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## **Native flowering plants along the Colorado River and their Pollinators**

The many microclimates and habitat types found along the Colorado River in the Grand Canyon provide an ideal environment for both insect and angiosperm biodiversity to flourish. In this ecosystem, high species diversity of plants and pollinators is generated from differences in water availability and elevation along the canyon walls, but also because flowering plants have evolved to attract different pollinators and pollinators have in turn evolved to more efficiently extract pollen and nectar from flowering plants. In this paper, I will present three examples of plant-pollinator relationships, which highlight the role of mutualism in the evolutionary diversification of plant and pollinator species. I will conclude by discussing how invasive plant and pollinator species can disrupt these highly co-evolved plant-pollinator interactions.

### **Introduction**

One of the primary drivers of the rapid diversification of angiosperms was the evolution of bees and other animal pollinators. Indeed, 88% of flowering plant species require animal pollination to successfully reproduce (Ollerton et al. 2011). In order for successful pollination to occur, compatible pollen must be transferred from the male part of a flower, the anthers, to the female part of the flower, the stigmas. Although beetles were the “original” pollinators in evolutionary history (Bao et al. 2019), bees are currently considered the most common pollinators of flowering plants across the globe, and bees pollinate more than half of all flowering plant species in the arid southwestern United States (Simpson and Neff 1987).

There are more than 20,000 species of bees in the world and 4,500 species are native to North America (Michener 2007). These species vary in nesting requirements, floral preferences, morphology, and behavior, but all bees are entirely dependent on flowers for pollen and nectar – their only food source. When bees visit flowers to collect nectar and pollen, they sometimes accidentally move pollen among plants, making them great pollinators of many flowering plant species. However, bees are not the only pollinators. Other animal pollinators include flies, beetles, butterflies, moths, wasps, hummingbirds, finches, bats, and even sometimes rodents (Willmer 2011).

Flowers have evolved specific floral traits to attract specific types of pollinators and have also evolved various traits to ensure that pollinators efficiently move pollen among flowers. For example, many plants will place pollen on hard-to-groom spots on pollinator bodies to ensure that it is successfully transferred to conspecific stigmas (Minnaar et al. 2019). Other plants make nectar and pollen rewards hard to access in order to limit the pool of animal pollinators that visit flowers (Willmer 2011). For instance, long, tubular flowers require that visitors have a long tongue or beak to access nectar and it's estimated that 6-8% of plant species have anthers with small slits or holes in anthers from which pollen can only be released through sonication or “buzz pollination” by highly specialized bees (Buchmann 1983).

This concept – that specific plants are adapted to attract specific pollinators and pollinators are attracted to specific floral traits – is referred to as the “pollination syndrome” framework and has been extensively studied within the field of pollination ecology (Willmer 2011). Yet the view that plant-pollinator interactions are harmonious one-to-one mutualisms has been contradicted by the finding that the vast majority of pollinators are generalist pollinators, which visit multiple plant species within a community (Waser *et. al.* 1996).

However, although the vast majority of visitors are generalists species, not all floral visitors are effective pollinators, and some speculate that specialist pollinators may be more effective than generalists. Specialists inherently display high floral constancy (defined as tending to consistently visit the same species of flower during a foraging bout) (Müller, 1996a; Müller, 1996b) and have other adaptations to effectively transport pollen from host plants. High floral constancy can increase plant reproduction (Brosi and Briggs, 2013), and thus the consistently high constancy of specialist visitors may make specialists more effective pollinators. For instance, a specialist bee pollinator is the most effective pollinator of *Echinacea angustifolia*, (Page *et al.* 2019) and likely many other plant species.

In the Grand Canyon, along the Colorado River, there are several examples of these concepts “playing out” in natural systems. These examples highlight how pollination systems vary and how plant and pollinator traits influence these relationships. First, the study of Prickly-Pear species in the genus *Opuntia* has demonstrated that cactus plants support highly diverse pollinator populations, including many species of ground-nesting cactus-specialist bees. The study of *Opuntia* species has also revealed that particular visit behaviors of cactus-specialist bees may simultaneously increase their foraging efficiency and their pollination effectiveness. Second, the study of flower color variation in the genus *Erythranthe* illustrates how pollinator preferences have shaped the evolution of floral traits in unique and sometimes surprising ways. Finally, while hummingbirds are traditionally considered the primary pollinators of Ocotillo, the study of this system provides an interesting example of the complicated relationship between nectar-robbing Carpenter bees and the plants they visit.

