Requirements for plant coexistence through pollination niche partitioning

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Plant–pollinator interactions are often thought to have been a decisive factor in the diversification of flowering plants, but to be of little or no importance for the maintenance of existing plant diversity. In a recent opinion paper, Pauw (2013 Trends Ecol. Evol. 28, 30–37. (doi:10.1016/j.tree.2012.07.019)) challenged this view by proposing a mechanism of diversity maintenance based on pollination niche partitioning. In this article, I investigate under which conditions the mechanism suggested by Pauw can promote plant coexistence, using a mathematical model of plant and pollinator population dynamics. Numerical simulations show that this mechanism is most effective when the costs of searching for flowers are low, pollinator populations are strongly limited by resources other than pollen and nectar, and plant–pollinator interactions are sufficiently specialized. I review the empirical literature on these three requirements, discuss additional factors that may be important for diversity maintenance through pollination niche partitioning, and provide recommendations on how to detect this coexistence mechanism in natural plant communities.

1. Introduction

It has often been suggested that pollination by animals played an important role in the evolution of flowering plant diversity [1–3]. On the other hand, pollinators are usually not thought to contribute to the maintenance of existing plant diversity. Whereas the classical mechanisms of diversity maintenance require a negative feedback of each population onto its own density (e.g. through increasing intraspecific competition or frequency-dependent predation; [4]), mutualistic interactions such as those between plants and pollinators are generally expected to result in positive feedbacks, thereby promoting growth of already abundant plant species at the expense of less common plants [5–7]. In contrast to this notion, in a recent opinion article, Pauw [8] suggested that under certain circumstances pollination by animals can maintain plant diversity. More specifically, the stabilizing mechanism proposed by Pauw requires that each plant’s reproductive success be limited by the availability of its specialized pollinator, but the pollinators’ population growth is not limited by availability of nectar and pollen, but rather by external resources such as nesting sites. If these requirements are met, Pauw argues that all else being equal, a rare plant species will be less pollen-limited than a more abundant plant, which allows the rare plant to increase in frequency. Thus, pollinators can act as limiting resources that promote plant coexistence via the classical mechanism of niche partitioning.

The purpose of this study is to investigate in detail under which conditions the mechanism proposed by Pauw can maintain plant diversity. Since pollinators are themselves consumers of plant resources, a decline in the frequency of their preferred floral resource may decrease their foraging success by increasing the cost of searching for flowers. If the reduction in net energy gain results in lower survival or reproductive output, the pollinator of a rare plant may in turn become rare, which reduces the reproductive success of its plant partner and may ultimately result in both the plant’s and pollinator’s extinction. This vicious circle of diminishing reproductive success may even occur when the upper limit of the pollinator’s population density is set by other resources such as nesting sites. It can therefore be expected that the mechanism of
diversity maintenance proposed by Pauw only stabilizes plant coexistence if the costs of searching for floral resources are low and pollinator populations are strongly limited by external resources. Furthermore, the stabilizing mechanism may break down as soon as pollinators cease to be perfectly specialized on one plant species. In the following, I test these ideas using a mathematical model of plant and pollinator population dynamics.

2. The model

The model used in this study is a modified version of the one developed by Kunin & Iwasa [6] and recently extended by Song & Feldman [9]. Both studies examined the effects of adaptive foraging of pollinators on plant coexistence. The original model describes the foraging success of pollinators and the pollination success of plants in relation to pollinator behaviour as specialists or generalists, but not the resulting population dynamics. Song & Feldman [9] added population dynamics of plants and assumed that the ratio of pollinators to plants remains constant, since a higher density of flowers should attract more pollinators from the surroundings to the local patch. By contrast, in this study, I model a closed system in which both plant and pollinator population dynamics depend on their local interactions. In addition, the model incorporates plant competition for abiotic resources (e.g. water, light and nutrients) and pollinator competition for nesting sites. Whereas in the above-mentioned studies individual pollinators either behave as perfect specialists or generalists, here I also consider intermediate degrees of specialization. As the focus of this study is not on inter-individual differences in foraging strategies, I assume that all individuals of the same pollinator species show identical foraging behaviour.

