
Floral colour diversity in plant communities, bee colour space and a null model

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Evolutionary biologists have long hypothesized that the diversity of flower colours we see is in part a strategy to promote memorization by pollinators, pollinator constancy, and therefore, a directed and efficient pollen transfer between plants. However, this hypothesis has never been tested against a biologically realistic null model, nor were colours assessed in the way pollinators see them. Our intent here is to fill these gaps. Throughout one year, we sampled floral species compositions at five ecologically distinct sites near Berlin, Germany. Bee-subjective colours were quantified for all 168 species. A model of colour vision was used to predict how similar the colours of sympatric and simultaneously blooming flowers were for bees. We then compared flower colour differences in the real habitats with those of random plant communities. We did not find pronounced deviations from chance when we considered common plants. When we examined rare plants, however, we found significant divergence in two of the five plant communities. At one site, similarly coloured species were found to be more frequent than expected, and at the other two locations, flower colours were indistinguishable from a random distribution. These results fit theoretical considerations that rare plants are under stronger selective pressure to secure pollination than common plants. Our study illustrates the power of linking such distinct biological traditions as community ecology and the neuroethology of bee vision.

Keywords: flower colour; community ecology; pollination; divergence; colour vision

1. INTRODUCTION

The diversity of flower colours has long fascinated scientists and non-scientists alike. It was scientists, however, who shattered the popular notion that flowers are God's ornaments of an otherwise dull world, designed solely to please us humans. Rather, they argued, flowers are plain sex organs, and their colours designed to lure animals into a dirty business that many plants cannot accomplish without help (Sprenzel 1793; Darwin 1876). Sprenzel called this somewhat unromantic discovery 'the uncovered mystery of nature', but close inspection reveals that many details of the mystery are far from uncovered. Seemingly trivial questions such as 'why don't all flowers have the same colour?' or 'what is the biological meaning of the diversity of flower colours we see?' remain unanswered. As a first step toward assessing the adaptive significance of any pattern of diversity, it should prove useful to see whether the observed pattern deviates from a null expectation based on some form of randomization, and if so, what form the deviation takes. We analyse this question taking into account how bees see colours.

While there are no good answers to the questions above, there are some ideas. For some time it was believed that different flower colours are the result of direct selection by different pollinator taxa with different innate colour preferences (e.g. Fægri & Van der Pijl 1979). However, as early as 1899, Bulman wrote 'As far as I am

able to judge, it matters not one iota to a bee whether the flower is blue, red, pink, yellow, white or green: so long as there is honey that is sufficient.' We know now that he was mostly right. While pollinators of some taxa do have innate preferences for certain colours (Lunau & Maier 1995) these aid mostly in the initial recognition of flowers by naive animals (Giurfa *et al.* 1995). Later, flower visitors learn to use flower colours as predictors of the rewards to be expected, so visiting most frequently those colours which they have experienced as most rewarding (Menzel *et al.* 1993), but see, for example, Banschbach (1994) for exceptions). Accordingly, we now find that the syndrome concept in pollination biology, which holds that different pollinator taxa have narrow innate affinities to particular floral traits (such as their colours), rests on shaky foundations (Waser *et al.* 1996). In summary, it is doubtful that innate preferences of pollinators for certain colours present a selective force strong enough to explain all the diversity of flower colours we see.

Another idea emerged quite a while ago. This is the idea that pollination systems are markets, in which there are products (pollen and nectar), advertising signals (e.g. floral colours) and careful shoppers, the pollinators (Heinrich 1979; Menzel & Shmida 1993; Chittka 1997). In this view, the advertising of one company (a plant species) should be distinguishable from that of another species, so as to be recognizable for the customer. Only by means of a distinct signal can the customer be faithful to one product. Such fidelity favours an efficient and directed pollen transfer between conspecifics (Kevan

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1978; Waser 1983*b*; Chittka *et al.* 1999). Conversely, pollinators straying between flowers of different species may lose pollen during interspecific flights (Feinsinger 1983) or even reduce seed set by clogging up stigmas with foreign pollen (Waser 1978; Thomson *et al.* 1982). In some closely related species, hybrids may be produced which are sometimes less viable than the parental species, so increasing selective pressures to diverge in floral advertising (Levin 1971).

