Variability in floral abundance can drive flower diversification and specialization

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Abstract

The angiosperms show remarkable floral diversity. However, the ecological processes involved in flower diversification remain poorly understood. In this article I propose that different species' floral abundances drive adaptation to different pollinators and promote different degrees of specialization. In this view, interspecific variability in abundance can foster floral diversification. I develop a mathematical model of pollen transfer considering the interaction of several pollination processes—pollen removal and carryover, intra- and interspecific competition for pollinator visitation, and interspecific pollen transfer—that are linked to floral abundance. To assess if and how floral abundance can generate floral diversity, I use the model to assemble plant-pollinator networks from simulated plant and pollinator communities. The model shows that evolution on highly specialized pollinators and pollinators with high pollen carryover capacity is favoured at low floral abundance, while evolution on more abundant pollinators is favoured at high floral abundance. Furthermore, floral specialization is favoured at low floral abundance, while generalization is favoured at high abundance. In simulated plant communities of variable floral abundance, different pollinator systems evolve among the different plant species. The model demonstrates a new mechanism by which floral diversity can be generated, contributing to our understanding of floral evolution and diversification.

Introduction

A defining feature of the angiosperms is their remarkable floral diversity. (Armbruster 2014; Hernández-Hernández & Wiens 2020). Darwin first recognized that the diversity of floral shape, size, colour and scent could be attributable to selection by pollinators (Darwin 1877). This realization has resulted in a large modern research program, spawning ecological, evolutionary and genetic studies, investigating how interactions between plants and pollinators drive floral evolution (Harder & Johnson 2009; Van der Niet & Johnson 2012). While we are now heading toward a strong mechanistic understanding of how flowers evolve (Moyroud & Glover 2017; Shan *et al.* 2019; Fattorini & Glover 2020), the ecological processes involved in flower diversification remain poorly understood (Kay & Sargent 2009; Johnson 2010; Van der Niet & Johnson 2012; Armbruster 2017).

Most of our understanding of how flowers diversify derives from two principles, which were combined into the Grant-Stebbins model (Johnson 2006, 2010). First, flowering plants should adapt to the most effective pollinator in a given environment (Stebbins 1970); that is, the pollinator that visits most frequently (number of visits) and efficiently (per-visit pollen transport efficiency) (Armbruster 2014). Second, since pollinator assemblages are geographically variable, plants should be under divergent selection in different environments, resulting in adaptation to different pollinators (Grant & Grant 1965).

However, the Grant-Stebbins model does not answer a fundamental question in floral evolution: why is there so much floral diversity within communities? In other words, why do the various species constituting plant communities rarely converge on a single most effective pollinator? Moreover, within-community diversity in degrees of flower specialization, spanning from specialization on a single species of pollinator to generalization

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on multiple unrelated pollinator species, is equally challenging to reconcile with the perception that plants should specialize on the most effective pollinator (Sargent & Otto 2006; Gómez *et al.* 2007).

In the last few decades, we have gained important insights into the processes governing pollination success, allowing a better understanding of the selective pressures acting on floral evolution (Mitchell *et al.* 2009b). Several studies emphasize the importance of community context in understanding the ecology and evolution of plant pollination (Caruso 2000; Sargent & Ackerly 2008; Mitchell *et al.* 2009a; Muchhala *et al.* 2010). Competition and facilitation among plant species for access to pollinator visitation, and interspecific pollen transfer play important roles in determining the outcome of pollination (Geber & Moeller 2006; Morales & Traveset 2008; Sargent & Ackerly 2008; Mitchell *et al.* 2009a; Pauw 2013). Furthermore, competition via interspecific pollen transfer offers a potential mechanism promoting divergence in pollinator use by favoring reduced pollinator sharing (Muchhala *et al.* 2010; Moreira-Hernández & Muchhala 2019). However, despite a more comprehensive understanding of pollination ecology, and several hypotheses having been proposed to explain either variability in pollinator use or degree of specialization (Waser *et al.* 1996; Johnson & Steiner 2000; Aigner 2001; Gómez & Regino 2006; Sargent & Otto 2006; Muchhala *et al.* 2010; Moreira-Hernández & Muchhala 2019), we still lack a theory explaining the broad patterns of floral diversity within and among communities.

A general mechanism promoting floral diversity both in pollinator use and degree of specialization might derive from the consideration that several processes governing pollination success—intraspecific competition for access to pollinator visitation, interspecific pollen transfer and pollen carryover—are modulated by floral abundance, which intrinsically varies among species within communities. It is therefore possible that different plant species of varying floral abundances face divergent selective pressures from a same pollinator assemblage. For example, interspecific pollen transfer is expected to have a stronger impact on populations of low abundance, as the proportion of interspecific pollinator visits increases with the proportion of heterospecific individuals in plant communities (Rathcke 1983; Feinsinger *et al.* 1991; Caruso 2002; Palmer *et al.* 2003; Sargent & Otto 2006; Mitchell *et al.* 2009a; Runquist & Stanton 2013). Likewise, opportunities for pollen loss, whether passively or due to pollinator grooming, should be greater for rare plant species because pollinators visiting rare plants spend more time between conspecific visits (Minnaar *et al.* 2019). Therefore, pollen carryover— the proportion of the removed pollen carried to the next conspecific flower—is expected to increase with floral abundance. conversely, intraspecific competition for pollinator visitation should be stronger at high floral abundance, as more flowers compete for visitation by the same pollinator community (Rathcke 1983; Geber & Moeller 2006; Duffy & Stout 2008; Pauw 2013; Benadi & Pauw 2018). While studies carried out at limited spatial scales often find increased per flower pollinator visitation with increasing floral density (due to greater attractiveness of larger flowering patches) (see Ghazoul 2005), at the landscape scale—the scale that ultimately matters for floral evolution—the opposite trend is observed: the number of visits received per flower decreases with a species abundance (see Pauw 2013 and references therein; Hegland 2014; Benadi & Pauw 2018; Bergamo *et al.* 2020). The reason for such scale dependency is simple: large floral patches are more attractive to pollinators, but a population composed of multiple large floral patches will saturate the pollinators available, leading to stronger intraspecific competition.

In this article, I propose that the pollination system offering the optimal evolutionary solution for a plant species is a function of the plant's relative abundance in a community. In this view, different pollinators and degrees of specialization are favoured at different floral abundances. Floral diversification can result from shifts in relative floral abundance associated with the colonization of new habitats or geographical ranges, creating new conditions under which floral diversification can occur. Abundance has been previously identified as a potential driver of floral specialization (Feinsinger 1983; Sargent & Otto 2006). However, the potential for variability in floral abundance to drive adaptation to different pollinators has never been considered before. To demonstrate the potential of floral abundance to foster floral diversity, I develop a simple mathematical model of pollen transfer considering the interaction of several pollination processes— pollen carryover, pollen removal, intra- and interspecific competition for pollinator visits, and interspecific pollen transfer. I use the model to assemble plant-pollinator networks from simulated plant and pollinator communities. In a community context, the interactions between plants and their pollinators are generally

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investigated in terms of networks of interactions. Using this approach, I assess if and how interspecific variability in floral abundance generates diversity in pollinator use and degree of specialization. In addition to supporting the conceptual model, the mathematical model is consistent with, and suggests explanations for, several patterns governing the evolution, diversification and community assembly of flowers.