The model describes a system of two plant species (with population densities $P_i$, $i \in \{1, 2\}$) and two pollinator species (with densities $A_j$, $j \in \{1, 2\}$). For simplicity, I assume that each plant individual has exactly one flower. The dynamics of this system take place on two different time scales: on a shorter time scale (within a season), pollinators move between neighbouring flowers, collecting nectar and transferring pollen. Within this shorter period, population sizes of plants and pollinators remain constant. On a longer time scale (between seasons), changes in population density take place. It is assumed that plants and pollinators have non-overlapping generations of equal length (e.g. annual species). Thus, at the end of each season, all individuals reproduce and die. Each population’s reproductive output is determined by the benefits gained from mutualistic plant–pollinator interactions as well as by intra- and interspecific competition for other resources.

(a) Flower visits

In a plant community with total plant density $P$ (with $P = P_1 + P_2$), the average travelling time $T$ of a pollinator between neighbouring flowers is calculated as $T = 1/(s\sqrt{P})$, where $s$ is the speed of travelling. If the pollinator is a specialist on flowers of plant species $i$, it will encounter suitable flowers at a rate of $1/(T/p_i)$ (with $p_i = P_i/P$, $0 \leq p_i \leq 1$). A perfect generalist encounters suitable flowers at rate $1/T$. For pollinators with intermediate degrees of specialization, the rate of encounter depends on the frequencies $p_i$ of the two plant species as well as the pollinators’ tendency to visit each of these plants. This tendency can be expressed as a probability $\alpha_i$, with $\alpha_j$ denoting the probability that a pollinator of species $j$ visits a flower of plant species $i$ upon encounter. Thus, for pollinator species $j$, the rate of successful encounters is $1/(T/\sum p_i \alpha_i)$. For perfectly specialized pollinators, $\alpha_j = 1$ for the preferred plant species and $\alpha_j = 0$ for the non-preferred plant.

If a pollinator decides to visit a flower, it requires time to handle the flower and collect nectar. Let $F_i$ be the average amount of nectar in flowers of plant species $i$. For a visitor of plant $i$, the handling time is $aF_i + c$, with $c$ being the minimum time required regardless of the available amount of nectar. Overall, the average rate of flower visits $V_j$ of a pollinator of species $j$ is

$$V_j = \frac{1}{T/\sum p_i \alpha_i + \left( \sum p_i \alpha_i (aF_i + c) / \sum p_i \alpha_i \right)}.$$

where the first term in the denominator is the pollinator’s average travelling time and the second term its handling time.

Following Kunin & Iwasa [6], the current nectar level of a flower is modelled as a saturating function of time $t$ since the last visit of a pollinator:

$$f(t) = f_{\text{max}}(1 - e^{-t/T_{\text{max}}}).$$

Here, $f_{\text{max}}$ denotes the maximum nectar volume a flower can hold and $g$ the rate of nectar replenishment. If flowers of species $i$ are visited at rate $R_i$, it can be assumed that the time between subsequent flower visits follows a negative exponential distribution with mean $1/R_i$. The expected amount of nectar $F_i$ available to a visitor of plant $i$ is then

$$F_i = \int_0^\infty R_i e^{-t/R_i} f_{\text{max}}(1 - e^{-t/T_{\text{max}}}) \, dt.$$

Integrating over all values of $t$ gives

$$F_i = \frac{g f_{\text{max}}}{g + f_{\text{max}} R_i}.$$

The rate at which flowers receive visitors depends on the densities of the two pollinator species ($A_j$), their visitation rates ($V_j$) and the proportion of visits they make to each plant species. Hence, the per-capita rate of flower visits received by plant species $i$ is

$$R_i = \frac{1}{P_i} \sum_j (A_j V_j f_i p_i \alpha_i).$$

Following Song & Feldman [9], for simplicity I assume that the energetic costs of travelling and flower handling are identical. Thus, the net energy intake rate $\Phi_j$ of pollinator $j$ is

$$\Phi_j = V_j \left( \frac{1}{\sum p_i \alpha_i} F_i \right) - E,$$

where $E$ is the energetic cost of foraging.

