

Plants and pollinators: will natural selection cause an imbalance between nectar supply and demand?

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Abstract

Pollination is an important ecological process. However, the needs of plants and pollinators are not always met. Pollen limitation commonly reduces seed set and bees often experience nectar dearth. Using a theoretical cost-benefit optimization model we show that natural selection acting at the level of individual plants and pollinators will result in positive feedback that exacerbates pre-existing imbalances between nectar supply and demand. When pollinators are scarce plants will be selected to produce more nectar to outcompete other plants in attracting pollinators, and when pollinators are abundant plants will be selected to produce less nectar. We encourage the testing of this novel hypothesis and propose several ways of doing this via comparative study and experimental manipulation. We also suggest that evidence for seasonal variation in foraging conditions provides preliminary empirical support. If our hypothesis is correct it means that pollination faces a particular challenge in balancing nectar supply with demand.

Evolutionary & Ecological Logic

Pollination is central to plant reproduction yet pollen limitation is widespread (Ashman et al. 2004; Burd 1994; Knight et al. 2005). Fig. 1 shows a standard theoretical cost-benefit model that determines optimal levels of nectar secretion in terms of plant reproduction for an individual plant at times of relative scarcity or abundance of pollinators. Optimal nectar production is higher when pollinators are scarce. The assumptions underlying the model are biologically realistic: (i) greater nectar production results in more pollinator visits (Wyatt and Shannon, 1986; Klinkhamer and de Jong, 1990) and generally (however, see Fisogni et al., 2011) increases plant reproductive success (e.g. Neiland & Wilcock, 1998; Larson, & Barrett, 2000), (ii) nectar has a non-zero cost of production (Southwick, 1984, Pyke, 1991); (iii) plant reproduction increases with pollinator visits and approaches the maximum in an asymptotic manner (Silander and Primack, 1978; Snow, 1982; Ashman et al. 2004; Morris et al., 2010).

How would these individual-level evolutionary responses affect nectar availability in the wider ecosystem? If pollinators are scarce, an individual plant can increase its reproductive success by producing more nectar and thereby attracting more of the available pollinators. That is, it becomes a superior competitor. However, the same logic also applies to other plants competing for the same limited number of pollinators. Overall, and via the action of natural selection at the individual level, this should result in increased nectar availability in the ecosystem. The same logic applies in reverse when pollinators are abundant and leads to an overall decrease in nectar availability.

Connectedness in the plant-pollinator network

For the scenario above to result in an ecosystem-wide effect, pollination interactions must form a well-connected network, in which particular plant species are pollinated by multiple pollinator species and *vice versa*. This scenario is shown in Fig. 2a. The high level of connectedness results in broad ranging competitive effects that can propagate across the plant-pollinator community.

For example, if (Fig. 2a) Plant Species 1 produces more or less nectar this will also affect Pollinator Species 3, even though it does not visit Plant Species 1, via its competition for nectar with Pollinator Species 2 that visits both Plant Species 1 and 3. Conversely, if plants and pollinators are not well connected (Fig. 2b), then natural selection for more or less nectar production and competition will still occur but will be localized, and affect particular sub-sets of the pollination community, but not the entire community and network. There are specialized cases, such as in the fig plant-fig wasp mutualism, in which pollination is largely as shown in Fig. 2b, even if in a few cases it falls short of being completely specific (Molbo et al., 2003), in which each plant species has only one pollinator wasp species (Janzen, 1979).

Empirical data on pollination networks indicate that species are typically well connected (Memmott, 1999; Vizenin-Bugoni et al., 2018). In addition many pollinators, including honey bees and bumble bees, are generalists that visit many plant species (Biesmeijer & Slaa 2006; Waser et al., 1996). Indeed, most plant species are visited by multiple pollinator species (Waser et al., 1996, Ashworth et al., 2015).