How floral abundance spurs flower diversification: a conceptual model

Since plants produce a finite number of gametes, optimizing reproductive success requires maximizing the number of ovules fertilized by a finite amount of pollen. When limited by pollinator quantity, plants should benefit from being less restrictive in their flower accessibility. Any visitor, regardless of its quality (pollen carryover efficiency and specialization), is likely to increase the number of pollen grains deposited on conspecific stigmas (Thomson *et al.* 2000; Thomson 2003; Muchhala *et al.* 2010). However, pollen grains have a higher probability of reaching conspecific stigmas when carried by more efficient pollinators. When enough pollinators are available to remove most pollen grains, pollinator quality becomes more limiting to plant reproductive success than pollinator quantity, and plants should specialize on the most efficient pollinator (Thomson *et al.* 2000; Thomson 2003).

Here I propose that the selective importance of pollinator quantity and quality is modulated by floral abundance. At high floral abundance, as more pollinators are required for sufficient pollination, plant reproduction is more strongly limited by pollinator quantity. Conversely, pollen loss to inefficient carryover and interspecific visits is reduced as floral density increases. Therefore, increased floral abundance should increase the selective importance of pollinator quantity while reducing the selective importance of pollinator quality. Under these conditions, plants should benefit from generalized pollination where more pollinators, but perhaps more wasteful ones, have access to flowers. At low abundance, the dynamic is reversed and plants should benefit from specializing on efficient carriers of their pollen.

While I have so far considered a dichotomy between low and high abundance, plants can exist in any state from extremely rare to ubiquitous. Likewise, pollinators inherently vary in their abundance (quantity component) and efficiency (quality component). As each pollinator offers a unique combination of the quantity and quality components of pollination, changes in a plant species' relative abundance in a community will shift the identity of the pollinator representing the most effective pollinator, and therefore, the pollination system resulting in a fitness optimum. In this view, floral abundance shapes the plant selective landscape. Variations in plant abundance move the fitness peak of the selective landscape toward different pollination systems, fostering floral diversification.

Model of pollen transfer

Here I develop a mathematical model determining how the optimal pollinator or set of pollinators for a plant population changes as a function of floral abundance. The model measures the proportion of pollen grains produced by a single flower of the focal species (hereafter focal flower) that reaches conspecific stigmas. In the model, this value is influenced by the interaction of several pollination processes—pollen removal and carryover, intra- and interspecific competition for pollinator visitation, and interspecific pollen transfer—that are linked to floral abundance, as described above. In the mathematical model, I treat pollinators as functional groups of pollinator species with similar attributes (morphology, behaviour) that produce similar selection on flowers (e.g. different species of hummingbirds, large-bodied bees) (Fenster *et al.* 2004). The model assumes that flowers are distributed homogeneously in space (i.e., that flowers of the same are not more likely to be near one another). The model therefore does not consider the potential for facilitation among species sharing the same pollinators, although facilitation is expected to beneficiate rarer species (Rathcke 1983; Steven et al. 2003; Essenberg 2012), contributing to the predicted increase in quantity limitation with abundance.

For a plant species a, the number of pollen grains produced per flower is represented by P_t. The proportion of grains removed with each pollinator visit to a focal flower is represented by R_i, and depends on both

the attributes of the pollinator i and of the focal plant species. While adaptation toward a pollination system could, theoretically, increase R, I am more interested in the causes of shifts between pollination systems rather the mechanisms leading to a subsequent better fit to the system, so the model does not consider evolution of R. With each new visit to the focal flower, the amount of pollen remaining in the anthers diminishes, and the amount picked up with each new pollinator visit diminishes proportionally to the number of visits received, resulting in an exponential decline of pollen removed with each new visit (Young & Stanton 1990; Robertson & Lloyd 1993). Considering that pollinator i is the only visitor (floral generalization is considered in equation 5), the total amount of pollen removed, P_r, from the focal flower by a given pollinator i is therefore

$$P_r = P_t \left[1 - (1 - R_i)^{V_{ij}} \right] (1)$$

where V_{ij} represents the number of visits by pollinator i to flower j, which is a subset of V_i, the total number of visits made by the pollinator in the plant community. The number of visits to the focal flower depends on the abundance of the focal species A_a and its proportional floral abundance in the community, $A_a / (A_a + \Sigma A_i)$ where ΣA_i represent the total abundance of flowers for each plant species visited by the pollinator i excluding the focal species. ΣA_i is related to pollinator generalization. The number of visits to the focal flower by pollinator i is therefore

$$V_{ij} = \frac{V_i \left(\frac{A_a}{A_a + \Sigma A_i} \right)}{A_a}$$

Which can be simplified as

$$V_{ij} = \frac{V_i}{A_a + \Sigma A_i} \ (2)$$

More simply, this second equation distributes the visits made by the pollinator i equally among all flowers visited by the pollinator, and therefore reflects competition for access to pollination by a specific pollinator i. In this model I treat all plant species as being equally attractive to each pollinator (variable attractiveness could be considered by weighting A_a by the relative attractiveness of the focal species). Considering the role of floral abundance and competition for a limited amount of pollinator visits, the number of pollen grains removed from the focal flower by a given pollinator can be expressed as

$$P_r = P_t \left[1 - (1 - R_i)^{\frac{V_i}{A_a + \Sigma A_i}} \right] (3)$$

The proportion of those grains removed by the pollinator i that reach a conspecific stigma depends on the pollen carryover capacity of the pollinator, C_i —the proportion of pollen carried over to each subsequent visit. For a given individual of the pollinator i, as with each new visit the amount of pollen remaining on the pollinator body declines at a rate C_i, the proportion of grains remaining on the individual pollinator follows an exponential decay (Lertzman & Gass 1983; Campbell 1985; Robertson 1992) (although longer or shorter than exponential tails have been observed; Morris *et al.*, 1994; Holmquist *et al.*, 2012). From the pollen grains deposited on the individual pollinator body, as pollen is lost with each visit, the amount that will reach a conspecific stigma is a function of the number of interspecific visits made by the pollinator before reaching a conspecific flower, which is a function of the reciprocal of the proportional floral abundance of the focal species in the community of flowers visited by pollinator i : $(A_a + \Sigma A_i) / A_a$. Therefore, assuming that the pollinator does not exhibit floral constancy (floral constancy could be considered by weighting ΣA_i by the reciprocal of the degree of floral constancy exhibited by the pollinator), the proportion of the removed pollen grains by individuals of pollinator "i" that reach conspecific stigmas is equivalent to

$$C_i^{\frac{A_a + \Sigma A_i}{A_a}}$$

Floral constancy can be considered as temporal specialization (Nickolas M. Waser 1986; Amaya-Márque 2009), and therefore has a similar impact on pollen transport as fixed specialization (not behaviourally

flexible), which is represented in the model by $A_a + \Sigma A_i$. Considering both the amount of pollen removed by the pollinator i and the proportion of this pollen that is deposited on conspecific stigmas, the total number of pollen grains deposited on conspecific stigmas, P_d , is expressed as

$$P_d = P_t \left[1 - (1 - R_i)^{\frac{V_i}{A_a + \Sigma A_i}} \right] \bullet C_i^{\frac{A_a + \Sigma A_i}{A_a}} (4)$$