The pollination success of a plant does not only depend on its visitation rate, but also on the probability that visitors carry conspecific pollen. Let $B$ be the degree of pollen carry-over, i.e. the maximum number of flower visits between pollen removal and deposition. If $B = 1$, pollinators can only transfer pollen to the next visited flower. For $B \to \infty$, a pollinator can fertilize a flower even if it has visited many flowers of other species after the last visit to the same species. Taking the degree of pollen carryover into account, the
expected amount of pollen received by a flower of plant species $i$ is

$$ \Psi_i = \frac{1}{R} \sum_j \left( A_i V_j \left( \frac{p_{i,j}}{\sum_k p_{i,k}} \left( 1 - \left( 1 - \sum_k \frac{p_{i,k}}{\sum_j p_{i,j}} \right)^b \right) \right) \right). \quad (3.7) $$

In addition to the plant species’ visitation rate $R_i$ (equation (3.5)), this expression contains a term specifying the probability that a visitor to the focal plant visited at least one flower of the same plant species during its previous $B$ flower visits.

(b) Population dynamics

At the end of each season, plants and pollinators reproduce and die. The number of offspring each individual can potentially produce (its fecundity) is a linear function of the amount of pollen received (for plants) or nectar collected (for pollinators) during the season. Here, $\beta_p$ denotes the conversion of pollen to seeds and $\beta_A$ the conversion of nectar to pollinator offspring. However, the realized number of offspring is usually lower than the potential number owing to competition for limited resources. Whereas the two pollinator species are assumed to require different types of habitat for reproduction (e.g. one may be stem-nesting, the other ground-nesting), habitat requirements of the two plants are assumed to be identical (i.e. seedling requirements for resources such as water, light and nutrients). Therefore, pollinators experience only intraspecific competition for nesting sites, whereas plants experience equally strong intra- and interspecific competition for seedling establishment sites.

In the model, competition among plants and pollinators is introduced by including a density dependence term. As density dependence function, I use the Skellam model [10], a time-discrete model of contest competition. This model can be derived from first principles based on the assumption that the distribution of individuals on sites follows a Poisson distribution [11]. Using the Skellam model, the dynamics of plant population $i$ are specified as

$$ P_i(t+1) = H_P \left( \sum_j \psi_i \psi_j P_j(t) \right) (1 - e^{-\sum_j \psi_i \beta_j P_j(t)/H_P}), \quad (4.1) $$

where $H_P$ denotes the carrying capacity for plants of both species together, i.e. the maximum number of plant individuals the habitat can sustain. Similarly, the population dynamics of pollinator $j$ are given by

$$ A_j(t+1) = H_A (1 - e^{-\phi_j \beta_j A_j(t)/H_A}), \quad (4.2) $$

with $H_A$ denoting the carrying capacity for pollinators of species $j$. Carrying capacities of pollinator species 1 and 2 are assumed to be identical.

(c) Numerical analyses

To investigate the effects of search costs, pollinator limitation by availability of nesting sites and specialization of plant–pollinator interactions on plant coexistence, I performed numerical simulations of the population dynamics of plants and pollinators. In these simulations, I tested whether a system consisting of a single plant species and its pollinator ($P_2$ and $A_2$, respectively) can be invaded by a second species pair ($P_1$ and $A_1$), whose initial density is a small fraction of the resident population’s density. Initial densities of $P_1$ and $A_1$ were systematically varied to determine the minimum density at which invasion is still successful (invasion threshold). In each simulation run, I first determined the equilibrium densities of the resident species alone by setting the invaders’ initial densities to zero. For subsequent simulations, initial densities of $P_2$ and $A_2$ were set to these equilibrium values and those of $P_1$ and $A_1$ to a fraction of the respective resident species. In all simulations, an equilibrium state was found by iterating the system of difference equations until the largest difference in population densities between subsequent time steps fell below a threshold value of $10^{-6}$. If in a simulation with invaders the invading plant species’ density at equilibrium was greater than zero, the invasion counted as successful.

Although the above co-invasion scenario represents the strongest test of a stabilizing effect of pollination niche partitioning, in reality immigration of a plant species alone into a system of a resident plant and two resident pollinators is probably more common. Therefore, I performed additional simulations with this alternative invasion scenario. Since perfectly specialized pollinators can only maintain a population in the presence of their preferred plant, parameter combinations with perfect pollinator specialization ($a_{ij} = 0$ for $i \neq j$) were only tested with the co-invasion scenario.

For parameters also present in the original model by Kunin & Iwasa [6], I used the default values provided there (table 1), which are based on empirical estimates from the published literature. All other parameter values ($H_A$, $H_P$, $\beta_A$, $\beta_P$, $E$) were chosen so as to allow population growth to a reasonable size under a wide range of conditions. Simulations and graphics were produced using the R language v. 3.1.0 for Linux [12].

