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Are flowers red in teeth and claw? Exploitation barriers and the antagonist nature of mutualisms

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Abstract The romantic perception of plant–animal mutualisms as a cooperative endeavour has been shattered in the last decades. While the classic theory of plant-pollinator coevolution assumed that partner coevolution is largely mutualistic, an increasing appreciation of the inherent conflict of interests between such partners has led to the realization that genes that confer a reproductive advantage to plants may have negative effects on their pollinators (and vice versa), giving rise to an apparent paradox: that antagonistic processes may drive coevolution among mutualistic partners. Under this new paradigm, mutualistic partners are bound by mutual interest but shaped by "selfish" antagonistic processes. Exploitation barriers mediated by resource competition among pollinators are a key element of this paradigm. Exploitation barriers involve traits such as tubular corollas, red flowers, toxic or deterrent rewards, and attractants of floral predators. Exploitation barriers result in resource partitioning, increasing floral fidelity of favoured pollinators and therefore plant fitness; but they often entail a physiological, behavioural or developmental cost for such favoured pollinators. Resource partitioning mediated by exploitation barriers is a very powerful driver of floral diversification, robust to variation in pollinator assemblages; hence, it may contribute to elucidating the occurrence of co-evolutionary changes in multi-species contexts. Exploitation barriers provide also a mechanistic basis for traitbased modelling of interaction networks, and represent a reason for caution in assuming fixed interaction identity or strength when modelling such networks (e.g. in rarefaction procedures used to estimate secondary extinctions). We propose to replace the misleading metaphor that depicts flowers and pollinators as cooperative partners by a metaphor in which plants and pollinator are traders, seeking to obtain different services from each other in complete disregard for the benefit of their mutualistic partner.

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Introduction

The expression "nature is red in tooth and claw" (Tennyson 1833) preceded Darwin's Origin of species by 9 years, yet it came to epitomize Charles Darwin's theories on natural selection. The expression was popularized as symbolizing the conflict between the goodnatured basis of Christian religion and the callousness of nature, a conflict that developed into an epistemological divide within the natural sciences: some scientists-concerned with the popular summing up of nature as indifferent and "red in tooth and claw"-tried to set some distance between Tennyson's canto and evolution, noting that the same nature that fosters competition also fosters cooperation among organisms (Tafarella 2008), while others argued that Tennyson's expression captures something fundamentally true about organisms: that their behaviour is, at bottom, self-interested (e.g. Dawkins 1976). Darwin was not foreign to the apparent contradiction between the antagonistic and cooperative nature of many organism's traits and behaviours. In a number of passages of the Origin of species, he presents "the body of each organism a kind of mini-Benthamite (Utilitarian) society ... engaged in trade-offs that try to achieve, on balance, what is best for the organism's reproductive prospects as a whole. This might entail a mix of aggressive and cooperative strategies" (Tafarella 2008).

In this (most often implicit) debate, mutualistic interactions-notably those between flowering plants and their pollinators-became the epitome of cooperation. If antagonistic interactions such as predation and parasitism evidence the "red toothed" character of nature and evolution, mutualisms show that the "positive forces" of cooperation have played a major role in shaping the Earth's organisms (e.g. Heinberg 2012). This perception had a long lasting effect on pollination research. Under the classical, cooperative paradigm, floral and pollinator traits evolved to (i.e. were selected because they) have beneficial effects on their corresponding partner (e.g. Westerkamp 1993). But the limitations of this model soon became apparent—notably for floral visitors, who often consume resources without exerting pollination, sometimes even damaging or destroying floral structures to access food. Various theoretical refinements accommodated these observations, e.g. by discriminating between "legitimate" and "illegitimate" pollinators (e.g. Lewis 1943; Inouye 1980), defining various categories of cheaters (nectar thieves, conditional parasites; e.g. Thomson et al. 2000) and stating that floral traits evolve to match solely the "most effective pollinator" (e.g. Stebbins 1970; Johnson and Steiner 2000). Similarly, flowers that cheat flower visitors into exerting their pollination service without obtaining a reward (e.g. nectarless flowers) were generally treated as evolutionary rarities (Ackerman 1986; Thakar et al. 2003; Schiestl 2005).