### **Prickly Pear: An example of specialist bee pollination and potential “benefits” of specialism**

*Opuntia* is a genus of flowering plants in the family Cactaceae comprising 150 species of flowering plants (Pinkava 2003). The genus naturally occurs throughout the Americas, including the Galapagos Islands, the Caribbean, and Canada, but most species are found in Mexico. Several species occur along the Colorado River in the Grand Canyon, including Beavertail Prickly Pear, *Opuntia basilaris*, Grizzly-Bear Prickly-Pear, *Opuntia polyacantha*, and Brown-Spined Prickly-Pear, *Opuntia phaeacantha* (Huisinga *et al.* 2006). *Opuntia* flowers are generally large and bowl shaped with brightly-colored petals and many yellow or green stamens (Grant and Hurd 1979). Finches pollinate the four species of *Opuntia* native to the Galapagos (Reyes-Agüero *et al.* 2006). However, bees, including several species of cactus-specialists, are the primary visitors of the vast majority of *Opuntia* species. Indeed, out of 36 species of *Opuntia* studied, more than 86 species of bees have been recorded as visitors (Reyes-Agüero *et al.* 2006). For instance, in central Texas, *Opuntia lindheimeri* is visited by at least 10 species of bees, four of

which specialize on plants in the family Cactaceae including *Perdita texana*, *Lithurge gibbous*, and *Diadasia rinconis* (Grant et al. 1979).

From a bee's perspective, one of the benefits of being a specialist is that specialist bees are generally better adapted to collect pollen from the plants on which they specialize. The Brazilian species *Opuntia brunneogemma* and *Opuntia viridirubra* are visited by 41 species of bees, including three specialist bees, *Lithurgus rufiventris*, *Cephalocolletes rugata*, and *Ptilothrix fructifera* (Schlindwein and Wittmann 1997). When specialist bees visit, they manipulate the stamens in such a way that pollen becomes available in the lower layer of the stamens, near the nectar furrow, and only specialist bees are able to gather pollen and nectar in this way (Schlindwein and Wittmann 1997). As such, specialist bees are much better at collecting pollen and nectar from *Opuntia* flowers as compared to other floral visitors. Specialist bees may also be better at moving and depositing pollen onto the stigmas of subsequently visited flowers because bees brush their bodies against the stigmas in the center of the flower when gathering pollen and nectar in this way.

Although no one has directly compared different pollinator taxa in their effectiveness as pollinators of *Opuntia*, early natural history reports speculate that specialists are the most effective pollinators of these plants (Grant and Hurd 1979). Comparisons of pollinator effectiveness have, however, been studied in other cactus systems, and the results from these studies confirm the hypothesis that cactus specialists are more effective pollinators of at least some cactus species. For instance, the most effective pollinators of *Ferocactus cylindraceus* and *Ferocactus wislizeni* are native cactus-specialist bees. In particular, the most effective pollinator of *Ferocactus wislizeni* is the specialist bee *Diadasia rinconis* (McIntosh 2005). Generalist bees in the family Halictidae also visit these two cactus plant species but visits from Halictid bees have reduced seed set compared to visits from specialist bees (McIntosh 2005). Overall, while the question of whether specialist bees are inherently better pollinators of the plants on which they specialize remains an unresolved question in the field of pollination ecology, it is certainly clear that cactus-specialist bees are diverse and important pollinators of plants in the arid Southwest.

### **Monkey-flowers: An example of pollinator-mediated reproductive isolation and floral trait selection**

Cardinal and Yellow Monkey-flower, two species in the genus *Erythranthe*, both occur along the Colorado River. Both species generally bloom from March – August and occur in the same habitat types – at lower elevations in the inner canyon, commonly in areas near seeps, springs, and perennial streams in side canyons (Huisinga et al. 2006). The genus *Erythranthe* is a very diverse genus, containing 111 species, and has long been studied by pollination ecologists as an example of how plant species maintain reproductive isolation.

Cardinal Monkey-flower, *Erythranthe cardinalis* is red and primarily visited by hummingbirds (Schmenske and Bradshaw 1999), while Common Yellow Monkey-flower, *Erythranthe guttatus*, is yellow and primarily visited by bees (Swiegart et al. 1999). Despite occurring in the same habitats, *Erythranthe* species maintain reproductive isolation by attracting different pollinators through their differential coloration, floral morphology, and nectar reward levels (Schmenske and Bradshaw 1999).

Red flowers are conventionally thought to be a “classic” floral trait of hummingbird-pollinated plants. However, when comparing the visitor communities on a suite of differentially colored F2 hybrids of bee-pollinated *Erythranthe lewisii* and hummingbird-pollinated *Erythranthe cardinalis*, Schmenske and Bradshaw (1999) found only a weak correlation between the anthocyanin and carotenoid concentration of flowers and hummingbird visitation preferences. In contrast, these authors found that bees showed a strong preference for flowers with lower concentrations of anthocyanin, avoiding red flowers with high concentrations of anthocyanin pigments. Indeed, it is hypothesized that red-coloration is not a mechanism to attract hummingbirds but rather a mechanism to reduce visitation by insects, including bees (Raven 1972).