To examine the effect of the cost of searching for flowers on plant coexistence, I simultaneously varied two parameters of the model: $s$, the flying speed of pollinators, and $H_P$, the carrying capacity for plants (see table 1 for ranges of parameter variation). While a higher value of $s$ obviously results in less time spent searching for flowers, $H_P$ has an effect on pollinator search costs, as well, because its value determines the density of the total plant population at equilibrium. Since the average travelling time $T$ between neighbouring flowers decreases with increasing total plant density $P$, higher values of $H_P$ make searching for flowers less costly for a pollinator. To study the effect of the strength of pollinator limitation by availability of nesting sites, simulations with variation of $s$ and $H_P$ were performed for two levels of the pollinators’ carrying capacity $H_A$.

In a separate experiment, the effect of pollinator specialization on plant coexistence was examined by varying each pollinator’s tendency to visit the non-preferred plant species ($a_{ip}$, with $i \neq j$) from zero (perfect specialization) to one (perfect generalization). As I expected the effect of pollinator generalization to be most pronounced under strongly limited pollen carryover, I simultaneously varied the degree of pollen carryover $B$ from 1 to 64. In addition, since most real plant–pollinator systems are moderately generalized [13], I repeated the first experiment (varying $s$ and $H_P$) with an intermediate degree of specialization ($a_{ij} = 0.5$) at two levels of pollen carryover ($B = 8$ and 64).

3. Results

In a perfectly specialized plant–pollinator system, both the flying speed of pollinators ($s$) and the plants’ carrying
capacity \((H_p)\) had positive effects on plant coexistence (figure 1a,b). High values of both parameters allowed invasion of a second plant–pollinator pair from low initial densities, while the lowest values tested did not result in successful invasion even for initial population densities of half the resident’s density. An increase in the pollinators’ carrying capacity \((H_A)\) had the opposite effect: as pollinator limitation by availability of nesting sites weakened, the invasion threshold increased for most combinations of \(s\) and \(H_p\) (figure 1, compare (b) to (a)).

**Table 1.** Parameter definitions and values tested in numerical simulations.

<table>
<thead>
<tr>
<th>symbol</th>
<th>definition</th>
<th>default value</th>
<th>range tested</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td>time required to collect one unit of nectar</td>
<td>4 s J(^{-1})</td>
<td></td>
</tr>
<tr>
<td>(s)</td>
<td>flying speed of pollinators</td>
<td>0.1 m s(^{-1})</td>
<td>(e^{-2.5}) – (e^{2.5})</td>
</tr>
<tr>
<td>(c)</td>
<td>minimum handling time per flower</td>
<td>0.5 s</td>
<td></td>
</tr>
<tr>
<td>(f_{\text{max}})</td>
<td>maximum nectar level</td>
<td>1 J</td>
<td></td>
</tr>
<tr>
<td>(g)</td>
<td>nectar replenishment rate</td>
<td>0.000025 J s(^{-1})</td>
<td></td>
</tr>
<tr>
<td>(B)</td>
<td>pollen carryover</td>
<td>1</td>
<td>1 – 64</td>
</tr>
<tr>
<td>(\alpha_{ij})</td>
<td>generalization level of (i \neq j)</td>
<td>0</td>
<td>0 – 1</td>
</tr>
<tr>
<td>(E)</td>
<td>energy expenditure of pollinators</td>
<td>0 J s(^{-1})</td>
<td></td>
</tr>
<tr>
<td>(H_A)</td>
<td>pollinator carrying capacity</td>
<td>200</td>
<td>200, 1000</td>
</tr>
<tr>
<td>(H_p)</td>
<td>plant carrying capacity</td>
<td>50 000</td>
<td>1000–100 000</td>
</tr>
<tr>
<td>(\beta_p)</td>
<td>conversion of pollen to plant offspring</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>(\beta_A)</td>
<td>conversion of nectar to animal offspring</td>
<td>1000</td>
<td></td>
</tr>
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**Figure 1.** Invasion threshold as a function of flying speed of pollinators \((s)\) and carrying capacity for plants \((H_p)\). (a,b) Results for perfectly specialized pollinators \((\alpha_{ij} = 0)\) and two different values of the pollinators’ carrying capacity \((a: H_A = 1000, b: H_A = 200)\). (c,d) Simulations were performed with an intermediate degree of pollinator specialization \((\alpha_{ij} = 0.5)\) and two degrees of pollen carryover \((c: B = 8, d: B = 64)\). The invasion threshold (shown as shades of grey in print) was determined by varying the initial density of the invading plant–pollinator species pair as a fraction of the respective resident species’ population density at equilibrium. The threshold was defined as the minimum initial density (expressed as a fraction of the resident’s density) that still allowed successful establishment of the invading plant species. Note that initial fractions of invaders were varied on a log scale so as to allow variation in smaller steps at lower initial densities. White areas of the graphs indicate parameter combinations that did not result in successful invasion even at the maximum initial density tested (50% of resident’s density). (Online version in colour.)
At an intermediate level of specialization ($a_{ij} = 0.5$), pollinator search costs had a qualitatively similar effect compared to a perfectly specialized system, but here the invasion threshold remained nearly constant over a much larger part of parameter space (figure 1c,d). Even with minimal pollen loss in heterospecific flower visits (pollen carryover $B = 64$, figure 1d) and high values of $s$ and $H_F$ (i.e. low search costs), a rare plant could only invade the community if its initial density was at least 5% of the resident’s density, compared to 0.1% in a perfectly specialized system. With a lower degree of pollen carryover ($B = 8$, figure 1c), invasion was only possible at an initial density of half the resident’s equilibrium density even when the pollinators’ search costs were extremely low.