The romantic perception of plant–animal mutualisms (notably plant–pollinator interactions) as a cooperative endeavour has been shattered in the last decades. While the classic theory of plant–pollinator coevolution often assumed that partner coevolution is largely mutualistic, an increasing appreciation of the inherent conflict of interests between such partners has led to the realization that genes that confer a reproductive advantage to plants may have negative effects on their pollinators (and vice versa), giving rise to an apparent paradox: that antagonistic processes may drive the coevolution among mutualistic partners (e.g. Westerkamp 1996). Under this new paradigm, which represents the focus of this Special Issue, mutualistic partners are bound by mutual interest but shaped by "selfish" antagonistic processes.

The main difference between these two perspectives of plant–pollinator interactions lays in the realization that the interests of the mutualistic partners are not fully aligned—most often, they differ or even conflict. Flowers are a source of resources (most often food) for pollinators, and pollinators compete for these resources both within and between species (e.g. Zimmerman and Pleasants 1982; Kato 1992). Floral visitors have two opposite effects on flowering plants: they enhance reproduction, but they also consume valuable resources and may inflict opportunity costs (by removing pollen that could be transferred more efficiently by other pollinators, depleting nectar, triggering irreversible changes in morphology or damaging floral parts). Plants will tend to reduce these resource and/or opportunity costs when doing so does not severely affect reproduction (e.g. in nectarless flowers).

Fitness effects of floral traits on mutualistic partners

Floral adaptations to favour pollen transfer can be classified in two broad groups. Some traits increase the probability that, if an individual visits two flowers of the same species, it collects pollen grains from the anthers of the first flower and deposits them on the stigma of the second one. Mechanisms increasing the precision with which pollen grains are deposited on and collected from the body of pollinators belong to this group. Other traits increase the probability that animals that transport pollen visit several flowers of the same species in succession, or that animals that do not transport pollen stay away.

Among this second group, there are also two types of traits, signals and exploitation barriers. Signals are traits that make flowers conspicuous and/or accessible to pollinators, in order to attract them. Exploitation barriers are traits that make access to floral resources, such as pollen or nectar, difficult. A given plant species may adapt to its most efficient pollinator by refining its signals, tailoring them to be particularly apt for such pollinators, or by making sure that animals that do not transport pollen optimally stay away. For signals, which have been emphasized by most classical approaches, floral adaptations increase the fitness of plant and pollinator. For exploitation barriers, this is not necessarily so.

Indeed, one of the most counterintuitive effects of exploitation barriers is that they may trigger adaptive changes in floral traits that, while enhancing plant fitness, have negative effects on the fitness of its mutualistic partners-including its most efficient pollinator (Rodríguez-Gironés and Santamaría 2010). To understand this, however, an explicit consideration of the foraging strategies of pollinators is crucial. Ignoring the foraging behaviour of pollinators leads to the conclusion that features that exclude less-effective pollinators are unlikely to evolve, particularly if these features interfere with the exploitation of flowers by more effective ones (Aigner 2001; Fenster et al. 2004). But, once we include such behaviour, it is straightforward to demonstrate that the optimal foraging strategy of two pollinator species that differ in the relative efficiency with which they exploit two flower types for which they compete is resource partitioning: at least one pollinator species behaves as a specialist, while the other species will behave as a specialist or a generalist depending on the ecological context (i.e. the relative abundance of pollinator species and flower types; Possingham 1992; Rodríguez-Gironés 2006, Rodríguez-Gironés and Santamaría 2005, 2006, 2007). Resource partitioning then results in increased flower fidelity within each of the two flower types (whether morphs or species) and the increase in assortative mating results in disruptive selection favouring the differentiation of traits mediating exploitation efficiency—i.e. the strength of the exploitation barrier. The increase in plant fitness, however, is not necessarily accompanied by an increase in pollinator fitness: whenever the exploitation barrier or the traits that may evolve to overcome it impose a physiological, behavioural or developmental cost on the pollinator (as it happens with most types of barriers, see below), the pollinator's fitness may decrease.

