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Passive partner choice through exploitation barriers

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Abstract   Floral features that affect the efficiency with which pollinators can harvest their resources, or the profitability they obtain from them, affect the foraging decisions of pollinators. Foraging choices of pollinators, in turn, affect pollen flow: increases in flower constancy lead to more efficient pollen transport. It follows that exploitation barriers—flower traits that differentially affect net intake rates of potential visitors—will promote resource partitioning and enhance pollen export. In this paper we first generalise foraging models to show that exploitation barriers can lead to partial resource partitioning even when flowers are randomly distributed in space. Then we develop a model to study how the foraging rules of pollinators, pollen removal and pollen deposition, affect pollen flow. The model shows that resource partitioning, even incomplete, can substantially increase the efficiency of pollen flow. Finally, we use computer simulations to demonstrate that exploitation barriers promoting partial resource partitioning can evolve. Many of the flower traits associated with pollination syndromes have small but consistent effects on the efficiency with which different taxonomic groups exploit flowers, and can be considered exploitation barriers. Even if these barriers are not strong enough to promote strict specialisation, and may have little effect on the female component of fitness when pollinators are not a limiting resource, they are likely to be selected because they enhance the male component of fitness.

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Introduction

Plant–pollinator interactions have given rise to adaptations in both plants and animals, and are in large part responsible for driving the evolution of a bewildering diversity of floral characteristics (Stebbins 1970; Gorelick 2001; Harder and Johnson 2009). Plants provide a variety of rewards to attract pollinators, ranging from food to oviposition sites, and in exchange they receive pollination services. However, not all plants provide rewards to pollinators, and not all animal visitors are effective pollen vectors (Jersáková and Johnson 2006; Gonzálvez et al. 2013). Plants and pollinators face the challenge of selecting the best partners from a pool of potential suitors.

Animals, the mobile partner, can use sensory inputs, innate preferences, learning and memory to select the flowers they visit (Meléndez-Ackerman et al. 1997; Weiss 1997; Raine and Chittka 2007; Goyret et al. 2008; Riffell et al. 2008; Dötterl et al. 2011; Burger et al. 2012). Upon detecting a flower-emitted cue, they can decide whether to approach the source of the cue and harvest its resources or ignore it. But flowers, the sessile partner, cannot make such choices: they have to accept pollinators' decisions. Their only option is to adopt traits that will influence the decisions of potential visitors—attracting effective pollinators or discouraging ineffective ones and parasites.

Flowers can discourage ineffective pollinators using exploitation barriers—traits that prevent visitors from reaching the resources or force them to invest more time and energy to harvest them. Exploitation barriers allow flowers to filter out some undesired visitors: short-tongued nectar feeders do not reach the nectar hidden at the bottom of long corolla tubes (Harder 1985), small bees are not able to open personate and keel flowers (Bohart 1957; Lebuhn and Anderson 1994) and many pollinators are unable to harvest the pollen of poricidal anthers (Buchmann et al. 1983; Thorp 2000). But exploitation barriers can also be subtle traits, such as colour (Raven 1972; Rodríguez-Gironés and Santamaría 2004) and fragrance (Galen et al. 2011)—because a change in colour or scent can make flowers more difficult to detect. In this paper we present a general framework to study the evolution of exploitation barriers, generalising a previous model investigating the conditions under which barriers that impose costs to effective pollinators can evolve (Rodríguez-Gironés and Santamaría 2005). The idea is to determine first their effect on the foraging choices of pollinators, and then to compute how foraging choices translate into pollen export and expected fitness.

If pollinators were optimal foragers, asymmetries in the efficiency with which pollinators can exploit the resources provided by different flowers could easily lead to resource partitioning. This result applies when search costs are similar for specialist and generalist pollinators (Possingham 1992; Rodríguez-Gironés 2006). When pollinators encounter flowers of different types in a random sequence, so that specialising on a single flower type implies skipping flowers and increases search costs, resource partitioning appears only if competition for resources is intense (Rodríguez-Gironés and Santamaría 2006). The first aim of this paper is to generalise these models to the more common situation, where flowers are randomly distributed in space but pollinators can detect them at a distance and can choose the direction in which they move. We use computer simulations to reach this goal.

The second aim is to determine how the foraging strategies of pollinators affect pollen flow. Most existing models of pollen transfer assume that, within a foraging bout, pollinators visit flowers of a single plant species (Galen and Rotenberry 1988; Harder and Thomson 1989; Thomson and Thomson 1992; de Jong et al. 1993; Harder and Wilson 1998; LeBuhn and Holsinger 1998; Sánchez-Lafuente et al. 2012). Although some computer simulation models study the effect of pollinator flower choices on pollen transfer (Rodríguez-Gironés and Santamaría 2007; Rodríguez-Gironés and Llandres 2008; Muchhala et al. 2010), the results of computer simulations are not easily generalised: to predict the effect of using different parameter values it is often necessary to run the simulation again. We therefore derive an analytical expression for the relationship between foraging strategy and pollen flow using as the starting point Sargent and Ottos's (2006) model.

Finally, we couple the two components—effect of barriers on foraging strategies and link between foraging strategies and pollen flow—to determine whether exploitation barriers can evolve if they only lead to incomplete resource partitioning. Although we analyse the results of each step for some specific parameter values, our aim is not to determine under which ecological conditions exploitation barriers can evolve, but to provide a tool with which to explore specific systems.