Pollinators of many species are not always faithful to just one plant species, but even if individuals do switch between species, such switches are not random. Bees tend to move less frequently between flower species whose signals are distinct (Waser 1983*a*; Wilson & Stine 1996; Chittka *et al.* 1999). Thus, divergent floral signals do promote flower constancy. It is intuitively appealing to argue, then, that the 'colour community' of a rich flowering meadow may be the result of selective pressures that have favoured divergence in visual display signals. Previous studies claimed a divergence in the colour of sympatric plants (Grant 1949; Heinrich 1979), but such observations were never based on a rigorous quantitative analysis taking into account how pollinators see colours, nor were they tested against a null model. Müller (1881), for example, observed that bee-pollinated flowers in the Alps flowering at the same time and place appear to a human observer to differ more strongly in colour than other plants. Related plants of the same genus that bloom together often differ in colour and other flower traits (Lewis 1953; Macior 1973; MacSwain *et al.* 1973; Armbruster *et al.* 1994). However, both non-randomness and adaptive significance of floral colour divergence remain to be demonstrated.

In addition, not all plants may benefit from having distinct signals. In common plants with dense populations, fitness may be constrained by factors other than pollination; therefore they may not be under strong selective pressures to diverge from competitors (Feinsinger 1983). Conversely, rare flowers which look dissimilar to any other flowers the bee has experience with may receive only exploratory visits (Smithson & MacNair 1997). Thus, convergence on common species may be advantageous in rare plants (Thomson 1983; Waser 1983*a*). Alternatively, rare plants have the option of boosting their nectar rewards to maintain pollinator interest, and diverge strongly from other plants to secure conspecific pollen movement (Feinsinger 1983).

Unfortunately, divergence or convergence in plant communities are not quite so easily proven (Waser 1983*b*; Armbruster *et al.* 1994). By picking flowers randomly from a flower store, you may end up with a rich colourful bouquet, which also includes some similar flower colours. But natural selection has neither made these flowers different from one another, nor has it favoured their similarity. In other words, to show that the colours of natural flowers indeed fill the colour space of bees (or any other phenotype space) in adaptive ways, the observed distribution of colours must be tested against a biologically realistic null model. In this work, we analyse the flower colours of sympatric plants and compare their colour distribution with that of randomly assembled plant communities. To assess flower colour from the perspective of insect pollinators, we employ a model of bee colour

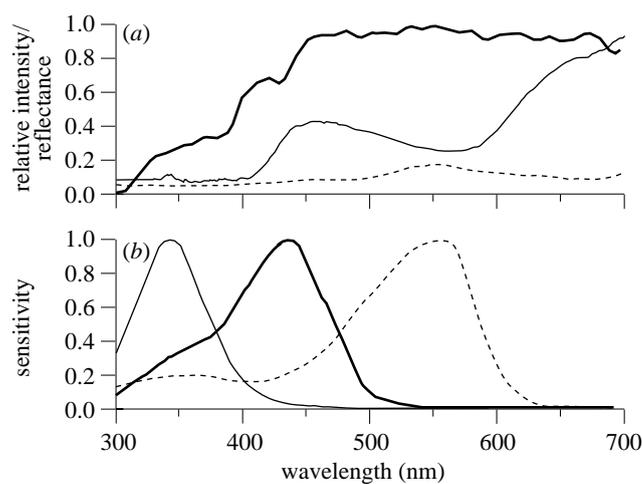


Figure 1. Functions that were used for calculating the colour loci in the bee colour space: the standard illumination light function D65 (Wyszecki & Stiles 1982; thick line in (a)) gives the spectral composition of normal daylight with which we assume our flowers and the background are illuminated. The reflection spectrum of green leaves forms the background (dashed line in (a)) to which the insect eyes are adapted while flying over the vegetation. The reflection spectrum of *Trifolium pratense* (Fabaceae) is given as an example for a flower colour (thin line in (a)). The signal generated by a photoreceptor when looking at the flower is a result of its own spectral sensitivity, the spectral composition of the coloured object and the illuminating light. (b) The spectral sensitivity functions of honeybees. Thin line, UV-receptor; thick line, blue receptor; dashed line, green receptor.

vision (Chittka *et al.* 1992). We test the following hypotheses: (i) simultaneously flowering species should differ more from each other than expected by chance, and (ii) flower colours should depend on the abundance of the plant species within a plant community. Rare plants should show a greater tendency to either converge on (or diverge from) other plants than common plants.

