

Flower colour diversity seen through the eyes of pollinators. A commentary on ‘Floral colour structure in two Australian herbaceous communities: it depends on who is looking’

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Pollinators arguably painted the world: before plants discovered the nifty trick to enlist insects as go-betweens for sex, terrestrial environments would have been largely green (or brown). Many habitats, at least during certain times of the year, display a remarkable diversity of flower signals – but what exactly shaped this diversity? Pollination systems are biological markets – flowers advertise their products (typically nectar and/or pollen of varied quality) by using signals (flowers) that must be conspicuous, attractive and memorable (just like product packaging in the supermarket). To explore plants’ advertising strategies adequately, one must consider the relevant pollinators’ sense organs, perception and cognition, which are profoundly different from those of humans (for example, most pollinators see ultraviolet light). A new study by Shrestha et al. (2019) uses cutting-edge colour analyses for a comprehensive analysis of the advertising strategies of over 100 flower species at two Australian sites, over the seasons. They found only weak support for the notion that sympatric flower colours diverge or converge more than expected by chance, and only at certain times of the year. Intriguingly, however, they discovered that whether or not such advertising strategies were detected at all depended on subtle differences between the colour vision systems of various bee pollinator species, highlighting that it is inadequate to use a one-size-fits-all model system such as the honeybee’s to predict how flowers will appear to a diversity of bee pollinators.

There are several strategies that plants could adopt in terms of their flower colour to secure pollination: 1) To be as distinct from sympatric plants' flowers as possible, to promote memorability by pollinators and thus flower constancy. Similarly, if plants strive to appeal to different innate colour preferences of available pollinator classes, this might lead to colours of sympatric flowers to diverge. 2) To be similar to one or more species of co-flowering plant, using Batesian or Mullerian mimicry, leading to colour convergence. 3) To diverge maximally from the prevailing background (e.g. leaves of the same plant). Alternatively, some of the diversity of flower colours might be explained by their phylogenetic background, or pleiotropic effects exerted on the flower pigments that are also used in vegetative tissues of the plants for purposes other than pollination such as reducing UV damage or reducing herbivory (Chittka et al., 2001).

One method of exploring whether sympatric species diverge or converge in colour is a hypothesis-driven approach focussing on particular plant species or small groups of species under various selection pressures. Another is a more community-oriented approach in which the plant assemblage present on a given site is studied comprehensively without any sampling bias (Bergamo et al., 2018, Gumbert et al., 1999), and this is the approach taken by Shrestha et al., (2019). The authors evaluated all flowering plant species found at two Southeast Australian nature reserves, which are notable especially for a spectacular diversity of orchid species (over a third all flowering species found are orchids). Both sites are specifically managed to ensure that non-native plants are kept out, so that they are representative areas of native Australian flora. This flora is interesting in that the continent has been separated from other major land masses for over 34 million years, 80% of plant species are endemic, and their pollinators are distinct from other (e.g. Eurasian) habitats too; e.g. bumblebees are absent and honeybees were only introduced in the 19th century. Over 1500 species of solitary bee are present, however, as are 11 species of social, stingless bee (Dyer et al., 2012).

The authors evaluated the diversity of flower colours on a fortnightly basis and quantified it in a bee colour space that takes into account the photoreceptors' spectral sensitivity and colour opponent coding (Chittka, 1992; Figure 1). Since the choice of colour model can affect predictions of colour similarity (Telles and Rodriguez-Girones, 2015), Shrestha et al. 2019 also consider the actual behavioural colour discrimination abilities of

the Australian native stingless bee *Tetragonula carbonaria* (and compared this with some other global pollinator species). They discovered that there was a tendency for colours to be more similar than expected by chance during the spring period of most abundant flowering (October-December), and a tendency for colours to be more diverse in the subsequent summer months (January-February), though this pattern was less clear when colour diversity was viewed through the eyes of non-native species. At other times over the year, there might have been too few plant species in bloom to establish robust statistics. One conclusion of Shrestha et al. (2019) is that a key selection pressure might simply be for flower colours to contrast strongly against the background, though a quantitative analysis of this question remains outstanding; one would have to demonstrate that the diversity of flower colours is explained by the particular backdrops against which each plant species displays its flowers (Chittka 1997).

Perhaps one reason for the observed mixed effects at a community level is that indeed different plant species pursue different strategies within these communities. Rare plants might benefit from having signals that mimic common species (Papadopulus et al. 2013), especially if the rare species is also poorly rewarding, as may be the case for a large number of orchid species, which are spectacularly species-rich at these field sites. Conversely, common plants (“market leaders”) might benefit more from having maximally distinct signals (Gumbert et al., 1999). Moreover, plant communities are not static in time or space. A plant that has a distinct colour in one community may be similar in appearance to co-flowering species in another site. Shrestha et al. (2019) observe this, seeing varying patterns in the colour communities of the two sites despite considerable overlap in the flora present. Consequently, the “best” colour at one location may be suboptimal at another, leading localised extinction, or to divergence in morphology or other sensory modalities such as scent, or even eventually to speciation. In some plants, flower colours might be constrained by factors wholly unrelated to pollination (Chittka et al. 2001). In the future, interfacing community level approaches such as those by Gumbert et al. (1999) and Shrestha et al. (2019) with an approach to explore the signalling strategies of focal plant species might be helpful. Perhaps the former can reveal interesting study cases, where, for example, members of the same plant species diverge in signal (as perceived by pollinators)

at different locations, so that one can then investigate the particular selection pressures that mediate such divergence.

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Fig. 1. Australian flower colours and their similarity in bee colour space. Measuring the spectral reflectance allows to predict how a flower will stimulate a bee's UV, blue and green receptors. The relative signals of these three receptors in turn allow to calculate flower colour loci in the colour hexagon. In this colour space, angular position from the centre indicates bee-subjective hue: flower loci in the "up" direction are predicted to stimulate predominantly a bee's blue receptors and are thus predicted to appear as bee-blue; loci in the lower left corner will be UV (invisible to humans), and flowers in the lower right corner are bee-green (other colours indicate mixtures between these extremes). Distances between flower colour loci indicate the extent to which the colours can be discriminated: large colour distances (such as between blue and yellow flowers) indicate

that flowers are highly dissimilar (which might indicate divergence), whereas small colour distances (such as those between various blue flowers, or among yellow flowers) might indicate that they might be confused by pollinators (possibly indicating convergence / mimicry). Photo credit: Mani Shrestha