The model

Resource partitioning

Pollinators, with few exceptions, are animals foraging for resources. If we assume that pollinators are optimal foragers and that they can specialise on a subset of available species without increasing travel times, models predict strong resource partitioning: within a community, any two pollinator species should share, at most, one plant species (Possingham 1992; Rodríguez-Gironés 2006). The assumption of costless specialisation is readily met if flowers of the same type are grouped in patches and pollinators must choose the patch where they forage. While this will often be a realistic assumption (many plants, particularly trees, produce large numbers of flowers), it is not universally valid. In alpine meadows, for instance, plants of different species, with a handful of inflorescences per plant, grow interspersed.

When pollinators encounter flowers in a random sequence, resource partitioning only ensues when competition for resources is strong: otherwise, pollinators should visit every flower they encounter (Rodríguez-Gironés and Santamaría 2006). While this result seems to undermine the idea that optimal foraging leads to resource partitioning, in a real meadow pollinators do not normally encounter flowers in a random sequence. Even if flowers have a random spatial distribution, pollinators can typically detect several flowers simultaneously and they can choose which flower to approach. Under these conditions, the average distance travelled from flower to flower may be quite similar for specialist and generalist pollinators, at least if pollinators specialise on common flowers. To model this situation, we have searched for the optimal foraging strategy with spatially explicit, individual-based simulations.

The simulations proceeded as follows (see "Appendix" for model details). Two pollinator species (X and Y) exploited the nectar produced by two flower species (A and B) randomly interspersed on a square lattice. In some simulations we assume that B flowers have two phenotypes: wild-type flowers, B, have no barrier and mutant flowers, B′, are endowed with the barrier. Upon harvesting the nectar from a flower, each pollinator

selected one of its eight nearest neighbours (avoiding the ones it had recently visited). The foraging strategy of an individual determined its probability of selecting flowers of one type or another (see "Appendix").

Pollinators differed in the efficiency with which they extracted resources from flowers. In the simulations, the time that a pollinator of species i (i = X or Y) required to exploit a flower of type j (j = A, B or B′), was the sum of two terms: a handling time, τ_{ij}, specific to each species pair, and a harvest time, proportional to the amount of nectar that the flower contained. The handling time oscillated between a minimal, $T_{min,ij}$, and a maximal $T_{max,ij}$ value (Eqs. 13 and 14 in Appendix): it got closer to the minimal value every time that the pollinator exploited a flower of the corresponding species (learning), and to the maximal value whenever it exploited a flower of the other species (forgetting and interference). Effects of practice on flower handling times are well known for pollinators (Laverty 1980; Lewis 1986).

Pollen flow

Our purpose is to estimate conspecific and heterospecific pollen loads on stigmas (a proxy for female fitness) and the number of pollen grains removed from a flower that end up on the stigmas of conspecific flowers (a proxy for male fitness). To this effect, we generalise the analytical expression derived by Sargent and Otto (2006). Although the expression relies on a number of simplifying assumptions, which will not always be met, it provides a useful starting point.

To estimate pollen flow, we need a number of parameters. Some of them we obtain from the foraging strategy of pollinators (estimated through computer simulations, field observations or otherwise): the average number of i pollinators that visit a j flower, v_{ij}, and the proportion of i pollinator visits that are paid to j flowers, p_{ij} (with $p_{XA} + p_{XB} + p_{XB'} = p_{YA} + p_{YB} + p_{YB'} = 1$). We also need to know the number of pollen grains produced by A and B flowers (N_A and N_B, respectively—we assume that wild-type and mutant flowers produce the same number of pollen grains), the probability that a pollen grain collected by an i pollinator at a j flower is eventually deposited on a stigma, γ_{ij}, and the fraction of pollen grains remaining in the anthers that i pollinators remove per visit to j flower, r_{ij} (Sargent and Otto 2006). Note that it is not uncommon for pollinators to remove a constant fraction of available pollen (Harder 1990; Thomson and Goodell 2001; Gonzálvez et al. 2013), and that this does not imply that pollinators can carry unlimited amounts of pollen. Bees harvesting pollen collect pollen at higher rates than they lose it, and return to their nest when they have a full pollen load. For pollinators not actively collecting pollen, the rate of pollen removal is typically lower and most pollen falls to the ground through grooming (Thomson 1986; Harder and Thomson 1989), so that pollen loads quickly reach a steady state in which, on average, the amount of pollen removed per flower equals the amount of pollen lost via grooming or deposition on other flowers.

We first calculate the number of pollen grains removed, on average, from flowers. Following v_{Xj} visits from X pollinators and v_{Yj} visits from Y pollinators, a j flower contains

$$N_{j,left} = N_j \cdot \left(1 - r_{Xj}\right)^{v_{Xj}} \cdot \left(1 - r_{Yj}\right)^{v_{Yj}} \tag{1}$$

pollen grains. The average number of pollen grains removed is therefore approximately

$$N_{j,removed} = N_j \cdot \left[1 - \left(1 - r_{Xj} \right)^{v_{Xj}} \cdot \left(1 - r_{Yj} \right)^{v_{Yj}} \right] \qquad (2)$$

Because X and Y pollinators visit flowers in a random sequence, the average number of pollen grains collected by i pollinators at j flowers is simply

$$N_{ij} = \frac{r_{ij} \cdot v_{ij}}{r_{Xj} \cdot v_{Xj} + r_{Yj} \cdot v_{Yj}} \cdot N_{j,removed} \qquad (3)$$

The number of pollen grains exported from a j flower to the population of k flowers (where k = A, B or B′) equals (Eqs. 3–5 and A1 of Sargent and Otto 2006)

$$\xi_{jk} = \sum_i N_{ij} \cdot \gamma_{ij} \cdot p_{ik} \qquad (4)$$

We now turn to the calculation of pollen loads at stigmas. The number of pollen grains that all j flowers export to k flowers necessarily equals the number of pollen grains that k flowers receive from j flowers. Hence, if the numbers of j and k flowers in the community are, respectively, F_j and F_k, then the average amount of k pollen on the stigmas of j flowers must be

$$\rho_{jk} = \frac{F_k}{F_j} \cdot \sum_i N_{ik} \cdot \gamma_{ik} \cdot p_{ij} \qquad (5)$$

In what follows, we denote by c_j and h_j conspecific and heterospecific pollen loads. When the community consists only of A and B flowers, conspecific and heterospecific pollen loads are simply $c_j = \rho_{jj}$ and $h_j = \rho_{jk}$, with $j \neq k$. When a plant species produces flowers of different types (for instance, when a population includes wild-type and mutant plants), we must consider all possible combinations.

