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Article Addendum

The importance of floral signals in the establishment of plant-ant mutualisms

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Visual and olfactory floral signals are essential for the establishment of plant-pollinator mutualisms. Different batteries of floral features attract different pollinators and may achieve specific relationships that are essential for the immediate plant reproductive success, and at an evolutionary time scale have been of vital importance in the radiation of Angiosperms. We have found that mutualistic services by ants, insects traditionally considered ineffective pollinators, are essential for the pollination of *Cytinus hypocistis* (Cytinaceae), a Mediterranean root holoparasitic plant. Diverse floral signals, mainly nectar characteristics and floral scent could be playing a key role in the attraction of different species of ants, which pollinate effectively the flowers. Surprisingly, the abundance of other insects foraging in this parasite was very low and, although this scarcity could be due in part to the presence of ants, we suggest that different floral features exhibited by *C. hypocistis* could be evolving for attracting ants. Based on some current findings, we suspect that the study of floral signals in Cytinaceae is critical in the understanding the divergence of pollination systems in this fascinating family of parasitic plants.

The flowers of angiosperms exhibit an amazing variety of floral and nectar colors,[1,2] floral morphology and displays,[3,4] floral scents[5] and nectar characteristics,[6,7] that may influence pollinator type and pollination quality. The existence of those signals help to the establishment of interactions among plants and pollinators, that range from drastic generalists, when flowers are visited by an elevated number of pollinators, to extreme specialists, being the plant pollinated by only one or a few species of pollinators.[8,9]

In the majority of terrestrial ecosystems, ants stand out as one of the most common floral visitors.[10] In spite of such ubiquity, ants have been largely considered as ineffective pollinators, mainly due to their small size, erratic behaviour and the presence of metapleural glands that produce antibiotic secretions reducing pollen viability.[11,12] Moreover, it has been postulated that ants act as nectar thieves and reduce visitation by other potential pollinator.[10] However, new findings are highlighting that their role on pollination is not fully understood. Recently we have described, combining a four-year field observation study with experimental pollination treatments at six study sites, a new ant-plant mutualism, between the holoparasitic plant *Cytinus hypocistis* (Cytinaceae) and different ant species,[13] joining a growing body of evidence stressing the prominent role that ants are playing in some plant-pollinator systems.[14-17] Nevertheless, in contrast to preceding studies where only one ant species pollinated the plants (but see refs. 17 and 18) in *C. hypocistis* as many as ten ant species behave as true pollinators. Moreover, our study has shown that the different ant species that pollinate *C. hypocistis* differ in their effectiveness as pollinators, as commonly observed in other pollinator guilds.[19,20] We therefore suggest that generalizations about the importance and quality of ants as pollinators should be avoided or made with caution unless backed by careful field measurements.

Our study system was a monoecious rootless, stemless and leafless holoparasitic plant with inflorescences appearing at ground level. Although *C. hypocistis* does not exhibit typical features of the purported 'ant-pollination syndrome',[21] a number of floral signals could be playing key roles in the establishment of the plant-ant interactions. Among them, the low stature of plants that make flowers to stay a ground level, in combination with sweet scented flowers that offer concentrated nectar and large quantity of pollen, are signals that may enhance the attractiveness of *C. hypocistis* to diurnal and nocturnal ants that pollinate flowers efficiently. Flying insect visits were unexpectedly low, and only a fly was a predictable visitor. The presence of ants can discourage flying pollinators from visiting the flowers,[22] but we suspect that this low number of visits can be explained by the floral features exhibited by *C. hypocistis* which, although probably still no specialized, may be becoming more important for attracting ants.

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It has been postulated that different species of animals are attracted by diverse sets of visual (colour and floral shape) and chemical (floral scent, nectar features) floral characteristics.[5,6,9] These features are critical for plant reproductive success,[23,24] and at an evolutionary time scale they have been of vital importance in the radiation of Angiosperms.[25] Although our study does not specifically deal with the relative importance of different floral signals, circumstantial evidence suggests that in the family Cytinaceae various signalling-related features could be essential for the establishment of plant-pollinator mutualisms. More specifically, floral scent seems to be an important channel of communication between these flowering plants and their pollinators and has been a likely key factor in the evolution of pollination mechanisms in this outstanding family of parasitic plants. In the only three studies conducted on plant-pollinator systems in the family Cytinaceae a remarkable diversity of mutualisms has been observed. First, in Mexico, the yeasty and unpleasant scent produced by the dark flowers of *Bdallophyton bambusarum* has been described to attract carrion flies,[26] a common pollinator guild in other parasitic plants such as Rafflesiaceae or Hydnoraceae, with a characteristic pollination system by deceit with flowers mimicking insect mating or egg-laying habitats.[27] Second, in South Africa, the crimson flowers of *Cytinus visseri* emit a strong scent dominated by aliphatic compounds that play a central role in attracting small mammals, the only flower visitors and pollinators of this species.[28] And third, our recent findings on *C. hypocistis* in Spain and Morocco point to an important effect of floral scent in attracting ants, its main pollinators. Although research on the importance of floral signals to attract pollinators in this family is still in its infancy, recent findings make of Cytinaceae an ideal model to study at an intra-family level the influence of divergent selection from pollinators on the evolution of high floral signal diversity. Mechanisms acting on plant-animals signalling obviously deserve further studies to provide an accurate picture of the importance of visual and chemical cues on the evolution of pollination systems in Angiosperms.

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