Exploitation barriers in an uncertain world

Another important aspect of exploitation barriers involves its robustness to changes in a variety of behavioural and ecological conditions. Modelling results suggest that resource partitioning is a very powerful driver of floral diversification, robust to the introduction of perceptual noise (which induces pollinators to make suboptimal foraging choices and reduces the strength of resource partitioning), to changes in the spatial distribution of flowers (patchy vs. random; Rodríguez-Gironés 2006; Rodríguez-Gironés et al. 2014), to the presence of floral visitors from a different guild (e.g. pollen-collecting bees) and to year-to-year fluctuations in population densities (Rodríguez-Gironés and Santamaría 2007). The reason for this robustness is double: the pervasiveness of resource partitioning as a response to (even small) differences in the structure and reward of co-occurring flowers, and the importance of floral constancy as a determinant of plant reproductive success. Both processes have received considerable empirical support (Rodríguez-Gironés and Santamaría 2010), albeit in relatively simple situations—since most field studies of resource partitioning and pollination efficiency concentrate on small subsets of species, and focus on one or a few localities and seasons.

This robustness extends also to variation in pollinator assemblages, and may contribute to elucidating the conundrum of current pollination biology: the occurrence of co-evolutionary changes in multi-species contexts. There are two reasons for it. Firstly, pollinator specialization through exploitation barriers does not entail lack of pollination when the favoured pollinator is rare or absent. In its absence, resources accumulate at flowers until it becomes profitable for other pollinators to exploit them, pollinating the flowers in the process. Secondly, the same exploitation barrier may foster specialization to different pollinators in different community contexts, and all but the most abundant plant species benefit from reducing pollen loss through an increase in the flower fidelity of pollinators (Feinsinger et al. 1982). Hence, exploitation barriers promote resource partitioning in all communities (Rodríguez-Gironés and Santamaría 2010).

Floral traits acting as exploitation barriers

Most traits with differential effects on the efficiency with which putative pollinators can harvest the resources provided by flowers can be considered exploitation barriers (Rodríguez-Gironés et al. 2014). These include traits related to floral morphology (long and/or constricted corolla tubes; personate corollas, such as in snapdragons; keel and bilabial blossoms; lack of landing structures, such as petals and bracts), habit (hanging flowers) and colour (red colour, which is less conspicuous to bees); as well as to anther and pollen characteristics (pore-dehiscing anthers for buzz pollination), reward profitability (diluted nectar), reward palatability (distasteful or toxic nectar and pollen), scent (selective attractants and repellents) and predation risk (mediated by ambush predators, such as crab

spiders or ants). Below, we will review briefly the traits that have been explored in the various papers that compose this Special Issue, elaborating briefly on the significance of the results presented for our current understanding of exploitation barriers.

Tubular corollas

Corolla tubes represent, probably, the best known example of resource barriers. The constriction and elongation of corolla tubes is broadly considered as a key trait in the evolution of hummingbird- and hawkmoth-pollinated flowers, as confirmed in this issue by Clark et al. (2014) for the Neotropical plant genus *Drymonia* (Gesneriaceae). Using phylogenetic analyses, they show that, within the *Drymonia*, constricted corolla tubes have evolved several times independently from ancestors with broad, bell-shaped corollas and that the trait is associated with hummingbird pollination (Clark et al. 2014). Their results suggest that corolla constrictions evolved as a barrier mechanism that precludes bees to visit flowers, but the trait may also enhance pollen placement—a possibility that remains to be investigated.

Zung et al. (2014) study the effect of corolla constrictions on the foraging behaviour of pollinators. Extending their previous work with captive bumble bees (Castellanos et al. 2004), they show in field conditions that flowers of *Penstemon strictus* with experimentally constricted corolla tubes receive fewer bumble bee visits than control flowers. The manipulation had a stronger effect on small than large bees, presumably because large bees had more ready access to nectar thanks to their longer proboscis. This experiment therefore confirms that corolla constrictions act as exploitation barriers and deter bumble bees from visiting flowers—regardless of any additional effect they may have on pollen placement. Corolla constrictions are often associated with other traits, such as the absence of landing platforms, that further increase handling times by bumble bees and decrease the rate at which they visit flowers (Zung et al. 2014).

Exploitation barriers allow nectar to accumulate until specialist pollinators visit flowers, making them a tempting booty for other pollinators that may attempt to access nectar illegitimately—that is, in ways that are less profitable for the plant. Lázaro et al. (2014) study how nectar production and corolla length of *Lonicera implexa* affect nectar robbing and reproductive success in populations with different pollinator ensembles. Nectar volumes modulate the effect of corolla length as a nectar barrier. Plant fecundity peaked at two different optima (long corollas with little nectar and short corollas with abundant nectar) and the specific combination of these two traits that maximised fecundity was related to the identity of pollinators within each population and year (Lázaro et al. 2014).