Evolution of exploitation barriers

To study the evolution of exploitation barriers we first need to convert pollen loads into seed production. For illustration, and without claiming any generality, we assume that all conspecific pollen grains landing on a stigma have the same probability of fertilising ovules, and that the number of seeds that a j flower produces equals

$$S_j = \begin{cases} 0 & if \quad c_j < 10 \cdot \delta_j \\ 1 + 99 \cdot exp\left(-0.0035 \cdot \left(c_j - 10 \cdot \delta_j \right) \right) & if \quad c_j \geq 10 \cdot \delta_j \end{cases} \qquad (6)$$

where

$$\delta_j = 5 \cdot \left(1 + \frac{h_j}{h_j + c_j} \right) \qquad (7)$$

This fitness function assumes that fruit set requires a minimum pollen load–abortion occurs if the number of fertilised seeds is below some threshold (Molau 1991; Hannan and Prucher 1996; Cruden 2000) and that about five pollen grains per ovule are required to maximise seed set (Murcia 1990; Schuster et al. 1993). Equation 7 further incorporates the assumption that seed set will decrease with h_j—due to interference processes, such as stigma clogging and allelopathy (Galen and Gregory 1989; Murphy and Aarssen 1995).

Knowing how pollen loads translate into seed set, the spread of a mutant allele coding for a barrier can be easily studied. We considered a population with plant species A and B.

Handling times for A flowers and wild-type B flowers were $T_{min,ij} = 2$ s for all pollinator species. Mutant B flowers, however, contained a barrier against Y pollinators, so that $T_{min,Y,B'} = 3$ s. The scope of learning, $T_{max,ij}/T_{min,ij}$, was the same for all flower–pollinator combinations. Throughout the simulations, 50 % of grid cells were occupied by A flowers. The remaining cells were occupied by wild-type or mutant individuals of species B—at the start of the simulations, there were 3 % mutant individuals. We fixed the frequencies of the different flower types for 50 pollinator generations and used the algorithm described in "Appendix" to estimate the foraging strategy of pollinators corresponding to these flower frequencies. After these 50 pollinator generations, we used the foraging strategy of pollinators to estimate pollen flow and seed set of wild-type and mutant B flowers, and from these seed sets we obtained the new frequencies of wild-type and mutant flowers. This process was iterated for 200 plant generations, or until the mutant invaded the population— we considered that the mutant allele had successfully invaded the population if it was present in at least 90 % of B flowers. For the calculations, we assumed dominance of the mutant allele and Hardy–Weinberg equilibrium between the mutant and wild-type alleles.

Results

Resource partitioning

To determine whether maximising intake rate leads to resource partitioning when flowers are randomly distributed in space, we simulated a 100-by-100 square grid with periodic boundary conditions. Each cell in the grid had the same probability of being occupied by an A or a B flower (no spatial correlation). The parameter determining nectar secretion rate (Eq. 10) was θ = 0.003. Two hundred pollinators, 100 of species X and 100 of species Y, exploited the nectar produced by A and B flowers. Their minimum handling times were

$$T_{jmin,XA} = T_{jmin,XB} = T_{jmin,YA} = 2 \tag{8}$$

$$T_{jmin,YB} = 2 + \delta T \tag{9}$$

We determined the optimal foraging strategy of X and Y pollinators as a function of the parameter δT, with $0 \leq \delta T \leq 1$—so that X pollinators were equally efficient at collecting resources from A and B flowers, while Y pollinators were less efficient collecting pollen from B flowers. For each value of δT, we also explored the effect that the scope for learning ($1 \leq T_{max,ij}/T_{min,ij} \leq 1.5$) had on flower preferences. In all simulations, the rate of learning was given by ζ = 0.25 (Eqs. 13 and 14) and pollinators avoided the last ten flowers they had visited. We ran ten simulations for each set of parameter values.

Resource partitioning increased with the scope of learning—which reduced handling time for pollinators specialising on a single flower—and with the strength of the exploitation barrier (Fig. 1). When the scope of learning was large ($T_{max,ij}/T_{min,ij} = 1.5$), pollinators selected their preferred flower on over 90 % of visits. But even when specialising on a single flower type did not reduce handling time ($T_{max,ij} = T_{min,ij}$) weak barriers (δT = 0.25 s) induced biases in flower choices. Pollinators affected by barriers preferentially visited flowers without barriers and, although to a lesser extent, pollinators unaffected by the barrier preferentially visited flowers with barriers—where interspecific competition for resources decreased (Fig. 1). Note that when $T_{max,ij}/T_{min,ij} > 1$ and δT = 0 pollinators benefit from specialising on a single flower (as learning reduces handling times)

but it makes little difference which flower they specialise on (as long as each species chooses a different one). For this reason, in Fig. 1 data for $\delta T = 0$ indicate the strength of preferences, but not which flowers pollinators preferred.