Positive & Negative Feedback in Plant-Pollinator Balance

What is intriguing in the scenario above is that the competition causes positive feedback. That is, existing imbalances, whether it is plants chasing scarce pollinators by providing more nectar or *vice versa*, will be exacerbated (Fig. 3). The behaviour of pollinators should also facilitate and encourage positive feedback thereby working against balance. Pollinators such as bees are very mobile, can rapidly assess nectar rewards, and are able to preferentially visit more rewarding feeding sites (Balfour et al. 2015; Seeley 1995). As such, pollinator behaviour will advantage flowers that produce more nectar. What about times when selection favours plants producing smaller amounts of nectar leading to relative resource scarcity for pollinators? Although pollinators should not visit flowers to collect nectar unless they make a net energy profit in doing so, the energy gains can be small (Balfour et al. 2015). Pollinators would seem to be exploitable to work for “low wages” at a time of nectar scarcity, provided these wages are above the minimum needed to make an energy profit. Bees are able to cope with small energy gains per flower because they can visit flowers at a great rate (Couvillon et al. 2015), thereby accumulating many small rewards. Most female bees and some wasps are nest builders and need to forage not just for their own needs but for the needs of their nest or colony. However, most other pollinators, such as butterflies and hover flies, do not provision a nest and so are only foraging for their personal energy needs. Here, small amounts of nectar may be sufficient and a rapid foraging rate not needed. Therefore, producing small quantities of nectar when pollinators are abundant may be a viable reproductive strategy for summer-blooming plants.

What about negative feedback to reduce imbalance? Via natural selection, plants that do not receive adequate pollination may prolong their flowering period (Udovic & Aker, 1981), decrease their need for pollinators in various ways such as by producing fewer but larger seeds (Huang et al., 2017), make better use of pollinator visits (Ashman and Morgan, 2004.), rely less on outcrossing (Harder and Aizen, 2010) or even adopt asexual reproduction (Lloyd, 1992). Furthermore, plants may also increase the display of signals that attract pollinators (e.g. visual or olfactory; Raguso, 2004). Indeed, there is evidence that scent advertisement is higher in early blooming species, when pollinators may be relatively scarce, than late flowering species (Filella et al., 2013). However, such phenomenon are unlikely to increase floral resource availability or, in turn, pollinator population growth rates (Ogilvie & Forrest 2017). Therefore, these adaptations are unlikely to significantly alter the balance between nectar supply or demand.

There are also several evolutionary and biological constraints within plant-pollinator communities which may prevent phenological matching between nectar demand and supply. For example, plant flowering phenology is thought to be a conservative character (Ollerton & Lack, 1992) and is partially determined by a number of factors including taxonomic membership (Kochmer, and Handel, 1986). Likewise, many groups of pollinators are constrained, for example, by their thermal windows (Lefebvre et al., 2018) and trait characteristics (Junker et al., 2013). Moreover, pollinator populations are may be strongly limited by resources other than pollen and nectar during times of nectar abundance, for example nesting sites and larval food resource (Benadi, 2015). Similarly, plant population are constrained by resources availability beyond pollen limitation, e.g. water and minerals (Kalske et al., 2012).

Evidence for and Testing the Positive Feedback Hypothesis

We suggest that the outcome of the combined evolutionary-ecological process outlined above will be to cause seasonal differences in the balance between nectar supply and demand, with one or more seasons characterized by relative nectar abundance in which plants chase scarce pollinators, and one or more seasons by relative nectar shortage in which pollinators chase scarce nectar. These imbalances would arise via positive feedback exacerbating pre-existing, but smaller imbalances. Thus, a pre-existing situation in which many plants bloom in spring in a temperate-climate region could lead to a situation in which spring-blooming flowers produce more nectar than summer-blooming flowers. Is there any evidence for seasonal imbalance? In addition, how can the positive feedback hypothesis be more directly tested?