With successively more generalized plant–pollinator interactions, the invasion threshold increased, especially for low values of the pollen carryover parameter $B$ (figure 2). For $B < 8$, the rarer plant species could only invade when the pollinators’ tendency to visit the non-preferred plant was less than half of that of the preferred plant. In perfectly specialized plant–pollinator systems ($a_{ij} = 0$) in which no heterospecific pollen transfer takes place, the invasion threshold was independent of pollen carryover ($B$).

With the alternative scenario of invasion of $P_1$ alone into a system of $P_2$ and both pollinators at equilibrium, the effects of search costs and external resource limitation were qualitatively similar to the co-invasion scenario (electronic supplementary material, figure S1, cf. figure 1c,d). Likewise, the influence of pollen carryover and pollinator generalization did not change qualitatively (electronic supplementary material, figure S2). However, for most parameter combinations, the threshold for successful invasion of $P_1$ was lower in the alternative scenario compared with the co-invasion scenario. Only at the lowest levels of the generalization parameter $a_{ij}$ did a co-invading plant–pollinator pair exceed the invasion success of the single plant invader (electronic supplementary material, figure S2).

4. Discussion

(a) When can pollen limitation promote plant coexistence?

Although interactions with pollinators have long been regarded as unimportant or even counter-productive for diversity maintenance in plant communities, the above simulation results demonstrate that the mechanism of pollination niche partitioning described by Pauw [8] can at least in theory promote plant coexistence. However, the results also suggest that without other coexistence mechanisms a rare plant species with very low initial density can only increase in the presence of the resident plant under a restricted set of conditions. Moreover, under some circumstances invasion may fail even if the invader’s initial population density is relatively high. In the following, I discuss the parameters that determine invasion success in this model and consider additional factors that may be important for plant coexistence through pollination niche partitioning. I conclude by describing potential experimental and observational studies aimed at detecting this coexistence mechanism in the field.

(i) Search costs

As the results of this study show, pollen limitation can only promote plant coexistence if the costs of searching for flowers are sufficiently low to enable a pollinator of a rare plant to forage without spending too much time travelling between flowers. Whereas in the model search costs are measured only in terms of travel time, for real pollinators searching for rare flowers often also comes at the cost of increased energy expenditure, since for most species the energetic costs of travelling exceed those of handling flowers [14–16]. Moreover, while the model assumes that energy expenditure of pollinators is independent of the speed of travelling, in reality the energetic requirements of fast-moving animals are generally higher than those of slower ones [14]. Thus, in contrast to the model’s predictions, fast-moving flower visitors such as bumblebees and hummingbirds may not necessarily be able to tolerate low densities of their preferred floral resources.