Pollen flow

Barriers that affect mainly effective pollinators are unlikely to evolve. Therefore, to study the effect of barriers on pollen flow we focused on the situation where the barrier deters the less effective pollinator. We compared conspecific and heterospecific pollen loads in two communities with handling times as in Eqs. 8 and 9. In the first community, handling times were identical for all plant–pollinator pairs ($\delta T = 0$). In the second, B flowers had a barrier that deterred Y pollinators ($\delta T = 0.25$ s). For each community, and for $T_{max,ij}/T_{min,ij} = 1$, 1.1 and 1.25, we used the algorithm described in the appendix to determine the foraging strategies of pollinators. From the foraging strategies we derived the number of visits that A and B flowers received from X and Y pollinators (v_{ij}) and the probability that, in a randomly chosen visit, i pollinators visited j flowers (p_{ij}). We then used Eqs. 1–5 to calculate average conspecific and heterospecific pollen loads at the flowers with barriers. We calculated pollen loads assuming that the proportion of available pollen removed per visit (r_{ij}) was 0.1 and 0.3 for all plant–pollinator combinations and the probability that a pollen grain was eventually deposited on a stigma was $\gamma_{ij} = 0.01$ for all combinations, except for pollen removed by Y pollinators at B flowers ($\gamma_{YB} \leq 0.01$).

In the presence of barriers, B flowers received more conspecific and less heterospecific pollen (Fig. 2). Increasing the scope for learning, $T_{max,ij}/T_{min,ij}$ and the pollen removal rate (r_{ij}) enhanced the beneficial effect of the barrier—although the effect of pollen removal rate was rather small. Not surprisingly, heterospecific pollen loads at B flowers were independent of the value of γ_{YB}. In terms of conspecific pollen load, however, the barrier was particularly useful when γ_{YB} was small (Fig. 2). Thus, when X pollinators were ten times more likely to transfer B pollen grains to stigmas than Y pollinators ($\gamma_{XB} = 0.01$, $\gamma_{YB} = 0.001$) the barrier lead to a 15 % increase in conspecific pollen loads even when $T_{max,ij} = T_{min,ij}$—despite the fact that biases in flower choices were weak: X pollinators selected A flowers in 47 % of visits, and Y pollinators in 57 % (Fig. 1). Note that, because Fig. 2 shows changes in average pollen loads in a community with two equally abundant flower species, it can be read as pollen import or export.

Evolution of exploitation barriers

In the previous section we have seen that exploitation barriers, once in place, can enhance reproductive isolation—increasing conspecific and decreasing heterospecific pollen loads. To study the evolution of exploitation barriers, however, we must consider the reproductive success of flowers with and without barriers within the same community. For barriers to evolve, mutant flowers presenting a barrier, even when rare, must achieve greater reproductive success than the barrierless wild-type flowers.

When $T_{max,ij}/T_{min,ij} = 1.25$, a barrier with $\delta T = 1$ s readily invades the population (Fig. 3). After 200 plant generations, the average proportion of mutant B flowers was greater than 60 % in all the conditions we tested. The effectiveness of the less-effective pollinator ($\gamma_{YB} = 0.003$–0.009 vs. $\gamma_{XB} = 0.01$), the average number of visits per flower that flowers received (5–30) and the proportion of available pollen removed per visit (0.1–0.3) had no consistent effect on the invasibility of the population by the B' mutant (Fig. 3).
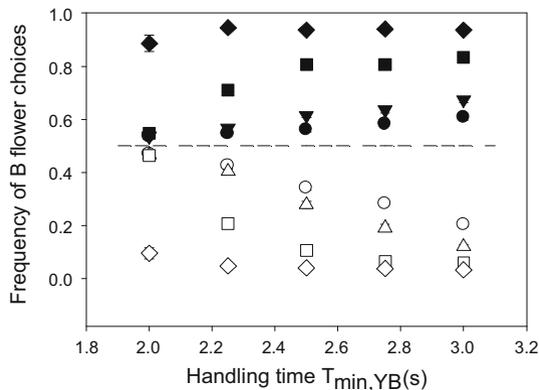
Fig. 1 Frequency with which pollinators choose B flowers as a function of the handling time for Y pollinators. The simulations assumed that all other handling times were equal to 2 s. *Black symbols* represent X pollinators, *empty symbols* Y pollinators. *Each symbol* type corresponds to a value of the scope for learning: $T_{max,ij}/T_{min,ij} = 1$ (*circles*), 1.1 (*triangles*), 1.25 (*squares*) and 1.5 (*diamonds*). *Error bars* (hardly visible due to the overlap with the *symbols*) are standard errors from 10 simulations. For $T_{min,YB} = 2$ s, *symbols* represent choice frequencies for the preferred (X pollinators) and unpreferred (Y pollinators) flower species, regardless of whether it was species A or B. The *dashed line* represents indifference (0.5 probability of visiting either flower species)

Discussion

Exploitation barriers and pollination syndromes

In this paper we provide a framework to evaluate the selective advantages of exploitation barriers—floral traits with differential effects on the efficiency with which putative pollinators can harvest the resources provided by flowers. The first step is to determine the effect of exploitation barriers on the foraging strategy of pollinators. This can be accomplished through analytical models (Possingham 1992; Rodríguez-Gironés 2006; Rodríguez-Gironés and Santamaría 2006) or, for more complex problems, computer simulations (Rodríguez-Gironés 2006; this study). Equipped with the optimal foraging strategies of pollinators, we can proceed to estimate pollen flow between different types of flowers—Eqs. 1–5.