Equation (4) determines the effect of specialization on a given pollinator on the pollination success of the focal plant species. The effect of specialization on different pollinators can be evaluated by comparing the value of P_d for exclusive pollination by different pollinators.

To determine the effect of pollination by different combination of pollinators (generalization on different subsets of the available pollinators), assuming random visitation order between individuals of the different pollinators, the total amount of pollen produced, P_t is distributed between the different pollinators visiting the focal species relative to 1) each pollinator's number of visits to the focal species and 2) their pollen removal rate. The individual contribution of each pollinator to P_r is summed and the total amount of pollen deposited on conspecific stigmas is therefore

$$P_d = \sum_{i=1}^n P_t \left\{ \frac{1 - \left(1 - \frac{\sum_{i=1}^n R_i}{n} \right)^{\sum_{i=1}^n \frac{V_{ij}}{A_a + \Sigma A}}}{\left[\frac{\left(\sum_{i=1}^n \frac{V_{ij}}{A_a + \Sigma A} \right)}{\left(\frac{V_i}{A_a + \Sigma A_i} \right)} \bullet \frac{\left(\frac{\sum_{i=1}^n R_i}{n} \right)}{R_i} \right]} \right\} \bullet C_i^{\frac{A_a + \Sigma A_i}{A_a}} (5)$$

By tracking pollen fate, the mathematical model explicitly measures the pollination system maximizing male reproductive success. However, selection through either male and female function is expected to reach the same solution in terms of optimal pollination system as long as pollen receipt and export are limiting and are governed by the same variables for each sex (i.e. pollinator identity and abundance).

Methods

Importance of pollinator quality and quantity

To determine the effect of floral abundance on the relative importance of the quantity and quality components of pollination for pollination success, using equation (4), I compared the impact of variations in those components on conspecific pollen receipt at different floral abundances. Equation (4) offers an explicit definition of which parameters constitute the quantity and quality components of pollination. Factors affecting pollen removal (the left part of the equation)—pollinator abundance and pollen removal rate—are defined as the quantity component. Factors affecting pollen deposition (the right part of the equation)—pollinator carryover capacity and specialization—are defined as the quality component. As a proxy for pollinator specialization, I used ΣA_i , the total floral abundance of all the plant species visited by the pollinator (see equation 4). The number of pollen grains produced by the focal flower deposited on a conspecific stigma (equation 4) was compared at low and high values of the parameters (Table 1) while maintaining the other parameters constant. The proportional change ($high – low$) / $high$ produced an estimate of the importance of variation of those parameters on pollination success. The importance of the different parameters for pollination success was compared for a range of floral abundances from 2 to 1500 (at least two flowers are required for cross-pollination).

Low, medium and high values of pollen carryover and pollen removal were parameterized based on data from the literature (Table 1). Robertson (1992) reported from a literature survey a range in pollen carryover from 50.2% to 94.7%. I used values of 0.55, 0.73 and 0.9 as low, medium and high values of pollen carryover in the model respectively. The values of pollen removal were selected following Thomson (2003) who modeled pollen delivery as a function of low and high values of pollen removal of 0.3 and 0.7 respectively. In the model, I used values of 0.3, 0.5 and 0.7 as low, medium and high values of pollen removal respectively. Those values encompass the pollen removal values measured in various systems (e.g. Wolfe and Barrett 1989, Young and

Stanton 1990, Harder 1990, Thostesen and Olesen 1996). Medium values of total number of visits by the pollinator in the community and abundance of the other flower species were selected to produce intermediate limitation by pollinator visits at intermediate floral abundance. This allowed variable degrees of limitation by pollinator visits within the range of floral abundance considered. The high and low values of total number of visits by the pollinator in the community and abundance of the other flower species represent a two-fold increase and decrease from the medium values respectively.

Because the number of pollen grains deposited on a conspecific stigma might be sensitive to the choice of values of the parameters used for the mathematical model, I compared the impact of variations in pollen carryover, pollen removal, pollinator visitation and specialization on conspecific pollen receipt at each possible set of values of the other parameters (low, medium, and high). I used those alternative values of the different parameters to set upper and lower values of the estimated importance of the quantity and quality components of pollination. Intermediate values of the importance of a parameter on pollination success correspond to the values obtained while all other parameters were set to medium values while upper and lower values correspond to the maximal and minimal values obtained among all the alternative values of the other parameters respectively. Essentially, the upper and lower values of the estimated importance of the quality and quantity components of pollination indicate the degree to which the estimate varies as a function of variation in the different parameters of the mathematical model and serve as a confidence interval.

Plant-pollinator network simulations

Using equation (5), I verified how variation in floral abundance affects the structure of plant-pollinator networks. Each simulated network was composed of a community of 10 pollinators and 12 plant species. The pollinator communities were assembled by randomly sampling for each pollinator values of carryover and removal from uniform distributions using the runif function in R (R core team, 2020) with maximal and minimal values of 0.9 and 0.55, and 0.7 and 0.3 for carryover and removal respectively, except for the simulations testing niche partitioning (see next paragraph and Table 2). The number of visits made by the different pollinators (relative to their abundance) was sampled from a Poisson log-normal distribution using the rpoilog function in the R package sads (Prado *et al.* 2018). Poisson log-normal distributions are often used to characterize community species-abundance distributions (Baldridge *et al.* 2016). After randomizing the plant species order, each plant species colonized the pollinator community successively until all species had colonized the community. For each colonization event, the plant species could evolve to be pollinated by any possible combination of pollinators in the community, and the combination resulting in the highest pollination success was selected as the evolutionary outcome for the plant species (assuming no restriction on the evolution of different pollination systems). Plant pollination success associated with the evolution of pollination by the different possible combinations of pollinators was calculated and compared by inputting the simulated parameters (see Table 2) in equation (5). Based on equation (5), the pollinators visited the plant species that evolved pollination by those pollinators relative to each plant species' floral abundance. For a given plant species the number of visits received by a pollinator was measured as $V_i / (A_a + \Sigma A_i)$ were V_i is the total number of visits made by the pollinator in the plant community, A_a is the floral abundance of the focal plant species and ΣA_i is the total floral abundance of the other plant species visited by the pollinator (see equation 2). Competition for visits by the different pollinators was dynamically updated with each new colonization event. After all species colonized the community, the number of visits by each pollinator to each plant species was determined and used to build the plant-pollinator networks.