In order to identify flower visitors that are able to sustain a population of their preferred plant species at low density and provide sufficient pollination services to this plant, ecologists need to study the relationship between a plant’s density, its visitation rate, and the survival and reproductive success of its pollinators. To my knowledge, until now no published study has addressed all of these factors, but some authors have measured travel times of bees in relation to plant density, confirming that larger distances between flowers result in longer flight durations ([17], but see [18]) and that flight duration is negatively related to the rate of brood cell provisioning [18]. While these results can be seen as evidence that decreasing flower density does indeed carry a fitness cost for bees, clearly more studies are needed to investigate how severely population growth of different pollinator taxa is affected by low resource density.

(ii) External resource limitation

A central requirement of the mechanism of plant coexistence through pollen limitation is that pollinator populations are limited by resources not provided through their mutualistic interaction with plants. If floral resources are the most limiting factor, the positive feedback between plant and pollinator population dynamics will ensure that their populations increase in parallel. In that case, abundant plant species are not more pollen-limited than rare species, and animal pollination does not contribute to plant coexistence.
As the results of this study show, stronger limitation by external resources lowers the invasion threshold for a rare plant entering the community. To find examples of this mechanism in the field, it would be helpful to know which flower visitor groups are most strongly limited by resources other than pollen and nectar. In reality, such external limiting resources could be nesting sites for bees and birds or larval food resources for flies, beetles and lepidopterans. Nest site limitation of bee populations has been addressed in several studies (reviewed by Roulston & Goodell [19]), but the results are equivocal owing to the difficulty of distinguishing the effects of nest site availability from those of other environmental variables. Nevertheless, given that most bee species have very specific nest site requirements, it is quite likely that nesting sites are at least as important as floral resources in regulating bee populations.

Since in virtually all insect pollinators apart from bees only the adult stage feeds on floral resources, population growth in these groups could be limited by availability of larval food. Larval food requirements and availability have mainly been studied in butterflies and moths, whereas information on other flower visitor groups is comparatively sparse. According to a meta-analysis of data on 30 European butterfly species, availability of larval food resources is the primary factor explaining variation in butterfly population sizes, whereas the effect of adult food (nectar) appears to be negligible [20]. Thus, in the case of Lepidoptera the requirement for strong limitation of population growth by external resources seems to be fulfilled.

(iii) Specialization and pollen carryover

Of the parameters examined in this paper, the degree of specialization (i.e. pollination niche partitioning) of plant–pollinator interactions proved to be critical for plant coexistence. Given the importance of the level of partitioning of non-mutualist resources for species coexistence (‘limiting similarity’, e.g. [21]), this result is not unexpected. Apart from having a considerable impact on the invasion threshold by itself, the model’s specialization parameter influences the strength of the effects of other factors such as pollen carryover and the two parameters affecting search costs. Its direct positive impact on plant coexistence can be explained as follows.

When the pollinator $A_1$ enters the system together with the rare plant $P_1$, it initially profits from the fact that its density is far below the carrying capacity set by the limited availability of nesting sites. Hence, this rare pollinator’s population is able to grow, while the more abundant pollinator’s population size ($A_2$) is kept constant by external resource limitation. If $A_1$ has a strong preference for the rare plant $P_1$, its increasing population can provide high per-capita visitation rates that enable $P_1$ to increase thanks to a temporary reproductive advantage over its abundant competitor $P_2$. However, this effect is diluted if $A_1$’s preference for $P_1$ over $P_2$ is weak. Since $A_1$’s encounter rate with the abundant plant $P_2$ is much higher than the probability to encounter a rare flower of $P_1$, most of $A_1$’s visits will go to the abundant plant even if its probability to visit $P_1$ upon encounter is only a fraction of that of $P_1$. Thus, with increasing level of generalization of $A_1$, the fitness advantage of $P_1$ is quickly diminished. If the degree of pollen carryover $B$ is low, $P_1$’s reproductive success may become even lower than that of $P_2$. Since $P_1$ is rare, the likelihood that a visiting pollinator has last visited a conspecific flower is much lower for $P_1$ compared with $P_2$. Therefore, with a low level of specialization of $A_1$ and $A_2$ and a low degree of pollen carryover $B$, $P_1$ can only invade a population of $P_2$ if its initial density is sufficiently high to overcome the reproductive disadvantage associated with being rare.