Using this framework, we have shown that exploitation barriers that lead to slight preferences (with probabilities of choosing the preferred flower over the non-preferred one less than 0.6) can be selected for if they encourage visits from a pollinator that is more effective at transporting pollen than alternative visitors. This has important consequences for the evolution of floral traits and, in particular, for our understanding of pollination syndromes (Fenster et al. 2004). Many of the phenotypic traits associated with pollination syndromes have small but consistent effects on the efficiency with which different taxonomic groups exploit flowers, or the profitability they obtain from exploiting them. As such, they can constitute exploitation barriers. These barriers are not strong enough to promote strict specialisation, and probably lead to weak preferences. But these small preferences can translate into substantial increases in the amount of pollen exported to conspecific stigmas. Enhancing pollen transfer may, or may not, increase the female component of fitness—but in the absence of associated costs, it will always be selected for its positive effect on the male component of fitness (Muchhala et al. 2010). Absolute

Fig. 2 Effect of barriers on pollen transfer. The figure plots conspecific (*black symbols*) and heterospecific (*empty symbols*) pollen loads in flowers with barriers, relative to their expected value in the absence of barriers, versus the relative pollination effectiveness of the pollinator affected by the barrier (γ_{YB}/γ_{XB}—where γ_{ij} is the probability that a pollen grain collected by an i pollinator at a j flower ends up on a stigma). Values greater than 1 indicate an increase in pollen loads, values smaller than 1 a decrease. *Panels* represent different values of the scope for learning: $T_{max,ij}/T_{min,ij} = 1$ (**a**), $T_{max,ij}/T_{min,ij} = 1.1$ (**b**) and $T_{max,ij}/T_{min,ij} = 1.25$ (**c**). *Circles* refer to $r_{ij} = 0.1$ and *triangles* to $r_{ij} = 0.3$. *Error bars* are standard errors from 10 simulations
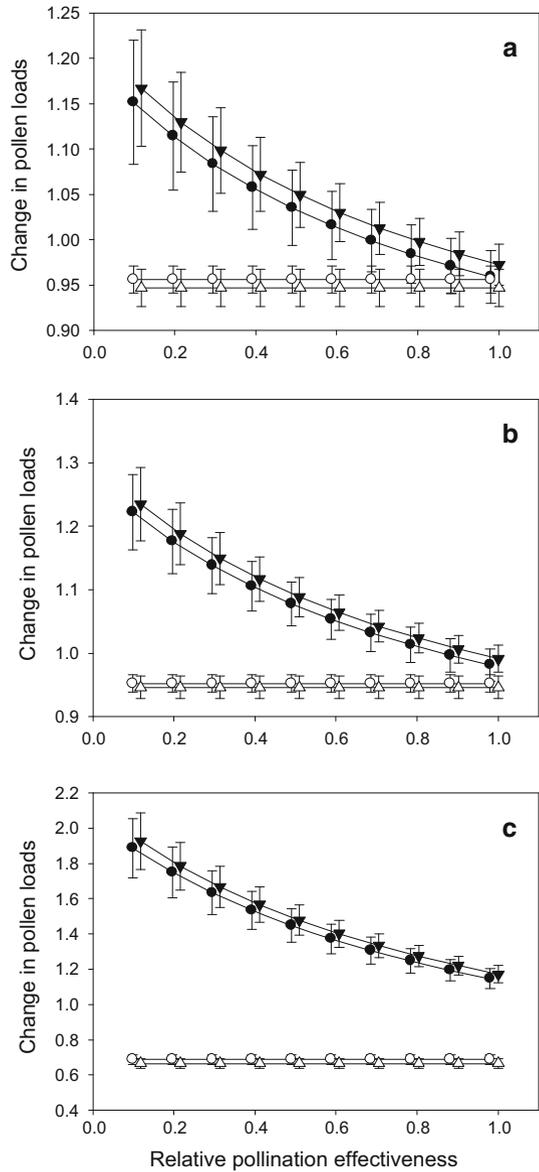
specialisation of pollinators may be required to promote sympatric speciation through ethological reproductive isolation (Grant 1994; Waser 1998; Gegear and Burns 2007), but not to promote the evolution of floral diversity (Armbruster and Muchhala 2009; Kay and Sargent 2009).

Flower specialisation on pollinators (barriers promoting pollinator preferences) may, in fact, be more likely to evolve than previously thought. It has been assumed that specialisation results in reduced visit rates (Muchhala et al. 2010), but this is not necessarily the case when pollinators are optimal foragers. When flowers specialise on a pollinator the