Sets of 100 simulations were run for plant communities of 1) variable floral abundance 2) all low-abundance species and 3) all high-abundance species. For the simulations with variable floral abundance, plant communities were assembled by randomly sampling each plant abundance from a Poisson log-normal distribution. For the simulations with plant species of low abundance, all plant species had the same abundance and their abundance was low enough that pollinator quantity was not limiting (see Table 2). For the simulations with plant species of high abundance, the plant species abundance was set so that pollination was quantitatively limited.

A final set of simulations was performed with all plant species of low abundance in which each pollinator had similar values of pollen removal, carryover and number of visits. I used this last set of simulations to verify if the model would produce niche partitioning between plant species as a result of selection to limit interspecific pollen transfer when floral abundance is low, and thus pollinator efficiency is more limiting than pollinator availability. Specifically, each pollinator's values of carryover and removal were determined by randomly sampling from uniform distributions with minimum and maximum values of 0.72 and 0.74, and 0.49 and 0.51 for carryover and removal respectively. Each pollinator's number of visits made in the community (relative to its abundance) was randomly sampled from a uniform distribution with minimum and maximum values of 1490 and 1510 respectively.

Pollination system evolution in a new community

Using the simulated plant-pollinator networks of the variable floral abundance plant communities, I tested how floral abundance affects the degree of floral specialization and if variation in floral abundance leads to adaptation to different pollinators. For each simulated plant-pollinator network, after all plant species had colonized the community, a new plant colonist invaded the community. I varied the new colonist's abundance and recorded the subset of pollinators on which the plant evolved at each abundance value.

Results

The impact pollinator abundance and pollen removal rate on plant pollination success increased with floral abundance while the impact of pollen carryover and pollinator specialization decreased with floral abundance (fig. 1A-D). Overall, the quality component of pollination was more important for plant pollination success than the quantity component at low floral abundance, while the quantity component was more important for pollination success at high abundance (fig. 1E).

For simulated plant communities in which plant species varied in floral abundance, the resultant plant-pollinator networks exhibited variable degrees of specialization among plant species (average number of links $\pm$ standard deviation $= 3.24 \pm 2.00$) (fig 2A, B). By contrast, in simulated plant communities where all plant species were of low abundance, most plant species specialized on a limited subset of the available pollinators (average number of links $\pm$ standard deviation $= 2.24 \pm 1.06$) (Fig 2C, D). Moreover, in low-abundance plant communities, specialization occurred even when all pollinators had very similar abundance, carryover and removal. In this case, pollinator visits were partitioned homogeneously among plant species, demonstrating the presence of niche partitioning in the plant community (Fig 2G, H). Conversely, in plant communities composed of abundant plant species, most species generalized on most of the pollinators available (average number of links $\pm$ standard deviation $= 7.79 \pm 2.43$) (Fig 2E, F).

The subset of available pollinators on which a new plant colonist evolved was a function of its floral abundance. At very low floral abundance, the colonist specialized on pollinators weakly exploited by the other plant species, thereby reducing competition via interspecific pollen transfer (Fig 3). Those less-preferred pollinators were often relatively rare and had a low carryover capacity, as pollinators with high abundance and carryover were generally exploited by several plant species. From very low to relatively low abundance, there was a tendency for the new colonist to shift to specialization on a subset of pollinators with high carryover rather than low competition. From intermediate to high abundance, the new colonist favoured more abundant pollinators. Generalization increased with abundance, but only at very high abundance were the majority of the available pollinators exploited.

Discussion

Many plant lineages and communities are characterized by high floral diversity (Van der Niet & Johnson 2012). However, the causes of floral diversification and specialization remain elusive (Kay & Sargent 2009; Johnson 2010; Van der Niet & Johnson 2012; Armbruster 2017). Here I propose that a species' relative abundance in a community determines the pollination system offering the optimal evolutionary solution (Fig

1, 3). Given that abundance is evolutionarily and ecologically labile (Ricklefs 2010; Loza *et al.* 2017), shifts in abundance associated with the colonization of new habitats or geographic ranges could promote floral diversification. This conceptual model complements the Grant-Stebbins model in which flower diversification results from geographical variation in pollinator assemblages (Grant & Grant 1965; Stebbins 1970). In this more holistic view, floral diversification is the result of variability in pollinator assemblages, floral abundance, and plant community composition. This perception considerably relaxes the conditions under which floral diversification occurs and offers an explanation for the variability in pollinator use and degree of specialization within and among communities.

In the simulated plant communities, flower specialization was observed at low abundance while generalization was favoured at higher abundance (Fig 2A, B, Fig 3), a pattern consistent with the frequently observed link between abundance and degree of generalization in plant-pollinator networks (Jordano *et al.* 2002; Bascompte *et al.* 2003; Vázquez & Aizen 2003). While the cause of this pattern is debated (Dorado *et al.* 2011; Fort *et al.* 2016), the model presented here suggests that the link between abundance and generalization can originate from a selective advantage of generalization at high abundance. Furthermore, simulated plant communities composed of plant species of low abundance resulted in widespread specialization while communities of high abundance species were associated with generalized pollination (Fig. 2). This observation is consistent with the widespread floral specialization characterizing highly diverse plant communities composed mostly of rare species, such as in Mediterranean and tropical climates (Johnson & Steiner 2000; Vamosi *et al.* 2006). In such communities, plants should be under stronger selective pressure for specialization in order to avoid pollen loss from inefficient carryover and interspecific pollen transfer (Feinsinger 1983, Johnson and Steiner 2000). In the model, the importance of reducing competition via interspecific pollen transfer was further supported by the evolution of niche partitioning in communities of rare plant species even when the different pollinators had very similar attributes (Fig. 2G, H). Interestingly, while at moderately low abundance plants specialized on a subset of pollinators with high carryover capacity, at very low abundance the species frequently specialized on pollinators of low abundance and carryover (Fig. 3). Those pollinators were less exploited by more abundant plant species, which instead evolved pollination by abundant and efficient carriers of their pollen, offering a competition-free space for very rare species. This pattern of plant community assembly can be explained by the increasing probability of interspecific visits with increasing plant rarity, exacerbating the importance of interspecific pollen loss at very low abundance. The propensity for rare plant species to fill up unexploited pollination niches has the potential to give rise to the evolution of unique pollination systems, potentially contributing to the impressive diversity in modes of pollination characterizing tropical and Mediterranean communities.