In the numerical simulations, the only exception to the general positive effect of pollinator specialization on plant coexistence occurred with highly specialized pollinators ($a_{ij} < 0.1$) in the alternative invasion scenario. Since in this constellation pollinator $A_1$’s preference for $P_2$ is very low, its equilibrium population density with $P_2$ as the only floral resource is close to zero (data not shown). When $P_1$ is introduced into such a system, it cannot establish a population owing to insufficient pollination by $A_1$. On the other hand, for all higher values of the generalization parameter $a_{ij}$, $P_1$ benefits from the comparatively high equilibrium density of $A_2$, which lowers the invasion threshold compared to the co-invasion scenario.

Apart from the above-mentioned special case, given the general importance of specialized pollination for the functioning of pollen limitation as a diversity-maintaining mechanism a critical question is whether natural plant–pollinator systems are sufficiently specialized for the mechanism to be effective. According to current knowledge, most pollination systems are moderately generalized [13], but examples of remarkably specialized interactions have been found, especially in the tropics and the temperate zone of the Southern Hemisphere [22]. For moderately generalized plant–pollinator systems, the results of this study suggest that pollination niches alone can only enable a rare plant to increase from low density if the degree of pollen carryover is very high. Since in reality pollen carryover is a more gradual process than the simple binary carryover model used in this study [23,24], it is difficult to compare carryover values of the model with empirical data. Moreover, most published empirical studies of pollen carryover only consider carryover between conspecific flowers, but not pollen loss to heterospecific flowers (but see [25–27]). Nevertheless, based on the limited available information, it seems likely that in most real plant–pollinator systems pollen carryover during heterospecific flower visits is comparable to the lower end of the range of carryover values tested here. For example, Murcia & Feinsinger [25] found that five intervening visits to a different species reduced pollen transfer of hummingbirds to six cloud-forest plants by an average of 76%. In a study by Flanagan et al. [27], intervening visits to *Lythrum salicaria* reduced conspecific pollen deposition by bumblebees on *Minula ringens* flowers by approximately 42%. Although certain plant species, e.g. many orchids, may achieve much higher degrees of pollen carryover by precisely positioning their pollen on particular parts of the pollinators’ bodies [28], it is likely that such efficient pollen transfer mainly occurs in highly specialized plant–pollinator systems. Therefore, the potential of pollen carryover to mitigate the negative effects of low degrees of pollinator specialization on plant coexistence is probably limited. On the other hand, in reality pollen loss through heterospecific flower visits could be reduced by small-scale spatial structure. Since conspecific plants typically grow in aggregations [29] and pollinators mostly move between neighbouring flowers, pollen loss may be less of an issue for a rare plant than predicted by the model.

(iv) Additional factors

In addition to the model parameters discussed above, several other factors could influence the potential of
pollination niches to act as a diversity-maintaining mechanism. First, whereas in the model pollinator populations are required to be limited by external resources such as nesting sites, in reality other factors with a negative density-dependent effect on pollinator populations could fulfill the same role. For example, natural enemies such as parasites or predators can—under certain conditions—impose density-dependent mortality on their hosts or prey [30]. Furthermore, in reality pollinators often forage at larger spatial scales than that of the single local plant community modelled here. On the one hand, this fact could facilitate plant coexistence through pollination niche partitioning. Pollinators would then only need to be specialized with regard to the local plant community, but could be generalists at a larger spatial scale. The dynamics of these generalists would likely be nearly independent from those of any single local plant population and hence immune to fitness reductions owing to high costs of searching for rare flowers. On the other hand, the number of pollinators visiting a local patch often increases with increasing abundance of flowers in that patch [31–33]. Such an aggregative response is to be expected when abundances of floral resources fluctuate asynchronously across the landscape. If the positive relationship between floral and visitor abundance results in a per-flower visitation rate that is independent of the plant species’ local density, locally abundant plant species will not be more pollen-limited than rarer species. In that case, pollen limitation does not promote plant coexistence. Thus, a stabilizing effect of pollen limitation seems more likely for globally specialized pollinators whose preferred floral resources increase and decrease approximately synchronously at a landscape scale.

Whereas the model described in this paper assumes fixed preferences of pollinators without intraspecific variation, in reality many pollinators are sufficiently flexible to adjust their individual foraging strategies depending on the abundance of each resource and the behaviour of other foragers. The consequences of adaptive foraging of pollinators for plant coexistence were explored in the theoretical studies of Kunin & Iwasa [6] and Song & Feldman [9]. Both pairs of authors noted that adaptive foraging produces a disadvantage for rare plant species, because optimally foraging pollinators are predicted to ignore a rare resource. However, according to Song & Feldman [9], if a plant species is able to overcome the rarity disadvantage through a high immigration rate, it may benefit from adaptive foragers specializing on this new resource.