Fig. 3 Invasibility of exploitation barriers. Average frequency of flowers with barriers after 200 plant generations versus the average number of visits received by flowers. *Each panel* represents a different proportion of available pollen grains removed per pollinator visit: $r_{ij} = 0.1$ (**a**), $r_{ij} = 0.2$ (**b**) and $r_{ij} = 0.3$ (**c**). *Bar shading* indicates the effectiveness of the least effective pollinator ($\gamma_{YB} = 0.003$, 0.006 and 0.009; $\gamma_{XB} = 0.01$). *Error bars* are standard errors from 10 simulations
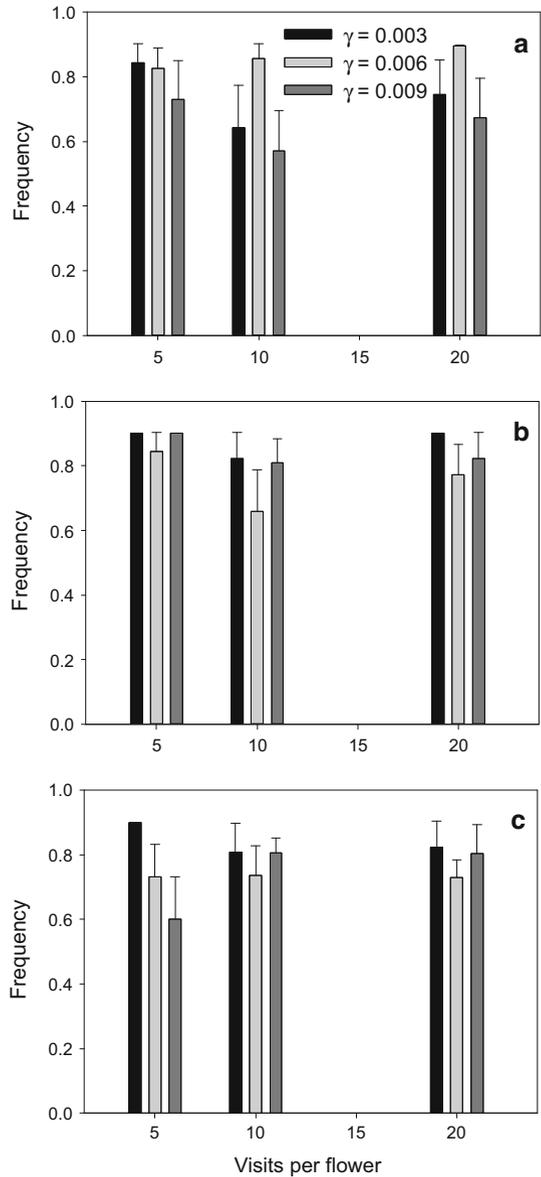
number of visits they receive may be unaltered: the increase in the rate at which the favoured pollinator visits flowers compensates for the decrease in visit rates of the alternative pollinator. For example, *Melastoma malabathricum* flowers receive the same number of visits in plants with or without nests of the predatory ant *Oecophylla smaragdina*. However, in plants with ant nests flowers are visited mainly by large *Xylocopa* bees, and in plants without nests by the small *Nomia strigata* (Gonzálvez et al. 2013).

Cognitive constraints and the community context

Evolutionary ecologists are increasingly incorporating the cognitive abilities of pollinators in their studies of flower evolution (reviewed in Schiestl and Johnson 2013). Pollinators can select flowers with specific traits (Meléndez-Ackerman et al. 1997; Gomez et al. 2006; Schiestl 2010; Parachnowitsch et al. 2012), and the cognitive constraints and biases of pollinators can influence and even be responsible for such choices, as suggested by the finding that many floral traits appeared after pollinators evolved a preference for such traits: most flower colours are conspicuous to insects, but the visual system of insects evolved before the radiation of flowering plants (Chittka 1996), and many floral fragrances are chemically similar to compounds that were already used in insect communication when the plant lineages evolved (Schiestl 2010; Ramírez et al. 2011; Schiestl and Dötterl 2012). Nevertheless, while to understand the flowers that pollinators exploit it is necessary to acknowledge their physiological, morphological and cognitive constraints, we believe that such information is not sufficient to fully predict flower choices. This is because constraints do not normally prevent pollinators from using flowers: they often make pollinators less efficient at exploiting flowers. The decision whether to exploit a flower type or not will depend on the balance between the time and effort pollinators must invest and the resources the flower offers.

Whether pollinators will include in their diet a certain flower type depends on the rate at which they can obtain resources from this and alternative flowers. Hence, the effect of floral traits on pollinators' choices must be studied in a community context (Rodríguez-Gironés and Santamaría 2004, 2005; Sargent and Otto 2006; Muchhala et al. 2010). Pollinators will include in their diet unsuitable species if they have no better choices (Feinsinger 1976), and they will make the effort to surmount barriers if the reward they obtain is high enough. For instance, where *Delphinium barbeyi* and *Aconitum columbianum* grow together, the former is visited mainly by *Bombus appositus* and the latter by *Bombus flavifrons*. But when one bumblebee species is experimentally removed, nectar accumulates in the plant it was exploiting until the other species starts harvesting it (Inouye 1978).

Determining the optimal foraging strategy of a set of pollinators exploiting the resources offered by a plant community is a daunting task. Indeed, except in the simplest communities, an analytical solution to this problem is not available. Nevertheless, the speed of modern computers makes it possible to obtain approximate solutions using individual-based simulations and rules of thumb as the ones we have implemented here. These simulations can incorporate perceptual and cognitive constraints, and their effect on the time that pollinators require to locate and exploit flowers (Rodríguez-Gironés and Santamaría 2007; Rodríguez-Gironés and Llandres 2008). Once we have an approximate solution for the optimal foraging problem, it is straightforward to estimate rates of pollen transfer (i.e. Eqs. 1–5) and hence plant reproductive success. We can therefore use this approach to determine the ecological conditions under which floral traits will evolve.

The nature of exploitation barriers

Any flower trait that differentially reduces the net intake rate of potential visitors constitutes an exploitation barrier. Many exploitation barriers will confront visitors with physical or physiological obstacles, favouring those individuals that can most easily surmount them. Such traits can evolve even if they reduce the exploitation efficiency of the most effective pollinators (Rodríguez-Gironés and Santamaría 2005). Consider for example flower

strength: large, robust flowers allow most visitors to land on them, providing a convenient platform from which to collect floral resources. The absence of a landing platform constitutes an exploitation barrier because it forces visitors to collect resources on the wing, a costly exploitation method that not all species can afford (Castellanos et al. 2004)—particularly when associated with other barriers, such as constricted corollas (Clark et al. 2014; Zung et al. this issue). Or consider the production of dilute nectar, which reduces the energy intake and increases the physiological costs (e.g. water excretion) for foraging insects and hummingbirds, favouring visitation by the latter (e.g. Irwin et al. 2004).