More recent work studying *Erythranthe cardinalis* has revealed that red-coloration on it’s own does not deter bees from visiting flowers, but when red-flowers are also oriented in a way that makes it harder for bees to access nectar, this increases the amount of time bees spend foraging per flower, reducing their per-visit foraging efficiency (Gegear et al. 2017). The authors speculate that bees avoid these red and oddly-oriented flowers because reduced foraging efficiency is undesirable for bees, which generally attempting to maximize rewards and minimize the energetic costs of foraging. Curiously, when flowers are oriented in a way that makes it harder for bees to access nectar, this alone does not reduce bumble bee visitation. It is only the combination of red flowers and unfavorable floral orientation that reduces bee visitation, suggesting that bees use the red-coloration as a cue to help them learn to avoid those flowers.

### **Ocotillo: An example of nectar-robbers as pollinators of the very same plant species they rob**

Another red-colored flowering plant that occurs along the Colorado River in the Grand Canyon is Ocotillo, *Fouquieria splendens*. Like *Erythranthe cardinalis*, Ocotillo is also considered to display “classic” hummingbird-flower traits. Ocotillo has long tubular flowers with hard-to-access nectar and its flowering phenology generally coincides with the migration of several hummingbird species (Waser 1979). Seed set in this species is positively correlated with year-to-year variation in hummingbird abundance, but small pollen-foraging solitary bees are some of the most abundant visitors to this plant (Waser 1979).

Large Carpenter bees, a group of pollinators in the genus *Xylocopa*, often use their large mandibles to pierce Ocotillo flowers near the base of the flower, “robbing” nectar in the process. Although this would seem like bad news for Ocotillo flowers, Carpenter bees can act as pollinators of this plant, particularly if they are foraging for pollen, which requires that bees visit “legitimately” (i.e. not by nectar-robbing) (Waser 1979, Scott et al. 1993). Indeed, in the nests of one species of Carpenter bee, *Xylocopa californica*, more than half of all pollen was from Ocotillo, suggesting that the relationship between Ocotillo and carpenter bees may be mutualistic rather than antagonistic (Scott et al. 1993).

### **How invasive plants and pollinators may disrupt these highly co-evolved relationships**

Introduced and invasive species have the potential to disrupt these highly co-evolved mutualisms and invasions are an important and potentially devastating element of

global change. Invasive plant species may compete with native plant species for pollinators (Morales and Traveset 2009) and if native plants are pollinator-limited, this can severely reduce plant reproduction. Although less well studied, the invasion of non-native pollinators also has the potential to severely disrupt native plant pollination (Morales et. al. 2017). For instance, while many bee species are declining globally (Potts et al 2010) managed species, such as honey bees, have also become successful invaders in new ranges (Stout and Morales 2009) and several studies suggest that honey bees compete with native bees for floral resources (Paton 1993).

At high densities, honey bees can be excessively effective at removing pollen from flowers and can deplete pollen resources across the plant community on a daily basis (Carneiro and Martins 2012) This could reduce pollen availability (Cane and Tepedino 2016) and potentially decrease the number of visits plants receive from native pollinators. If honey bees are effective pollinators of native plants, this may have little consequence for native plant pollination (at least in the short term). However, if honey bees are ineffective pollinators of native plants, the replacement of native bee visits with honey bee visits may have devastating consequences for both native bees and the plants they pollinate.

For instance, in the deserts of Southern Utah, honey bee invasions have been implicated in the decline and potential extinction of *Perdita meconis*, a rare specialist bee pollinator of the endangered Bearclaw Poppy, *Arctomecon humilis* (Portman et al. 2018). In surveys conducted from 1988-1993, before the invasion of honey bees, *Perdita meconis* were frequent visitors of these flowers. However, in surveys conducted from 2012-2017, honey bees were the most abundant visitor and *Perdita meconis* seemed to have become locally extinct. Honey bees strip flowers of pollen early in the morning, before any other bees can visit. Although *Perdita meconis* populations may have declined for other reasons, there is compelling evidence that competition with honey bees contributed to the decline and possible extinction of this rare bee species. Honey bees are not very effective pollinators of *Arctomecon humilis*, and plant populations with more honey bees have reduced seed set, suggesting that the replacement of native bee visits with honey bee visits has a negative effect on plant pollination in this system (Portman et al. 2018).

## Conclusions

In conclusion, many of the unique plant-pollinator interactions one can observe along the Colorado River in the Grand Canyon illustrate several interesting examples of how coevolution shapes diversity. Although we often think of competition as the principal driver of diversification in a “survival of the fittest” framework, mutualistic relationships can also exert strong selective pressures on evolution. Pollination ecology has changed a lot in the past 50 years, but cactus-specialist bees, the evolution of “classic” hummingbird-flower traits, and the complicated role of nectar-robbing carpenter bees as pollinators will certainly continue to fascinate ecologists and shape our understanding of the natural world. Unfortunately, the invasion of exotic plants and pollinators may disrupt the highly intricate relationships between native plants and their native pollinators, with potentially devastating consequences for native plant pollination. Preventing the invasion of potentially disruptive species is one way we can attempt to conserve this beautifully diverse ecosystem.

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