The mathematical model and the simulated plant-pollinator networks demonstrate that, from low to intermediate abundance, plants should specialize on a subset of pollinators offering the optimal combination of pollination quantity and quality components (Fig. 1, 3). However, as plant abundance increases and most pollinators are not sufficiently abundant to remove the majority of pollen grains, highly generalized pollination should be favoured. But what happens at the extreme end of the plant abundance spectrum, when the entire pollinator community cannot provide enough visits to prevent pollen limitation? In those conditions, perhaps the best strategy is for plants to relax their dependence on biotic pollen vectors. While the evolution of wind pollination from animal pollination has mostly been attributed to reduced reliability of animal pollinators, most wind-pollinated plants are characterized by large population size and high density (Culley *et al.* 2002; Friedman & Barrett 2009). Indeed, it seems doubtful that any combination of pollinators could adequately pollinate the thousands of flowers per square metre characterizing the bloom of temperate deciduous trees or Poaceae grasslands. Moreover, despite wind representing a relatively inefficient system of pollen transport, the high abundance characterizing most wind-pollinated plants reduces the importance of pollen vector efficiency.

In the model, in order to demonstrate the role of floral abundance in determining the optimal pollination system, plants could evolve on any combination of pollinators without evolutionary restrictions. Plants, however, have constrained abilities to track the most effective pollination system (Fenster *et al.* 2004). Evolution occurs along the lines of least resistance contingent on the genetic material available, making some

shifts in pollination systems more likely to occur in certain plant lineages (Stebbins 1970; Van der Niet & Johnson 2012). Those evolutionary limitations represent an important nuance in flower diversification. Plants should adapt to the most effective pollination strategy that represent a line of least resistance. Therefore, many plants are expected to not be optimally adapted to their pollination environment. For instance, bilateral symmetry is considered to facilitate floral specialization (Sargent 2004) and radially symmetrical flowers may have limited ability to evolve floral specialization.

Even in the absence of evolutionary constraints, because there is a net flux of genes from large to small populations, the smallest, and often peripheral, populations of a given plant species are expected to match the local selective pressures relatively poorly (García-Ramos & Kirkpatrick 1997; Kirkpatrick & Barton 1997; Kay & Sargent 2009). Considering the importance of floral abundance in determining the optimal pollination strategy, small peripheral populations should rarely match such optimal conditions. Furthermore, large fluctuations in population abundance might prevent adaptation to the most effective pollinator when such fluctuations happen fast enough that adaptive tracking is not possible.

Several theoretical models emphasize the importance of fitness trade-offs in the evolution of flower specialization (Aigner 2001; Sargent & Otto 2006; Muchhala 2007). Such trade-offs are expected to occur when adaptation to a pollinator decreases the effectiveness of pollination by other pollinators. However, despite having been detected in some studies, fitness trade-offs in the effective use of different pollinators are often weak or absent (see Armbruster 2014, 2017). Hence, it seems unlikely that floral specialization is the sole result of trade-offs. Here, similar to Muchhala et al. (2010), who investigated the role of interspecific pollen transfer in flower specialization, I demonstrate that specialization can evolve without trade-offs. Rather, specialization should be advantageous when pollinator quantity is less limiting than pollinator quality.

When present, fitness trade-offs in the effective use of different pollinators should increase floral specialization. However, the model presented here is consistent with the perception that floral specialization might be governed not only by adaptation to increase pollen removal and deposition by the most effective pollinator, but also by the exclusion of less efficient ones (Thomson 2003; Castellanos et al. 2004; Muchhala et al. 2010; Armbruster 2017). Paralleling evolution toward the most effective pollinator, exclusion of less efficient pollinators through the evolution of pollinator filters could produce trade-offs if it also excludes efficient but infrequent pollinators. In other words, pollinator filters might rarely allow to single out unwanted pollinators. For instance, the evolution of long nectar spurs prevents access to pollinators with short mouthparts, even if some of those pollinators might act as occasional but efficient visitors. Plants might therefore often evolve a high degree of evolutionary specialization despite several visitors acting as effective pollinators due to the limited capacity to maintain pollination by a subset of effective pollinators while precisely excluding the ineffective ones.

Conclusion and future directions

In virtually all communities, species vary widely in their abundance. In this article, I demonstrate that this variability could explain a part of the angiosperms' remarkable floral diversity. The model presented here offers a potential framework to understand the evolution toward different pollination systems. According to this model, the optimal pollination system is a function of the pollinator assemblage (which varies geographically according to the Grant-Stebbins model), the plant community in which a species is embedded, and its floral abundance. This more holistic view, integrating the plant community context with selection exerted by different pollinators, promises to improve our understanding of the ecological processes involved in flower diversification.

Future studies should investigate how this mechanism operates in natural systems. In support of the model, some studies have shown that the strength of selection on floral traits can be affected by floral density (see Eisen et al. 2020 and references therein). An important next step would be to investigate how floral abundance affects the strength and direction of selection exerted by different pollinators. Such studies should be performed at the scale of whole populations to encompass representative variability in the pollination processes affected by floral abundance. Studies investigating how different pollination systems are associated

with distinct floral abundances could also be very informative, although such studies would require careful consideration of historical contingency and spatiotemporal variability in species' abundances.

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REFERENCES

Aigner, P.A. (2001). Optimality modeling and fitness trade-offs: when should plants become pollinator specialists? *Oikos* , 95, 177–184.

Amaya-Márque, M. (2009). Floral constancy in bees: a revision of theories and a comparison with other pollinators. *Rev. Colomb. Entomol.* , 35, 206–216.

Armbruster, W.S. (2014). Floral specialization and angiosperm diversity: phenotypic divergence, fitness trade-offs and realized pollination accuracy. *AoB Plants* , 6, plu003.

Armbruster, W.S. (2017). The specialization continuum in pollination systems: diversity of concepts and implications for ecology, evolution and conservation. *Funct. Ecol.* , 31, 88–100.

Baldridge, E., Harris, D.J., Xiao, X. & White, E.P. (2016). An extensive comparison of species-abundance distribution models.*PeerJ* , 2016, e2823.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. U. S. A.* , 100, 9383–9387.

Benadi, G. & Pauw, A. (2018). Frequency dependence of pollinator visitation rates suggests that pollination niches can allow plant species coexistence. *J. Ecol.* , 106, 1892–1901.

Bergamo, P.J., Susin Streher, N., Traveset, A., Wolowski, M. & Sazima, M. (2020). Pollination outcomes reveal negative density-dependence coupled with interspecific facilitation among plants. *Ecol. Lett.* , 23, 129–139.

Campbell, D.R. (1985). Pollen and gene dispersal: the influences of competition for pollination. *Evolution.* , 39, 418–431.

Caruso, C.M. (2000). Competition for pollination influences selection on floral traits of ipomopsis aggregata. *Evolution.* , 54, 1546–1557.

Caruso, C.M. (2002). Influence of plant abundance on pollination and selection on floral traits of *ipomopsis aggregata* .*Ecology* , 83, 241–254.