Other exploitation barriers have a negative effect on some species, but no effect on others: the unaffected species will make a disproportionate fraction of the visits to flowers with such barriers. For instance, flowers with distasteful or toxic nectar can reduce or prevent visitation by some foragers without affecting others (Rhoades and Bergdahl 1981; Adler 2000; Shuttleworth and Johnson 2009; Nicolson et al. this issue).

Barriers must be defined relative to a baseline—the ancestor phenotype from which the barrier evolves. At least for some pollinators, exploiting flowers with barriers must be more costly than exploiting flowers without barriers. This change can come about in two ways: the flower may evolve a trait that interferes with exploitation (see examples above), or it can lose a trait that facilitates exploitation. It is for this reason that traits that, in themselves, increase the foraging efficiency of some species without affecting the foraging efficiency of other species can become exploitation barriers when they evolve from a trait that increases the foraging efficiency of all species. To be precise, in this context the barrier would be the shift from a trait that facilitates exploitation for all pollinator groups to a trait that only facilitates exploitation for some groups, as this shift makes flower exploitation costly (relative to the primitive phenotype) for some pollinators. This can, for instance, be the case of scents and colours that help some species locate flowers (diminishing their search time) but do not affect the foraging efficiency of those species unable to detect the chemical or visual cue (Shuttleworth and Johnson 2009)—lack of scent does not hide flowers from pollinators, it simply does not make flowers conspicuous (Raguso 2008). If these scents or colours, which are perceived only by a subset of pollinators, evolve from an ancestral type which is easily detectable by all pollinators, the shift constitutes a barrier. On the other hand, if these scents or colours evolve from an ancestor inconspicuous to all pollinators, then the shift does not constitute a barrier.

Exploitation barriers also differ in the mechanism through which they affect pollinators. Barriers can change the time that visitors require to find flowers (scent and colour) and exploit them (personate flowers), the amount of energy they must invest (absence of landing platforms), the risk they face (recruitment of predatory ants), the amount of resources they can collect (tubular corollas) or the physiological costs involved (diluted and toxic nectar). A good understanding of the sensory ecology and physiology of pollinators is essential to determine how barriers work.

Model limitations

The first and foremost limitation of our model is that real-world pollinators are not, strictly speaking, optimal foragers. Indeed, the existence of deceptive flowers, which offer no reward to pollinators (Jersakova et al. 2006), demonstrates that pollinators do not always visit the flowers that maximise their intake rate. Despite these exceptions, however, pollinators are efficient foragers (Pyke 1979; Houston et al. 1988) and determining their optimal foraging strategy, or a rule of thumb that approximates it, is a good starting point for modelling the effect of pollinator behaviour on pollen removal and deposition.

The model of pollen transfer that we present is extremely simple. It could be extended to include more complex communities, the effect of geitonogamy (de Jong et al. 1993; Sánchez-Lafuente et al. 2012), the placement and layering of pollen loads on the body of pollinators (Harder and Wilson 1998), the loss of viability over time of pollen grains (Thomson and Thomson 1992) and, most obviously, asymmetries in the probability of pollen transfer from pollinator to stigma (Castellanos et al. 2003; Gonzálvez et al. 2013). Nevertheless, even this simple model suffices to show how small changes in pollinator behaviour can translate in substantial changes in pollen exchange.

Finally, the evolutionary section relies on a rather artificial fitness function. The aim of this paper is not so much to demonstrate that the foraging behaviour of pollinators can affect the evolution of floral traits, or to determine the ecological scenarios under which this can happen, as to provide a framework that can be used to study specific systems— using parameters and fitness functions inspired (or measured) in the system under study. It is partly for this reason that we have explored a rather narrow range of parameter values. The take-home message of this paper should not be "the foraging behaviour of pollinators helps us understand the evolution of floral traits", but "we can evaluate whether a specific floral trait evolved because of its effect on the foraging strategy of pollinators".

Beyond plant–pollinator interactions

Plants produce rewards to attract pollinators, which provide a service to plants while harvesting the reward. After producing the reward, however, plants have no way to withhold it or in any other way retaliate against ineffective pollinators. Plants cannot actively choose their partners, but must do so passively through the use of exploitation barriers.

Plant–pollinator interactions are not the only example of mutualism without active partner choice by one of the interacting species. Firstly, interactions where partners greatly differ in size prevent active partner choice by the larger partner. Many animals, including ungulates, termites and birds, engage in mutualistic interactions with bacteria (McFall-Ngai 1998; Soler et al. 2010) and almost 50 % of the plant species studied engage in mycorrhizal relationships with fungi (Smith and Read 2008). Secondly, interactions between sessile and mobile partners often restrict the possibility of active partner choice by the former. Besides plants and pollinators, examples include interactions between plants and frugivores (for seed dispersal), myrmecophorous plants and ants (for biotic defences), plants and predators (for tritrophic defences) or anemone and fish ("trading" nutrition for protection).

To understand partner choice in these mutualisms, Archetti introduced in the biological literature the "contract game" (Archetti 2011). The contract game assumes that one individual (called the principal) invites another (called the agent) to perform a service, offering a reward in exchange. There are, however, low- and high-quality agents, the principal gets a higher payoff if it interacts with a high-quality agent and the quality of an agent is known only to itself. The Nash equilibrium of the contract game is to design the contract in such a way that only high-quality agents benefit from engaging in the inter-action (Archetti 2011). Because the contract is the set of rules determining the payoff to each player, to ensure that only high-quality agents benefit from entering the interaction principals must introduce exploitation barriers.