Nectar robbing is not limited to insect-pollinated flowers. It is also common in the guild of tubular, bird-pollinated plant species at the Cape Floral Region of South Africa (Geerts and Pauw 2009). While long-billed Malachite Sunbird specialized in flowers with long corolla tubes, short-billed sunbirds foraged legitimately on those with short corolla tubes— and robbed long-tubed flowers by piercing the corolla. It is worth noting that the presence of Malachite Sunbirds depressed robbing rates by short-billed sunbirds at long-tubed flowers—as predicted by resource partitioning process associated to exploitation barriers. This suggests that the effect of exploitation barriers might be operative even when facing the "shortcut" imposed by nectar robbers.

Red flowers

The association between red colour and hummingbird pollination has received considerable attention. Once the subject of controversy, centred on whether it reflected the inconspicuousness or the invisibility of red colour to bees (Chittka and Waser 1997), Rodríguez-Gironés and Santamaría (2004) pointed out that invisibility was not required for red colour to function as an exploitation barrier, so long as bees found it easier to find flowers of other colours, and a number of studies have shown now that "red flowers" may be one of a few combinations of colours that function as anti-bee exploitation barriers (Spaethe et al. 2001, Lunau et al. 2011). Phylogenetic studies show that evolutionary shifts from bee to hummingbird pollination are often associated to switches to red colour, accompanied by other exploitation barriers such as tubular corollas and/or reflected petals (e.g. Beardsley et al. 2003, Thomson and Wilson 2008). Moreover, an experimental study showed that a single-allele substitution changing flower colour from yellow to red may suffice to trigger a shift from bee to hummingbird pollination (Bradshaw and Schemske 2003). While it is clear how red colour could act as an exploitation barrier, and the perceptual basis of the hypothesis has been well established, it remains to be shown whether flower colour fosters resource partitioning when bees and birds compete for nectar.

In temperate systems where bees are among the main pollinators, red colour is rare but not absent. Some authors have suggested that part of this red-flower floras reflect an adaptation to pollination by beetles, typically in bowl-shaped flowers such as poppies (Dafni et al. 1990); while other part may be a reminiscence of past climates and ecosystems, when bird pollinators were still common (e.g. Burquez 1989, Valido et al. 2004). Alternatively, because bees are probably not the only insects lacking photoreceptors in the red part of the spectra, red flowers could be favoured as a different type of exploitation barriers—against antagonists such as floral or seed predators. Such predators could disfavour red flowers if they have difficulties detecting them or if red flowers produce fewer seeds because they receive fewer pollinator visits. Veiga et al. (2014) evaluated this possibility using a polymorphic population of *Gentiana lutea*, a mountain species in which flower colour varied from yellow to orange. Pollinator visits were virtually restricted to bumblebees (95 %) but a large proportion of fruits were subjected to seed predation by Lepidopteran larvae. Red flowers were disfavoured by both selection agents: they received less pollination visits and hosted more seed predators, and both effects resulted in decreased seed production-thus in selection favouring yellow flowers. Although consistent selective pressures from pollinators and seed predators do not explain colour polymorphism in G. lutea, the study points out to a promising avenue of work which addresses the concomitant effects of exploitation barriers on mutualistic and antagonistic visitors.

Toxic or distasteful rewards

Most pollinators are lured to the flowers by their food rewards: nectar and/or pollen. Pollen consumed by bees cannot fertilize ovules, and bees can use more than 95 % of the flower's pollen to feed their larvae (e.g. Schlindwein et al. 2005). Flowers have evolved several mechanisms as protection against excessive pollen harvesting by bees, including morphological traits (e.g. inconspicuous and pore-dehiscing anthers, keel and bilabiate flowers) and the chemical composition of pollen (pollen toxicity and/or low nutritional quality; Praz et al. 2008). In contrast, the primary function of nectar is to reinforce pollinator choices. Hence, distasteful or even toxic nectar only makes sense if it filters out undesired consumers. A recent review (Adler 2000) indicated that secondary compounds in nectar and toxic nectar are geographically and phylogenetically widespread, although their ecological significance is poorly understood. Several hypotheses have been proposed to explain its