Several lines of evidence indicate that nectar is considerably more available in spring than summer, suggesting a seasonal imbalance. For example, honey bee (Couvillon et al. 2014b) and bumble bee (Pope and Jha, 2018) foraging distances are greatest during summer. Honey bee colonies gain more weight during spring (Balfour et al., 2017; Garbuzov et al., 2020) and a greater proportion of foragers returning with empty crops in summer than spring (Couvillon et al. 2014a). In addition, standing crops of nectar in lavender flowers are greater in spring than summer (Wignall et al., 2020). Summer is also the season of intense nectar competition among flower-visitors (e.g. Inouye, 1978; Weatherwax, 1986; Balfour et al., 2015) during which foragers compete for flowers containing minute quantities of nectar (c. 0.1 μ l; Williams, 1998; Balfour et al., 2015) and nectar robbing among honey bee colonies occurs (e.g. Sakofski et al., 1990). Furthermore, it is likely that there are simply more flower-visiting insects on the wing in summer (Balfour et al., 2018) available to pollinate. For example, two major pollinators, honey bees and bumble bees, will be most abundant in summer as by then their colonies have reached maximum populations (Balfour et al., 2018).

In parallel with these findings, previous research in temperate-climate areas shows that species blooming earlier in the year tend to have lower seed or fruit set (e.g. Motten et al., 1981; Thomson, 2010; Kudo and Ida, 2013). It has been suggested this is due to low pollinator activity at this time of year. However, a formal measure of the seasonal ratio of pollinators to floral rewards is still lacking.

The positive feedback hypothesis needs to be tested, ideally by testing predictions that arise from it. Here we propose two tests, and encourage other biologists to devise more. The first test uses phylogenetically independent contrasts to compare the nectar secretion rates of native plants growing in a particular region in which there is existing background ecological information to suggest suitable seasons to compare. For the situation in southern England this would be spring versus summer (e.g., March-May v. July-August), with the *a priori* prediction being that spring-flowering plants produce more nectar per flower than summer-flowering plants. Specifically, we propose comparing the nectar secretion rates of sequentially blooming species within multiple families across seasons.

One advantage of flowering plants as a study group is that they are diverse. As a result, obtaining an adequate number of species to study should be possible. We propose that study species should be native and bloom exclusively or predominately in one of the designated seasons. Additional variables that are likely to affect per-flower nectar secretion such as flower size, plant type (herb, shrub, tree), and habitat can be included as additional variables and controlled for. In principle, any species that are not wind pollinated and for which their phylogentic position can be determined could be studied. In practice, focusing on particular taxa could give practical advantages. In the Lamiaceae, the flowers of many species are large enough to allow nectar volumes in individual flowers to be quantified using capillary tubes (Balfour et al. 2015). In addition, Lamiaceae produce little pollen, so the main reward is nectar. Although the Asteraceae are highly-attractive to insects (e.g. Warzecha et al., 2018), their flowers are aggregated into dense inflorescences and it is difficult to accurately quantify their nectar volumes (Dósa, 2008).

Our second suggested test is experimental/manipulative and also uses native plant species that bloom exclusively or predominantly in one of the two seasons to be compared. Plants of multiple species would be reared under controlled conditions to retard or advance their bloom (Wignall et al. 2020). We predict that plants that normally bloom in the pollinator-scarce season will attract more pollinators per flower per unit

time when caused to bloom in the pollinator-abundant season and *vice versa* .

Balance in Other Mutualistic Ecological Processes

Pollination is one of a number of ecological processes, that often involve mutualism, in which one group of organisms carries out an important function which helps sustain the ecosystem. Is pollination unique in that natural selection can, as we argue, cause an imbalance in supply and demand? Or could similar phenomenon occur in other mutualistic groups?

Frugivory is perhaps the closest to pollination, especially as animal frugivores also play an important and often mutualistic role in the reproduction of their plant partners by dispersing their seeds. Fruit production, like nectar production, has a non-zero cost to the plant (Encinas-Viso et al., 2014). The majority of frugivores are highly mobile and eat fruit from multiple species, which often varies seasonally in terms of which fruit is consumed (Herrera, 2002; Corlett, 2011) and the proportion of fruit in their diet. Plant-frugivore interactions often involve many species, forming complex networks of mutualistic partners (Vidal et al., 2014). Frugivores also differ in their effectiveness as seed dispersers (Calvino-Cancela et al., 2009). Therefore, if the supply of fruit is seasonal and limiting (Milton, 1980), imbalances in this system would seem likely. However, this area remains poorly understood (Calvino-Cancela et al., 2009). Nevertheless, we would expect phenological supply and demand fluctuations to be more likely in habitats in which seed dispersers show pronounced seasonal variation in diet, habitat use, or foraging behaviour (Campos-Arceiz, 2008).