The contract game is not unlike our earlier single-species nectar concealment model (Rodríguez-Gironés and Santamaría 2005): the single plant species is equivalent to the principal, the pollinator and parasite to the high and low-quality agents. It therefore suffers

from the same limitations. Among others, it assumes that high- and low-quality agents must pay a cost to engage the interaction with the principal (although high-quality agents typically pay a smaller cost) and, most important, it ignores resource competition and the community context. As we have seen, exploitation barriers need not impose a cost on all putative partners. As for the importance of competition, the nectar concealment model led to radically different solutions depending on whether the two pollinator species competed for the nectar produced by one (runaway evolution) or two (stable equilibrium) plant species (Rodríguez-Gironés and Santamaría 2005).

The reason why it is essential to consider the community composition in plant–pollinator interactions is that the benefit pollinators obtain from visiting a plant depends on how many other pollinators are doing it—and this expected benefit must be gauged against the expected benefit from visiting other flower types. When the benefit an agent obtains from interacting with a principal is independent of what other agents are doing, it is probably safe to use the contract game, which is simpler than the approach developed in this paper. When, however, the benefit that agents obtain is frequency dependent, passive partner choice will have to be studied in a community context.

Appendix

Generalities

We used a genetic algorithm to calculate the optimal foraging strategy of pollinators. Each generation 200 pollinators (100 of each species) foraged on a 100×100 square lattice (with periodic boundary conditions) containing one flower per cell. Cells were randomly assigned to plant species each generation (equal probability of belonging to each species; no spatial correlations). Pollinators, endowed with a genetically determined foraging strategy, foraged throughout the season (for most generations, 20,000 time units). At the end of the season a new generation of pollinators was produced: pollinators that obtained more nectar produced more offspring, and mutations were introduced to probe new foraging strategies. The process was iterated for 10,000 generations.

Nectar production

The volume of nectar per flower, V, increased according to

$$V = 1 - e^{-\theta t} \tag{10}$$

where θ is a parameter that determines the rate of nectar production and t represents the time since the flower was last visited.

Movement rules

At the beginning of each generation, pollinators were located at random positions of the grid. Thereafter, pollinators moved from the flower they occupied to one of its nearest

neighbours, consumed the nectar encountered and moved on to a new flower. The program kept track of the amount of nectar ingested by each pollinator through the season. The foraging strategy of a pollinator simply determined to which flower it moved. It was coded in two genes (pollinators were haploid, and had a single copy of each gene) determining the attractiveness of flowers of each species, α_A and α_B. A pollinator on a flower had 8 nearest neighbours, indexed by $l = 1, 2, \ldots 8$. Each neighbour was assigned a weight,

$$w_l = \frac{\alpha_l}{d_l} \tag{11}$$

where d_l represents the distance the pollinator must travel to reach the flower ($d_l = 1.414$ for flowers along the diagonal, and $d_l = 1$ otherwise), and the probability that the pollinator visited flower l was 0 if it was being exploited by another pollinator or had been visited by the focal pollinator in the ten previous rounds, and otherwise

$$p_l = C \cdot e^{w_l} \tag{12}$$

where C is a normalisation constant.

Time budgets

The duration of a foraging cycle (time from the departure from one flower to the departure from the following flower) was equal to the sum of three terms: travel time, handling time and ingestion time.

We assumed that all pollinators flew at the same speed, equal to 1 grid cell per time unit. Travel time was therefore equal to 1 or 1.414 time units—depending on whether the pollinator travelled along one axis or along the diagonal.

Handling time, τ_{ij}, had a species-specific component—determined by the phenotype of flowers and pollinators—and an individual component—determined by experience. The minimum and maximum handling times, $T_{min,ij}$ and $T_{max,ij}$, were determined by the flower and pollinator species. Unexperienced individuals required a greater time, $T_{max,ij}$, to get access to the nectar provided by the flower. Every time an i pollinator visited a j flower, the corresponding handling time decreased according to

$$\tau'_{ij} = \varsigma \cdot \tau_{ij} + (1 - \varsigma) \cdot T_{min,ij} \tag{13}$$

Due to cognitive constraints, however, the handling time increased when the individual visited a flower of the opposite species (Laverty 1980; Lewis 1986). Specifically, we assumed that every time pollinators visited a flower of the opposite species, handling times at j flowers increased according to

$$\tau'_{ij} = \varsigma \cdot \tau_{ij} + (1 - \varsigma) \cdot T_{max,ij} \tag{14}$$

As a result of 13 and 14, if a pollinator specialised on a particular flower type it achieved the minimum handling time at that flower type—at the cost of experiencing the maximum handling time if it once visited the other flower species. For pollinators visiting both flower types, handling times oscillated between their maximum and minimum values.

It takes longer to exploit flowers with more resources—a process encoded in the ingestion time. For simplicity, we assumed that ingestion time was proportional to the amount of nectar consumed.

Selection

At the end of the season we normalised the amount of intake consumed by the kth pollinator, I_k:

$$\bar{I}_k = \frac{I_k - I_{min}}{I_{max} - I_{min}} \qquad (15)$$

where I_{max} and I_{min} represent the maximum and minimum intakes by pollinators of the focal species. From this normalised intake we obtained the individual payoff, ω_k:

$$\omega_k = e^{2 \cdot \bar{I}_k} \qquad (16)$$

Payoffs were used to select the "parents" of the pollinators that constituted the following generation. We selected parents at random, with probabilities proportional to ω_k, with the constraint that one individual could not produce more than five offspring. Of every ten parents chosen, nine produced identical offspring. For the tenth parent, preference genes, α_A and α_B, had a 0.2 probability of mutating. Mutations steps were normally distributed, with mean zero and standard deviation 0.03. Preference genes were constrained to lie in the interval $(10^{-4}, 10)$.

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