2. MATERIAL AND METHODS

(a) *Determination of species assemblage composition*

Five ecologically distinct locations of 500 m² each were selected in the nature reserve Unteres Annatal–Lange Dammwiesen in Strausberg, Brandenburg, Germany. These were an open maple forest, a dense hazel shrub community, a dry grassland meadow, a humid meadow and a roadside plant community. Every fortnight from March to October 1993, all insect-visited plant species flowering at each site were identified. We categorized plants as rare if we found fewer than ten specimens in the sample area. Other plants were categorized as common.

(b) *Calculation of colour loci in bee colour space*

The floral reflectance spectra of the plants were measured from 300–700 nm by means of a flash photometer (resolution of 1 nm, see Menzel & Shmida (1993) for details). In order to assess how our flower colours are perceived by bees, we need to plot their loci in colour space. A colour space allows a graphical representation of an animal's colour perception. It must be designed so that distances between loci generated by two object colours are correlated with the animal's ability to discriminate

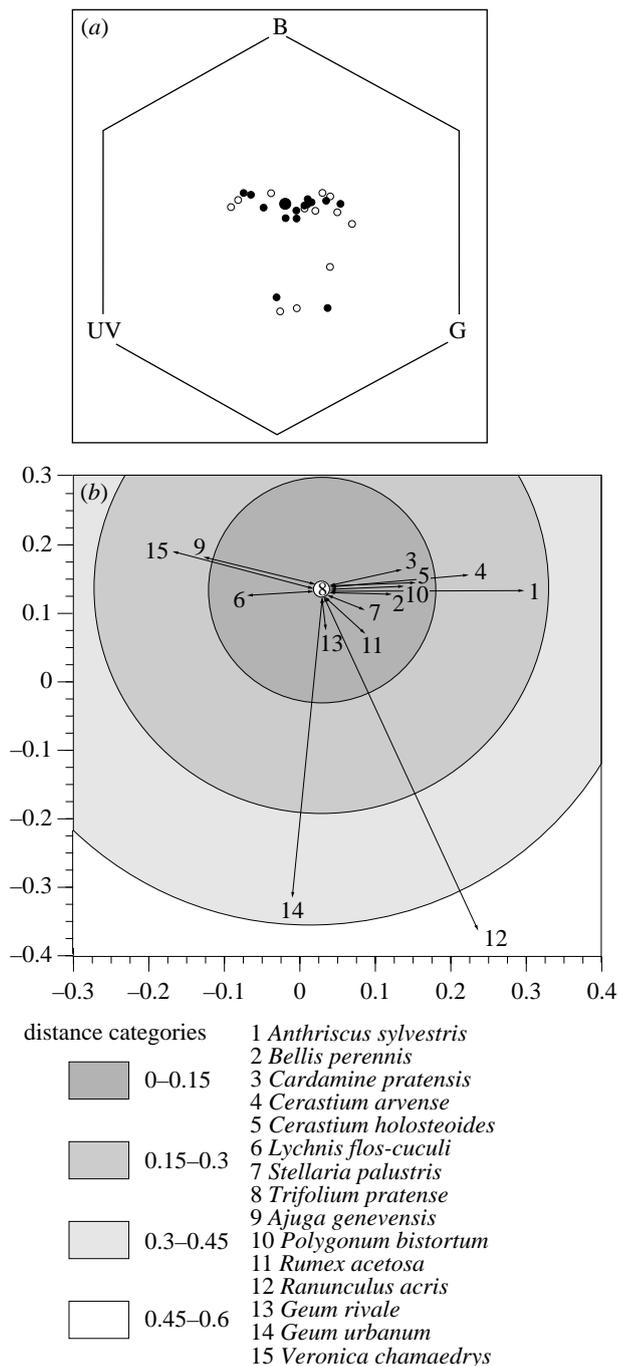


Figure 2. Loci of floral colours in bee colour space. The colour loci of all species flowering at the humid meadow in May are shown in the colour hexagon (filled circles in (a)), and in an enlarged section of this colour space (b). The angular position of a colour in the colour hexagon informs us how a bee will perceive this colour. For example, red clover (*Trifolium pratense*; large filled circle; see figure 1 for reflectance spectrum) lies in the direction of the blue corner; thus it is predicted to be bee-blue. The further two colour loci lie apart, the more dissimilar these colours appear to a bee. The loci of a randomly assembled plant community are marked with open circles. These are more dispersed than the loci of the natural community, and thus are predicted to be more distinct from one another (a). The colour distances from *T. pratense* towards all other species are marked with arrows (b). The concentric circles show the distance categories used in the analysis. In this particular month, eight species had colours similar to that of *T. pratense* of a distance below 0.15 (species:

those colours. To generate an appropriate colour space we need to know not only the reflectance functions of the objects in question, but also the spectral sensitivities of the animal's colour receptors, and the spectral distribution of the illuminating daylight. Finally, we must predict what signals the colours cause these receptors to send to the brain, and how the brain integrates the signals. The honeybee's ultraviolet (UV), blue and green receptors are maximally sensitive at about 340, 430 and 540 nm, respectively (Menzel & Backhaus 1991; figure 1b). The wavelength positions of these receptors are evolutionarily conservative (Chittka 1996); very similar curves can be found in a large number of flower-visiting bees. Bees are the predominant visitors (and also, on average the most efficient ones; Fægri & Van der Pijl 1979) to most of the flower species in our habitats. In addition, the colours of flowers visited by other systematic groups of pollinators are statistically indistinguishable from those visited by bees at our study site (Waser *et al.* 1996). For these reasons, it is appropriate to use honeybee spectral sensitivity functions as representative for most species of bees, and to use bee colour space to describe floral colours.

The receptors adjust their sensitivities to the light reflected from the predominant background. This adaptation process makes the receptors more sensitive if there is less light in the spectral range of their spectral sensitivity. Thus, the UV receptor is relatively more sensitive than the blue and green receptors, because there is less UV in the light reflected from the most common background, green foliage (Chittka *et al.* 1992). The response of a photoreceptor (its voltage signal) can be predicted by calculating the integral of adapted spectral sensitivity, the object reflectance spectrum and the illumination spectrum (Backhaus 1991). Figure 1 shows the functions used for these calculations: the standard illumination function, a typical background which was obtained by averaging the reflectances of several leaves, the reflectance of a representative flower and the spectral sensitivities of the honeybee's photoreceptors. This calculation is done for all three colour receptor types. The result is a set of three receptor signals for the UV, blue and green receptors. These values are normalized so that they range from 0 (no signal) to 1 (maximum signal). The set of relative signals so obtained is then used to generate a colour point in the colour hexagon (figure 2). This is done by using the three relative signals as vectors, plotted at angles of 120° in the hexagonal colour space, starting in the centre, so that at maximum excitation, a vector reaches all the way from the centre to one of the corners of the hexagon. The relative length of the three vectors determines where a colour is located. If, for example, a flower stimulates the UV receptor more strongly than the blue and green receptors, the colour locus will be in the UV corner of the colour hexagon. We therefore predict that the bee perceives it as UV.

The colour space allows us to estimate the perceptual similarity of different colours for a bee. The shorter the distance between two colour loci in colour space the more similar the corresponding colours appear to a bee. This relationship was experimentally confirmed for several species of bees (Chittka *et al.* 1992). The experimental paradigm was that the bee was trained to collect sucrose solution at one of two (or more)

Figure 2. (Cont.) 2, 3, 6, 7, 10, 11, 13), four species had colour distances between 0.15 and 0.3 (species: 1, 4, 9, 15) and one species each had a colour distance within the next two colour categories (0.3–0.45: species 14; 0.45–0.6: species 12).

colours. The reward was then removed and the bee was required to choose between the trained colour and several other ones. The shorter the distance between loci in colour space, the more visits the bee will make to the second colour, to which it was not trained.

(c) *Statistical analysis of colour distance distributions*

Because we analysed species composition at each site every fortnight from spring to autumn, 15 communities of sympatrically flowering species were obtained per site. However, many of the species were in bloom for more than two weeks. Therefore, each phenological community does not constitute an independent data set. To avoid using a pair of flower colours more than once in our study, we constructed only one colour distance distribution (Chittka 1997) per site. To this end, we identified all pairs of flower species that were observed in bloom together at least once during the study period. For these species, the perceptual colour distances in colour space were calculated. The colour distance distribution for each site is thus made up of all the colour distances so obtained. In order to compare these distance distributions with random species assemblages we created 1000 artificial plant communities with the same number of plant species as in the five real ones. This was done by randomly selecting species out of the pool of 168 species that were found in the five plant communities. Analyses were performed for (i) distances between common plants only, and (ii) distances from rare plants, where distances are calculated both to common and to other rare plants.