possible functions (e.g. encouraging specialist pollinators, deterring nectar robbers, preventing microbial degradation of nectar, and altering pollinator behaviour), resting on the assumption that its benefits must outweigh possible costs; but is also plausible that toxic nectar provides no benefits to plants and occurs due to previous selection pressures or pleiotropic constraints. A number of recent papers suggest, however, that toxic nectar may function as an exploitation barrier, deterring floral visitors only if alternative, non-toxic sources are present (e.g. Gegear et al. 2007, Tan et al. 2007) and having contrasting effects on different visitors (Adler and Irwin 2005, Johnson et al. 2006).

In this Special Issue, Nicolson et al. (2014) present the results of a series of experiments with *Erythrina caffra*, a coral tree from the Cape region (South Africa) whose nectar had deterrent effects (unrelated to sugar composition) on sunbirds and honeybees, but not on generalist bird pollinators such as bulbuls. This result might seem counterintuitive because sunbirds are generally regarded as specialist pollinators. However, in this specific case, flowers of *E. caffra* are better suited for pollination by generalist birds (who contact the anthers and stigma and carry visible pollen loads on their faces) than by sunbirds (who feed on nectar without contacting the reproductive parts of flowers) or honeybees. Similar results had been reported for *Aloe vryheidensis*, whose dark and bitter nectar rich in phenolic compounds was readily consumed by bulbuls, but not by sunbirds and honeybees (Johnson et al. 2006).

All these results pave the way for future work testing the potential role of toxic or distasteful nectar as an exploitation barrier. For this purpose, however, existing data should be complemented with observational and manipulative experiments allowing to estimate the consumption rates and effects on plant (male and female) reproductive success of the different floral visitors—and at varying frequencies of ("most" vs. "less" efficient) pollinators and (deterrent vs. palatable) plants. The striking parallel with other plant–consumer systems (such as fruit dispersal and herbivory) suggest also a great potential for comparative studies.

Floral predators

Flowers attract visitors and provide excellent hunting platforms for ambush predators such as crab spiders, mantids, ambush and assassin bugs, and predatory ants. Whenever floral ambush predators have differential effects on different pollinators (such as those with large vs. small body sizes; Gonzálvez et al. 2013), they may promote resource partitioning along the predation risk gradient. While ambush predators, notably crab spiders, affect the behaviour of insect pollinators at ecological and evolutionary scales, most of them are probably too scarce to impose strong selection forces on flower traits (Rodríguez-Gironés et al. 2013).

Ants may constitute an exception to this rule. In particular, the weaver ant, *Oecophylla smaragdina*, a keystone predator in South-East Asian forests, uses the flowers of a wide range of species as hunting platforms for incoming pollinators (Rodríguez-Gironés et al. 2013). Several studies explore the adaptations used by myrmecophytic plants to prevent ants from interfering with pollination ("pollinator protection" hypothesis). This is most commonly done through the production of floral ant repellents (Ghazoul 2001; Kessler and Baldwin 2007; Junker et al. 2007). But ants can also enhance plant reproductive success: *Melastoma malabathricum* shrubs, pollinated by large carpenter bees, *Xylocopa* spp., increased their reproductive success when they harboured ant nests—and *M. malabathricum* flowers attracted, rather than repelled, weaver ants (Gonzálvez et al. 2013). Ant repellents in flowers may have evolved to prevent weaver ants from exploiting floral nectar

("nectar protection" hypothesis). Gonzálvez et al. (2014) compared both hypotheses using a survey of 32 tropical plant species. Their results validate both hypotheses, suggesting that ant repellents can function as direct or indirect exploitation barriers: they can prevent ants from removing nectar without effecting pollination (direct barriers) and, when flowers are pollinated by large bees, the absence of ant repellents—or even the presence of ant attractants—can result in ants chasing away small ineffective pollinators (indirect barriers).