An essential prerequisite of plant coexistence through pollen limitation is that pollination by animals is necessary to maximize either the quantity or the quality of offspring produced. In reality, many animal-pollinated plant species have alternative means of reproduction in the form of self-fertilization or vegetative propagation [34]. However, self-fertilization often comes at the cost of reduced offspring quality, i.e. lower fitness compared to outcrossed individuals [35–38]. Thus, an abundant plant species whose reproduction is limited by availability of pollinators may be able to escape from pollen limitation by selfing, but the offspring produced in this manner will be less viable than the offspring of a rare plant that is able to reproduce exclusively by outcrossing. Therefore, as long as rarer plants have an advantage with respect to offspring quality, the mechanism of diversity maintenance should also function for plant species that do not exclusively rely on animal pollination for reproduction.

(b) Empirical tests of plant coexistence through pollen limitation

Despite the caveats mentioned in the previous section, our current knowledge of plant–pollinator systems suggests that partitioning of pollination niches could contribute to diversity maintenance at least in some plant communities. But how can we detect this mechanism in the field? In the following, I describe a number of experimental and observation-based approaches that may be used to infer the presence of this stabilizing mechanism, and discuss their respective strengths and weaknesses.

In general, without manipulating the community in question, ecologists can detect a stabilizing mechanism in one of two ways: either directly, by measuring the relationship between the vital rates of a species and its frequency in the community, or indirectly, by identifying characteristic patterns in the distribution of species in space or time that are indicative of the mechanism’s presence. In the case of diversity maintenance through pollen limitation, the direct method involves testing for negative frequency dependence of a plant species’ flower visitation rate, pollen receipt and seed set. To make sure that seed set determines fitness in this population, one would then ideally monitor seedling survival until the reproductive stage. Besides being time-consuming, the main disadvantage of this method is that it requires a gradient of frequencies of the focal species either in space or in time. Such a gradient may not always exist, and if it does, other factors such as community composition or abiotic conditions will often vary along the gradient as well. In that case, the effect of the species’ frequency can only be separated from other factors if there are no strong collinearities between them. In addition, this kind of study requires a decision on the spatial scale at which a species’ frequency is measured. Since natural plant and pollinator populations usually do not have clearly defined boundaries, this is a difficult choice to make. As a rule of thumb, the size of the foraging range of a pollinator of the focal plant species might be a good choice (i.e. easily several hectares).

Less direct evidence of a possible stabilizing effect of biotic pollination can be found in patterns of pollination niche overlap of co-occurring plant species. Since the stabilizing mechanism requires a certain degree of niche differentiation, we can assume that in the absence of other mechanisms of diversity maintenance plant species with very similar pollination niches should not be able to coexist. However, niche partitioning in itself is only an indication of the presence of competition for pollination. Without further information, especially on the factors limiting pollinator population growth, we cannot be sure that it has a stabilizing effect.

Since observation-based methods to determine the presence of plant coexistence through pollination niche partitioning clearly have their limitations, experimental manipulations could be used instead. A particularly strong test of this coexistence mechanism would be to remove a pollinator population’s external resource limitation by providing a sufficiently large amount of the resource in question (e.g. by installing trap nests as additional nesting sites for solitary bees: [39]). If the manipulation not only results in higher pollinator numbers, but also increases population growth of the
flowering plants visited by them, it is very likely that pollen limitation prevents competitive exclusion in this particular plant community.

(c) Conclusion

How large numbers of plant species with very similar resource requirements are able to coexist is a long-standing question in ecology [40]. The mechanism of plant coexistence through pollen limitation described by Pauw [8] may be part of the answer to this puzzle. Since this mechanism can only function under a specific set of conditions (see above), it cannot maintain diversity under all possible circumstances.

How frequently real plant–pollinator systems fulfil the requirements for diversity maintenance through this mechanism is still largely unknown. I hope that this article will encourage empiricists to study these factors more closely as well as directly test for a stabilizing effect of pollen limitation using one of the methods described above.

Competing interests. I have no competing interests.

Funding. I received no funding for this study.

Acknowledgements. I would like to thank Anton Pauw, Carsten Dormann, Florian Hartig and two anonymous reviewers for helpful comments on an earlier version of this paper.

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