Another very important ecosystem process is provided by the many decomposer organisms which break down organic matter and in doing so release plant nutrients into the soil. Whether or not it is considered a mutualism, this system is much less likely to result in positive feedback causing imbalance for several reasons. First, decomposer organisms lack the mobility (Rantalainen et al., 2004) of pollinators and so are not as free, for example, to serve particular trees that provide more dead leaves in the autumn. Second, their resource is not as ephemeral. Nectar does not persist in the environment. By contrast, dead leaves and other organic matter may persist for a long duration thereby buffering temporal imbalances.

Mycorrhizal-plant relationships also have parallels with pollination. Multiple fungi interact with individual plant hosts (Johnson et al., 2012) and vice-versa (Weremijewicz and Janos, 2013). As with the interactions between plants and nitrogen fixing bacteria, the partners will generally lack mobility. In these mutualisms, and also in brood-site pollination mutualisms such as those between fig plants and fig wasps, there may also be processes that control the mutualism to the benefit of one or both partners (e.g., Jander & Herre 2010; Wang et al. 2013). Selection dynamics of these communities has been likened to human economic markets (e.g. Werner and Kiers, 2015; see also Noe & Hammestein, 1995).

Concluding remarks

Our imbalance hypothesis may shed light on the surprising fact that seed production is often pollen limited (Ashman 2014; Knight et al. 2015; Burd 2004). This is surprising because, according to Bateman's principle (Bateman 1948; Burd 2004), female reproductive success is usually limited by resources not males. Bateman's principle appears to work better for animals than plants, and there are animal species with massively female-biased sex ratios in which the few males are still able to fertilize most of the females (Dyson & Hurst 2004; Jiggins et al. 2000). Pollen limitation is probably in part a consequence of plants "mating" via intermediaries in the form of pollinators. Ashman (2014) notes that the leading hypotheses for pollen limitation are that the situation is not at equilibrium, for example due to human interference, or that it is at equilibrium but subject to great stochastic variability (Burd 1994). Our hypothesis suggests that we should not necessarily expect the equilibrium to be a balance in terms of pollination-system needs. Rather it may be an equilibrium of costs and benefits than exacerbates imbalance rather than an equilibrium of needs. The flip side of the coin to pollen limitation, meaning that there is not enough pollinator activity, is nectar dearth, meaning that bees and other pollinators struggle to find nectar. Dearth is frequently observed by beekeepers (e.g. Mogren et al., 2018). Although pollination is a mutualism it would seem that one of the two partner classes is, on average, frequently underserved or exploited by the other (Bronstein, 2001; Nepi et al., 2018).

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Fig. 1. Optimum nectar production by a plant. The optimum occurs where the slope of the reproductive success curve and the nectar production cost curve are equal, shown by the positions of the red tangent lines. When there are many pollinators a plant reaches a given level of reproductive success at a lower level of nectar production.

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Fig 2. Connectedness in pollination community. In a) pollinator species each visit multiple plant species and plant species each have multiple pollinator species. As such, competitive effects can propagate across the whole pollination community even though not all pollinator species visit all plant species and *vice versa* . In b) each pollinator species only visits one plant species and *vice versa* . Competitive effects are, therefore, confined within the 3 species pairs of plant and pollinator.

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Fig 3. Positive feedback for increased or decreased nectar production. If pollinators are scarce relative to plant pollination needs, nectar conditions will be good for pollinators. However, rather than being selected to produce less nectar, which would put the supply and demand of nectar into a better balance, plants are actually selected to make more nectar to attract the scarce pollinators in competition with other plants. The reverse situation occurs when pollinators are abundant. Natural selection will favour lower nectar production by plants, which results in worse nectar conditions for pollinators.