Ant repellents are not the only mechanism by which plants can protect their pollinators. In the tropical genus *Macaranga* a specialized structure formed by flower-enclosing bracteoles provides feeding and breeding chambers to small-sized pollinators, such as trips and hemipterans (Yamasaki et al. 2014). These chambers act as size-dependent refuges against ant predation, effectively excluding potential pollinators of larger size (such as bees, wasps, flies and beetles) that regularly visit other species lacking this specialised structure. Because in open flowers ant disturbance is likely to select for large-bodied pollinators (which represent unlikely prey for much-smaller ants), while those with flower-enclosing bracteoles select for small-sized pollinators, the radiation in bracteole morphology can be interpreted to reflect the exploitation-barrier effect of ant predation. The suggestion is exciting, but more studies are needed before such an assertion can be contemplated.

Interaction networks

While classical pollination studies often focused on the analysis of pairwise interactions, it is becoming increasingly clear that most ecological and evolutionary process take place in a multi-species context. Borrowing a battery of techniques from the analysis of interaction networks, the study of pollination networks has made enormous advances (Bascompte et al. 2006; Bascompte and Jordano 2007; Olesen et al. 2007). To date, however, these analyses have been primarily descriptive, focusing on the topological properties of pollination networks, and it is only recently that experimental and modelling work started to be used to unravel the ecological mechanisms behind such properties and the evolutionary consequences thereof (e.g. Santamaría and Rodríguez-Gironés 2007; Okuyama and Holland 2008; Campbell et al. 2011; Guimaraes et al. 2011).

In the search for such mechanisms, one of the key questions concerns the inter-relationships between the functional and phylogenetic diversity of the two network components: plants and flower visitors. In a simulation study based on a quantitative flowervisitor network with measurements of flower traits, Junker et al. (2014) showed that functionally diverse plant communities support a higher diversity of flower visitors, which interact with their plant partners in more complementarily specialized and less connected networks. Exploitation barriers filter out undesired visitors while attracting desired ones, and are probably a key driver of such specialization. At any rate, the higher number of niches offered by functionally-diverse plant communities seems to have positive effects on the animal species exploiting them, suggesting that conservation and restoration efforts could benefit from prioritizing, respectively, the conservation and build-up of functionally diverse communities.

It is, however, important to stress here the labile nature of resource specialization triggered by exploitation barriers. This (ecological) lability is not contradictory with the evolutionary robustness proposed above. Resource specialization takes place under certain conditions, mainly a balance in the frequencies of the various pollinator species/morphs (as well as the plant species/morphs) necessary for resource competition to take place. When such conditions are not met, e.g. if one one of the pollinator species/morphs is dominant,

resource specialization does not take place and the pollinator will visit all flowers. In a seeming paradox, it is precisely such lability that ensures the provision of plant pollination by less efficient pollinators when the most efficient ones are rare or absent, thus facilitating the evolution of exploitation barriers.

Such lability has two important consequences. Firstly, the apparent properties of the interaction network depend strongly on the ecological context—a specialist pollinator may behave as a generalist in the absence of other competitors. Secondly, because the identity and strength of realised interactions depend tightly on the composition of both the plant and flower-visitor community, the properties of observed networks cannot be extrapolated to their subsamples: in the absence of dynamic simulations of resource use based on the traits of interacting species, the properties of such sub-networks cannot be reliably estimated. This is a strong limitation of all existing studies simulating the impact of species loss on network characteristics (e.g. Memmott et al. 2004; Rezende et al. 2007; Kaiser-Bunbury et al. 2010; Pocock et al. 2012), likely to severely limit their usefulness. Hence, while gathering the data and knowledge necessary to undertake such simulations requires considerable effort, this is an area where future research efforts are urgently needed.

Conclusion

We no longer see plants and pollinators as devoted partners in an unconditional mutualism. Traits beneficial to flowers may be detrimental for pollinators (and vice versa). We therefore propose to replace the misleading metaphor that depicts flowers and pollinators as cooperative partners by a metaphor in which plants and pollinator are traders, seeking to obtain different services from each other in complete disregard for the benefit of their mutualistic partner (Noë and Hammerstein 1995). Such metaphor provides a more useful framework to accommodate the determinant role of competition (both between pollinators and between plants) in shaping plant–pollinator relationships, and to understand numerous phenomena that, under the "cooperation paradigm", seem perplexing—most notably, the pervasiveness of exploitation barriers that "make use" of competitive interaction among pollinators to optimise plant pollination, often at the cost of decreasing pollinator fitness and/or triggering the evolution of traits that overcome such barrier (i.e. evolutionary arms races between plant and pollinators).

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