We group all colour distances into categories of a width of 0.15, where 2 is the maximum theoretical distance between two opposite corners of the colour hexagon. Real flower colours are rarely farther apart than 0.75, and such colours are extremely distinct for a bee. Conversely, two colours whose distance falls into the lowest category are so similar that these colours are likely to be confused. Natural and random communities are compared with respect to the number of colour pairs that fall into each distance category. We predict that if selection has worked to favour divergence of floral signals, short colour distances (between 0 and 0.15) will be underrepresented in nature and large colour distances overrepresented. If selection has favoured colour convergence, we expect the opposite. We analysed the distribution of colour distances in the distance categories by comparing the real colour distance distributions with the average frequencies of colour distances in the random communities by means of chi-square contingency tables.

3. RESULTS

A total of 168 insect-pollinated plant species flowered at the five different sites. The list of species and their flowering times are presented in the electronic Appendix A which can be found on the Royal Society Web site. The number of plant species at the sites ranged from 24 in the maple forest to 97 in the dry meadow. Figure 2 gives an example of the floral colour loci at the humid meadow in May. The distribution of colour distances between common species throughout the year is presented in figure 3a. At none of the sites, significant deviations from chance are found.

A different picture emerges when we evaluate distances between rare plants and other plants (figure 3b). Deviations from the random distribution of colour

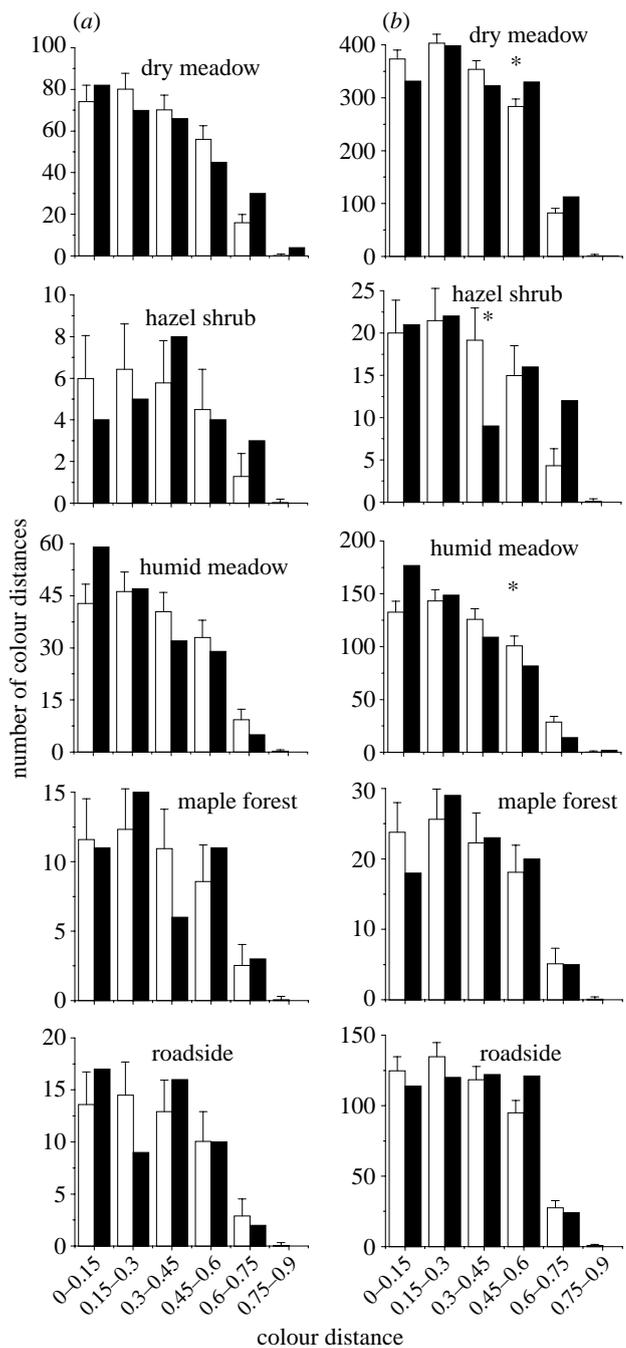


Figure 3. Number of distances between colour pairs in distance categories at the five sites (filled columns) and in random communities (open columns). In the natural plant communities different absolute numbers of colour pairs occur. The open columns indicate the average of the 1000 random communities, range bars being standard deviations. (a) Colour distances among common plants. (b) Distances from rare plants to all other plants. Significant deviations ($p < 0.05$, χ^2 contingency tables) between natural and artificial colour distance distributions are marked with asterisks.