Castellanos, M.C., Wilson, P. & Thomson, J.D. (2004). "Anti-bee" and "pro-bird" changes during the evolution of hummingbird pollination in*Penstemon* flowers. *J. Evol. Biol.* , 17, 876–885.

Culley, T.M., Weller, S.G. & Sakai, A.K. (2002). The evolution of wind pollination in angiosperms. *Trends Ecol. Evol.* , 17, 361–369.

Darwin, C. (1877). *The various contrivances by which orchids are fertilised by insects* . John Murray, London, UK.

Dorado, J., Vazquez, D.P., Stevani, E.L. & Chacoff, N.P. (2011). Rareness and specialization in plant–pollinator networks.*Ecology* , 92, 19–25.

Duffy, K.J. & Stout, J.C. (2008). The effects of plant density and nectar reward on bee visitation to the endangered orchid*Spiranthes romanzoffiana* . *Acta Oecologica* , 34, 131–138.

Eisen, K.E., Wruck, A.C. & Geber, M.A. (2020). Floral density and co-occurring congeners alter patterns of selection in annual plant communities. *Evolution.* , in press (accepted).

Essenberg, C.J. (2012). Explaining variation in the effect of floral density on pollinator visitation. *Am. Nat.* , 180, 153–66.

Fattorini, R. & Glover, B.J. (2020). Molecular Mechanisms of Pollination Biology. *Annu. Rev. Plant Biol.* , 71, 487–515.

Feinsinger, P. (1983). Coevolution and pollination. In:*Coevolution* (eds. Futuyma, D.J. & Slatkin, M.). Sinauer Associates, Sunderland, MA, pp. 282–310.

Feinsinger, P., Tiebout, H.M. & Young, B.E. (1991). Do tropical bird-pollinated plants exhibit density-dependent interactions? Field experiments. *Ecology* , 72, 1953–1963.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.D. (2004). Pollination syndromes and floral specialization.*Annu. Rev. Ecol. Evol. Syst.* , 35, 375–403.

Fort, H., Vazquez, D.P. & Lan, B.L. (2016). Abundance and generalisation in mutualistic networks: solving the chicken-and-egg dilemma. *Ecol. Lett.* , 19, 4–11.

Friedman, J. & Barrett, S.C. (2009). Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants. *Ann. Bot.* , 103, 1515–1527.

Garcia-Ramos, G. & Kirkpatrick, M. (1997). Genetic models of adaptation and gene flow in peripheral populations. *Evolution.* , 51, 21–28.

Geber, M.A. & Moeller, D.A. (2006). Pollinator responses to plant communities and implications for reproductive character evolution. In:*Ecology and evolution of flowers* (eds. Harder, L.D. & Barrett, S.C.H.). Oxford University Press, New York, NY, pp. 102–119.

Ghazoul, J. (2005). Pollen and seed dispersal among dispersed plants.*Biol. Rev.* , 80, 413–443.

Gomez, J.M., Bosch, J., Perfectti, F., Fernandez, J. & Abdelaziz, M. (2007). Pollinator diversity affects plant reproduction and recruitment: the tradeoffs of generalization. *Oecologia* , 153, 597–605.

Gomez, J.M. & Regino, Z. (2006). Ecological factors that promote the evolution of generalization in pollination systems. In:*Plant–pollinator interactions: from specialization to generalization* (eds. Waser, N.M. & Ollerton, J.). University of Chicago University Press, Chicago, IL, pp. 145–166.

Grant, V. & Grant, K. (1965). *Flower pollination in the Phlox family* . Columbia University Press, New York, NY.

Harder, L.D. (1990). Pollen removal by bumble bees and its implications for pollen dispersal. *Ecology* , 71, 1110–1125.

Harder, L.D. & Johnson, S.D. (2009). Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation. *New Phytol.* , 183, 530–545.

Hegland, S.J. (2014). Floral neighbourhood effects on pollination success in red clover are scale-dependent. *Funct. Ecol.* , 28, 561–568.

Hernandez-Hernandez, T. & Wiens, J.J. (2020). Why are there so many flowering plants? A multi-scale analysis of plant diversification.*Am. Nat.* , 195, 000–000.

Holmquist, K.G., Mitchell, R.J. & Karron, J.D. (2012). Influence of pollinator grooming on pollen-mediated gene dispersal in *Mimulus ringens* (Phrymaceae). *Plant Species Biol.* , 27, 77–85.

Johnson, S. (2006). Pollinator-driven speciation in plants. In:*Ecology and Evolution of Flowers* (eds. Harder, L.D. & Barrett, S.C.H.). Oxford University Press, New York, NY, pp. 295–306.

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Johnson, S.D. (2010). The pollination niche and its role in the diversification and maintenance of the southern African flora. *Philos. Trans. R. Soc. B Biol. Sci.* , 365, 499–516.

Johnson, S.D. & Steiner, K.E. (2000). Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* , 15, 140–143.

Jordano, P., Bascompte, J. & Olesen, J.M. (2002). Invariant properties in coevolutionary networks of plant-animal interactions. *Ecol. Lett.* , 6, 69–81.

Kay, K.M. & Sargent, R.D. (2009). The role of animal pollination in plant speciation: integrating ecology, geography, and genetics. *Annu. Rev. Ecol. Evol. Syst.* , 40, 637–656.

Kirkpatrick, M. & Barton, N.H. (1997). Evolution of a species' range. *Am. Nat.* , 150, 1–23.

Lertzman, K. & Gass, C. (1983). Alternative models of pollen transfer. In: *Handbook of experimental pollination biology* . Scientific and Academic Editions, New York, NY, pp. 474–489.

Loza, M.I., Jimenez, I., Jorgensen, P.M., Arellano, G., Macia, M.J., Torrez, V.W., *et al.* (2017). Phylogenetic patterns of rarity in a regional species pool of tropical woody plants. *Glob. Ecol. Biogeogr.* , 26, 1043–1054.

Minnaar, C., Anderson, B., L de Jager, M. & Karron, J.D. (2019). Plant–pollinator interactions along the pathway to paternity. *Ann. Bot.* , 123, 225–245.

Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M. & Karron, J.D. (2009a). New frontiers in competition for pollination. *Ann. Bot.* , 103, 1403–1413.

Mitchell, R.J., Irwin, R.E., Flanagan, R.J. & Karron, J.D. (2009b). Ecology and evolution of plant–pollinator interactions. *Ann. Bot.* , 103, 1355–1363.

Morales, C.L. & Traveset, A. (2008). Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Crit. Rev. Plant Sci.* , 27, 221–238.

Moreira-Hernandez, J.I. & Muchhala, N. (2019). Importance of pollinator-mediated interspecific pollen transfer for angiosperm evolution. *Annu. Rev. Ecol. Evol. Syst.* , 50, 191–217.

Morris, W.F., Price, M. V., Waser, N.M., Thomson, J.D., Thomson, B. & Stratton, D.A. (1994). Systematic increase in pollen carryover and its consequences for geitonogamy in plant populations. *Oikos* , 71, 431.

Moyroud, E. & Glover, B.J. (2017). The evolution of diverse floral morphologies. *Curr. Biol.* , 27, R941–R951.

Muchhala, N. (2007). Adaptive trade-off in floral morphology mediates specialization for flowers pollinated by bats and hummingbirds. *Am. Nat.* , 169, 494–504.

Muchhala, N., Brown, Z., Armbruster, W.S. & Potts, M.D. (2010). Competition drives specialization in pollination systems through costs to male fitness. *Am. Nat.* , 176, 732–43.

Nickolas M. Waser. (1986). Flower constancy: definition, cause, and measurement. *Am. Nat.* , 127, 593–603.

Van der Niet, T. & Johnson, S.D. (2012). Phylogenetic evidence for pollinator-driven diversification of angiosperms. *Trends Ecol. Evol.* , 27, 353–361.

Palmer, T.M., Stanton, M.L. & Young, T.P. (2003). Competition and coexistence: exploring mechanisms that restrict and maintain diversity within mutualist guilds. *Am. Nat.* , 162, S63–S79.

Pauw, A. (2013). Can pollination niches facilitate plant coexistence? *Trends Ecol. Evol.* , 28, 30–37.

Prado, P.I., Miranda, D. & Maintainer, A.C. (2018). sads: maximum likelihood models for species abundance distributions. R package version 0.4.2. https://cran.r-project.org/package=sads.

R core team (2020). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rathcke, B. (1983). Competition and facilitation among plants for pollination. In: *Pollination Biology* (ed. Real, L.). Academic Press, New York, pp. 305–329.

Ricklefs, R.E. (2010). Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proc. Natl. Acad. Sci. U. S. A.* , 107, 1265–1272.

Robertson, A.W. (1992). The relationship between floral display size, pollen carryover and geitonogamy in *Myosotis colensoi* (Kirk) Macbride (Boraginaceae). *Biol. J. Linn. Soc.* , 46, 333–349.

Robertson, A.W. & Lloyd, D.G. (1993). Rates of pollen deposition and removal in *Myosotis colonsoi* . *Funct. Ecol.* , 7, 549.

Runquist, R.B. & Stanton, M.L. (2013). Asymmetric and frequency-dependent pollinator-mediated interactions may influence competitive displacement in two vernal pool plants. *Ecol. Lett.* , 16, 183–190.

Sargent, R.D. (2004). Floral symmetry affects speciation rates in angiosperms. *Proc. R. Soc. London. Ser. B Biol. Sci.* , 271, 603–608.

Sargent, R.D. & Ackerly, D.D. (2008). Plant-pollinator interactions and the assembly of plant communities. *Trends Ecol. Evol.* , 23, 123–130.

Sargent, R.D. & Otto, S.P. (2006). The role of local species abundance in the evolution of pollinator attraction in flowering plants. *Am. Nat.* , 167, 67–80.

Shan, H., Cheng, J., Zhang, R., Yao, X. & Kong, H. (2019). Developmental mechanisms involved in the diversification of flowers. *Nat. Plants* , 5, 917–923.

Stebbins, G.L. (1970). Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. *Annu. Rev. Ecol. Syst.* , 1, 307–326.

Steven, J.C., Rooney, T.P., Boyle, O.D. & Waller, D.M. (2003). Density-dependent pollinator visitation and self-incompatibility in upper Great Lakes populations of *Trillium grandiflorum* . *J. Torrey Bot. Soc.* , 130, 23.

Thomson, J. (2003). When Is It Mutualism? *Am. Nat.* , 162, S1–S9.

Thomson, J.D., Wilson, P., Valenzuela, M. & Malzone, M. (2000). Pollen presentation and pollination syndromes, with special reference to *Penstemon* . *Plant Species Biol.* , 15, 11–29.

Thostesen, A.M. & Olesen, J.M. (1996). Pollen removal and deposition by specialist and generalist bumblebees in *Aconitum septentrionale* . *Oikos* , 77, 77–84.

Vamosi, J.C., Knight, T.M., Steets, J.A., Mazer, S.J., Burd, M. & Ashman, T.L. (2006). Pollination decays in biodiversity hotspots. *Proc. Natl. Acad. Sci. U. S. A.* , 103, 956–961.

Vazquez, D.P. & Aizen, M.A. (2003). Null model analyses of specialization in plant–pollinator interactions. *Ecology* , 84, 2493–2501.

Waser, N.M., Chittka, L., Price, M. V., Williams, N.M. & Ollerton, J. (1996). Generalization in pollination systems, and why it matters. *Ecology* , 77, 1043–1060.

Wolfe, L.M. & Barrett, S.C.H. (1989). Patterns of pollen removal and deposition in tristylous *Pontederia cordata* L. (Pontederiaceae). *Biol. J. Linn. Soc.* , 36, 317–329.

Young, H.J. & Stanton, M.L. (1990). Influences of floral variation on pollen removal and seed production in wild radish. *Ecology* , 71, 536–547.

Table 1. Description of the parameters and parameter values used in the mathematical model

Parameter	Description	Value
P_t	Number of pollen grains produced by the focal flower	
R_i	Proportion of pollen grains removed per visit to the focal flower by an individual of the pollinator "i".	Low
		Mediu
		High
V_i	Total number of visits made by the pollinator "i" in the plant community	Low
		Mediu
		High
ΣA_i	Total floral abundance for each plant species visited by the pollinator "i", excluding the focal species	Low
		Mediu
		High
C_i	Proportion of pollen grains carried to each subsequent flower by an individual of the pollinator "i"	Low
		Mediu
		High
A_a	Abundance of the focal species	2-150

Table 2. Description of the parameters and parameter values used in the plant-pollinator network simulations. Equation (5) was used to determine the number of visits from each pollinator to each plant species. See Methods for justification of the values.