distances occur in three of the plant communities, but these do not all show the same trend. Large colour distances of 0.45–0.75 are more common than expected by chance in two plant communities, the dry meadow and the hazel shrub. In the dry meadow, fewer colour distances are found in the intermediate colour distance

category with distances of 0.3–0.45. We interpret this to mean that selection has favoured distinct colour signals of rare plants in these habitats. On the other hand, the humid meadow shows a particularly high number of colour distances in the shortest category. At this site, large distances of 0.45–0.75 are less common than in the artificial communities. Thus, in the humid meadow, flower colours appear more similar to each other (to a bee's eye) than expected by chance.

4. DISCUSSION

For the first time, to our knowledge, we were able to show that flower colours in natural plant communities indeed show patterns that cannot be explained by assuming that they have been randomly assembled. However, there is no simple and unidirectional trend across all habitats. The diversity of common plants did not show any divergence from random. In one habitat, however, we found convergence of rare flower colours, whereas in two habitats, rare flowers appeared to be more distinct than expected.

The reason for the differences between habitats is unclear. At sites with random colour distributions or a tendency for convergence, a high percentage of flower colours may stem from related species or species whose flower colour is subject to phylogenetic constraint (Chittka 1997). Or, even if there are fitness costs resulting from floral similarity and thus pollinator inconstancy, some plants may adapt to minimize the costs themselves, rather than adapting to discourage pollinators from switching (Feinsinger *et al.* 1987). In other cases, sympatric plant species which share inconstant pollinators may place pollen in different places on insect visitors (Armbruster & Herzig 1984).

But at two sites, we found a clear and significant divergence effect of rare species. This scenario is exactly what one would expect following theoretical considerations by Feinsinger (1983). He pointed out that plants with dense populations are under low pressure to diverge from others in signal. When plants of the same species are strongly aggregated in space, any visitor is likely to remove and deposit conspecific pollen efficiently, even if the pollinator switches species outside the patch. But rare species might often have difficulties in maintaining pollinators sufficiently interested to secure their constancy. Such plants have two options (Waser 1983*b*). One possibility is that the rare species produce a high reward and diverge strongly in signal from sympatric species. Under such conditions, long travel times may be outweighed by sufficient rewards, so that pollinators may be constant and transport pollen efficiently between conspecific plants. The other possibility is that the signals of rare plants converge on those of other plants, to form a mimicry ring (Feinsinger 1983; Waser 1983*b*). Such mimicry may increase pollinator frequency, but impair the quality of the pollinator service, so that more heterospecific pollen gets placed on stigmas (Thomson 1983; Campbell & Motten 1988; Kunin 1993). In two of our study sites, rare plants show a significant tendency to diverge from sympatric plants, and so appear to employ the first strategy. Further research will show whether the divergent species are indeed those that produce more nectar.

Plant communities could be shaped in two principal ways. If they are stable over evolutionarily significant periods of time, species could coevolve floral traits in a process of *in situ* evolution (Connell 1980). If this is the case, flowers might have undergone character displacement under conditions of sympatry, but not at other sites where they are the sole flowering species (Waser 1983*b*; Armbruster *et al.* 1994). Further research may show if such a pattern is indeed realized in nature. Conversely, if the composition of plant communities changes at a faster rate than the evolution of floral traits it is not possible for a species to adjust its characters to other co-flowering plants (Wilson & Thomson 1996). Plant communities are often highly dynamic (Feinsinger 1987) and in our study area significant changes in vegetation composition could be demonstrated over a time period of 40 years (Meißner 1992), a period which is most likely too short to allow *in situ* evolution. Our results open up the possibility that rare species, which are probably often recent invaders of a plant community, might fare best if they possess a strongly divergent advertisement. In this view, species are entities with fixed traits, which are either preadapted to occupy a previously unoccupied niche in a signalling community, or they will fail to establish themselves in that community (ecological sorting, cf. Rummel & Roughgarden 1985; Armbruster *et al.* 1994). In our study, we cannot distinguish between character displacement and ecological sorting, because we do not have any assessments of within-species variability of flower colour, and too few flower species occurred at more than a single site. But our results clearly show that the colours of flowers in some natural plant communities are indeed non-random, and exploring the adaptive significance of these patterns is certainly worth further research. Sprengel's 'uncovered mystery of nature' has many layers of covers yet to be uncovered!

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