Parameters	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations	Values in the different sets of simulations
	Variable floral abundance species	Variable floral abundance species	Low abundance species	Low abundance species	Low abundance species	Low abundance species	High abundance species	High abundance species	High abundance species	High abundance species	Low abundance species with similar pollinators	Low abundance species with similar pollinators
P_t		1000	1000			1000	1000			1000		1
R_i	Max	0.7	Max	Max	0.7	0.7	Max	Max	0.7	0.7	Max	0
	Min	0.3	Min	Min	0.3	0.3	Min	Min	0.3	0.3	Min	0
V_i	Mu	7	Mu	Mu	7	7	Mu	Mu	7	7	Max	1
											Min	1
	Sigma	0.7	Sigma	Sigma	0.7	0.7	Sigma	Sigma	0.7	0.7		
C_i	Max	0.9	Max	Max	0.9	0.9	Max	Max	0.9	0.9	Max	0
	Min	0.55	Min	Min	0.55	0.55	Min	Min	0.55	0.55	Min	0
A_a	Mu	5			100	100			1000	1000		1
	Sigma	0.7										

Figure 1. Importance of different pollination processes for plant pollination success as a function of floral

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abundance, as determined by the mathematical model. Comparison of pollination success expected for low, medium and high values of A) pollinator abundance, B) pollinator specialization, C) pollen removal and D) carryover at variable floral abundance (see Table 1 for parameter values). E) Importance of the quantity component of pollination, represented by pollinator abundance, and the quality component, determined by pollinator specialization and carryover as a function of floral abundance (measured as the average between the importance of pollinator specialization and carryover). F) Hypothetical representation of the pollination systems offering the highest pollination success at different floral abundance. Specialization on pollinators with high pollen carryover and level of specialization is favoured at low floral abundance (hypothetical examples; hawkmoths and hummingbirds). At intermediate abundance, specialized pollination by more abundant pollinators (hypothetical example; bees) is favoured. At high floral abundance, most pollinators are not sufficiently abundant to remove most pollen grains and generalization becomes more advantageous. When floral abundance is too high for the pollinator community to remove most pollen grains, reliance on abiotic pollen vectors is expected.

Figure 2. Plant-pollinator networks resulting from simulated communities of different plant species and pollinator attributes. A, B) Plant-pollinator networks formed with plant species of variable floral abundance result in variable levels of generalization among plant species. C, D) Networks composed entirely of low-abundance plant species result in high level of specialization. E, F) Networks composed entirely of high-abundance plant species result in widespread generalization. G, H) Networks composed of low-abundance plant species that interact with a pollinator community composed of functionally similar pollinators result in specialization and niche partitioning among plant species for the use of the different pollinators. In A, C, E and G, the thickness of the links represents the number of visits of a pollinator to a plant species. In B, D, F and H, grey squares denote interaction between a plant and a pollinator and darker shades represent higher frequencies of interaction.

Figure 3. Degree of generalization and attributes of the pollinators on which a plant species colonizing simulated plant communities evolved as a function of its floral abundance. The parameter values represent the average values of pollen carryover capacity, specialization and abundance of the pollinators on which the new colonist evolved and degree of floral generalization of the new colonist. The parameter values on the y-axis were normalized so that the minimum value corresponds to 0 and the maximum value corresponding to 1. The standard error of the mean parameter values among the 100 simulations is presented as the shaded area around the mean values.
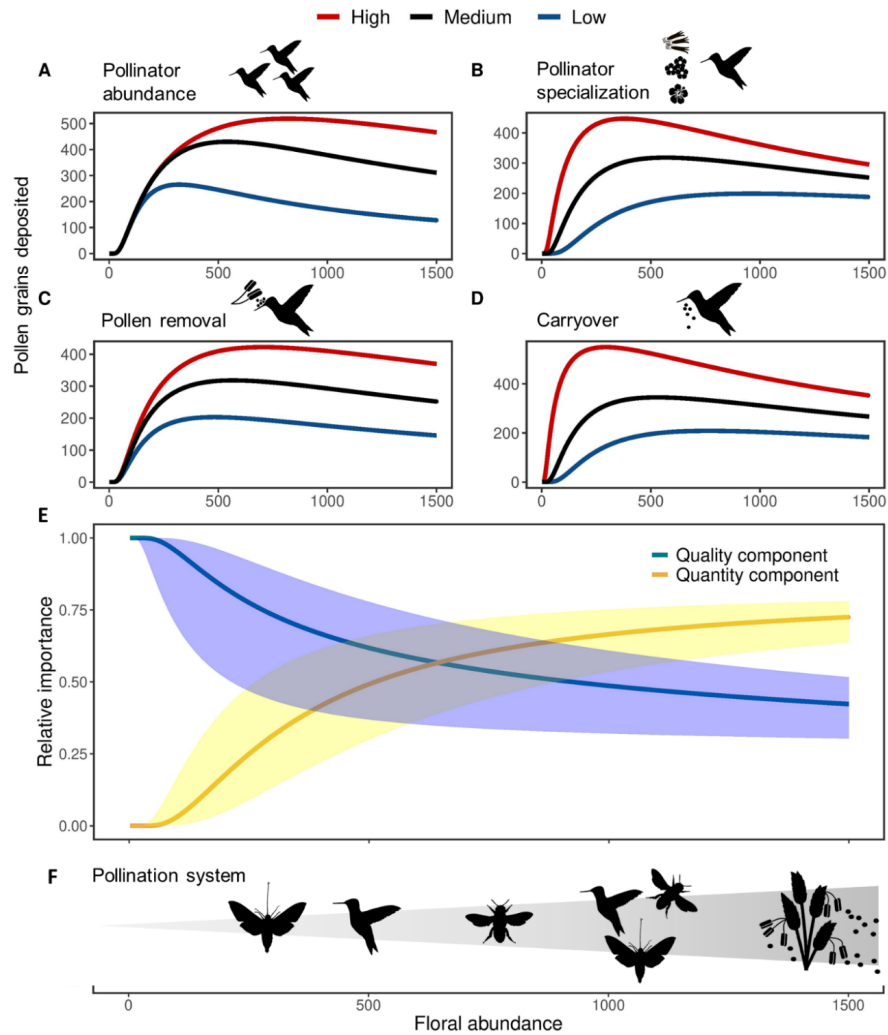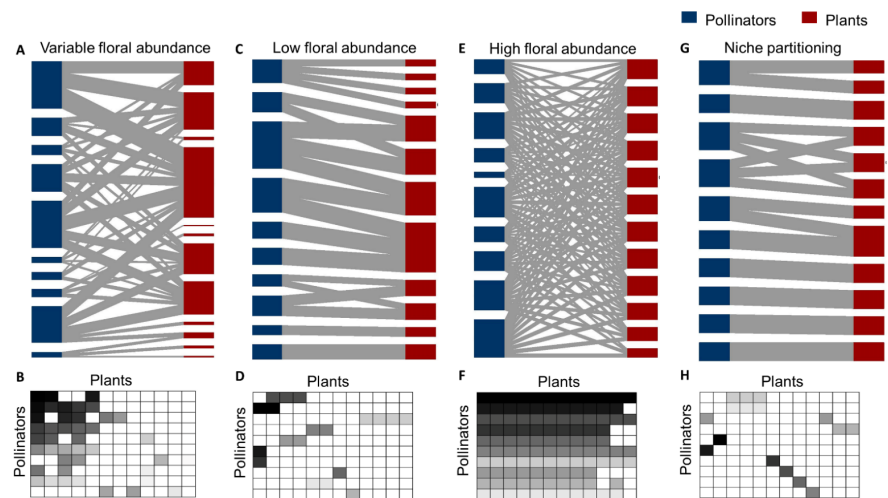
Figure 1.

Figure 2.

Figure 3.