# What's the Buzz About Flower Color Diversity?

## by Julienne Ng and Robert G. Laport

There is no denying that flowering plants (angiosperms) exhibit a dazzling array of flower colors, from white, all the way through the colors of the rainbow to black, and even in the UV spectrum. Perhaps most amazing is that we often see a broad swath of this diversity just by looking at a single plant community. This incredible diversity of flower color has led biologists, at least since Darwin, to wonder how and why such flower color variation arose. Given the vital role animals play in helping flowering plants disperse pollen and reproduce, many ideas about flower color evolution have revolved around pollinator. For example, plants may exploit new pollinators with differing color preferences or there may be competition among plant species for pollinator visits. However, other hypotheses unrelated to pollinators have also been proposed, including flower color diversity arising as an adaptation to environmental conditions or because flower color genes are influenced by other plant characteristics needed for survival.

**The relationship between pollinators and plants**

Many flowering plants largely rely on animals to disperse their pollen. Plant species that are most successful in producing offspring are those that increase the chance that pollinators visit multiple individuals of the same species depositing pollen along the way. Pollinator movements among different species results in wasted pollen, either because fertilization does not occur or, if it does, unfit hybrid offspring might be produced (those having fewer ovules, reduced pollen receptivity, or reduced seed production). To ensure pollen is moved between individuals of the same species, flowering plants must produce an attractive visual or olfactory cue that entices pollinators to repeatedly visit the "correct" species. Coloration is a highly conspicuous signal that serves to increase the probability of pollinator visitation and fertilization (Figure 1). Therefore, if a chance genetic mutation occurs that alters flower color in a species, and particular pollinators increase their visits to the new color variant because it is preferable to the old color, then the new flower color would become more widespread after several generations due to natural selection.

**Hypothesis I: Flower color diversity is driven by differences in preference between different types of pollinators**

The close interaction between flowering plants and their pollinators gave rise to the idea that different pollinators may have different flower color preferences. Therefore, a plant species with a flower color different from others in the community could exploit this preference and increase the likelihood that a particular pollinator type will only visit and fertilize other individuals of the same species. This hypothesis is bolstered by the observation that plants pollinated by the same types of pollinators often have flowers that look the same ("pollination syndromes"), even though the plant species might be distantly related. For example, bee-pollinated flowers are often blue or purple with short, wide corolla tubes and small volumes of concentrated nectar. Moth-pollinated flowers are typically white, with long, narrow corollas that are very fragrant at night. Hummingbird-pollinated flowers tend to have long, red floral tubes that are scentless, but contain copious amounts of dilute nectar. Given these associations, we might expect that the diversity of colors in a field of wildflowers is a function of a diverse pollinator community, and some studies have supported this tight association between flower color and pollinator preferences. For example, Colorado populations of a larkspur, *Delphinium nelsonii,* are typically blue-flowered but on occasion, white flowers are found. The rare white flowers (only about 0.1% of Colorado populations) are thought to have arisen from chance mutation, but remain at a low frequency because blue flowers are favored by the species' main pollinators, hummingbirds and bumblebees (Waser and Price, 1981). In another study, researchers made hybrids between the pink-flowered, bee-pollinated monkey flower *Mimulus lewisii* and the red-flowered, hummingbird-pollinated *M. cardinalis* that looked just like one parent or the other, but with the flower colors switched. Just this shift in flower color was sufficient to elicit a change in pollinator type (Bradshaw and Schemske, 2003).

**Hypothesis II: Flower color diversity is driven by specialization of individual pollinators or particular species of pollinators, regardless of pollinator type**

The idea that flower color diversity is driven by differences in preference between different types of pollinators is complicated by the fact that many flowering plants do not exhibit such tight associations with their pollinators. In fact, if you observe floral visitors for any length of time, you will find that many deviate from their expected pollination syndrome. This was shown in a study (Elam and Linhart, 1988)) of white, pink and red-flowered fairy trumpets (*Ipomopsis aggregata*) in the Front Range of Colorado in which researchers found that hummingbirds and hawkmoths did not discriminate between the different flower colors, instead visiting and cross-pollinating all flowers regardless of color (Figure 2). Another piece of evidence supporting that flower color and pollinators are not always tightly linked, is that many groups of plants share the same pollinators yet exhibit a diversity of flower colors. Therefore, an alternative explanation for flower color diversity is that different flower colors arise as a result of competition among plant species (or varieties within a species) for visits from individual pollinators or particular species of pollinators. For example, if a community of plant species flower at the same time, are all pollinated by hummingbirds and exhibit the same color flower, then it is likely that the hummingbirds will visit several different species transferring pollen between them, thus wasting pollen resources. It would therefore be advantageous for plants to exhibit a flower color different from others in the community to take advantage of the tendency of a pollinator (e.g. a single bird) to move between flowers that look the same during a foraging bout, a phenomenon referred to as flower constancy. Therefore, even though the pollinator type as a whole might visit a variety of different flower colors, any given individual or species of pollinator might be faithful to only a single color, which would effectively prevent hybridization and maintain a variety of flower colors through natural selection.

**Hypothesis III: Flower color diversity is driven by environmental differences**

While interactions with pollinators are clearly important for flowering plants, there are other factors that could influence flower color diversity. Environmental differences may cause changes in flower color, as different populations are likely to experience unique habitat conditions, such as soil type, temperature, and access to water. For example, imagine the stress of living at high elevations in the Rocky Mountains with huge fluctuations in daily temperature and intense UV radiation! Flavonoid pigments can help protect plants against environmental stresses, such as harmful UV-light, extreme heat, and drought conditions. By producing more anthocyanin pigments (a class of flavonoids responsible for many of the colors we see in flowering plants) in the stems and leaves to protect itself from environmental stress, a plant may also produce anthocyanins in floral tissue as a by-product, altering the color of the flower. This could explain why the buds of the yellow stonecrop, *Sedum lanceolatum* are red-tinged in the parts of its range where it experiences more sun (Figure 3), and why our very own state flower, the Rocky Mountain Columbine (*Aquilegia coerulea*), exhibits bluer flowers at higher altitudes than at lower elevations in Colorado. But, changes in flower color need not only arise as a by-product of pigment production elsewhere in the plant. Plants may express particular characteristics when dealing with the challenges of their environment, such as the production of compounds that protect against being eaten, or leaf hairs that help prevent thermal stress in arid and/or sunny environments. Natural selection on one of these traits could also influence unrelated traits, such as the biochemical pathways responsible for flower pigmentation. One gene affecting multiple traits ("pleiotropy") is common in both plants and animals, and explains, for example, why blue-eyed, white cats are often deaf. Therefore, if natural selection favors certain characteristics that help a plant survive in a given environment (e.g. leaf hairs), and the genes for these traits also affect flower color, we may see differences in flower color simply because they arose as a side effect of the evolution of other traits.

We have discussed just some of the hypotheses that have been proposed to explain the striking diversity of flower coloration and researchers are still trying to determine the relative importance of each of these. While some studies have shown that the competing interests of plants and their pollinators are important drivers of flower color evolution in many species, other studies have shown support for factors such as environmental variation and adaptation as a significant force. Together, this suggests that flower color evolution

(Cont. on next page)

## PHOTOS

**Figure 1**

**Figure 1.** Variation in flower color can be seen at different levels: among different plant species, among different individuals of the same species (see Figure 2), on the same individual and even within an individual flower! A number of species exhibit flowers that undergo a change in color with age, such as these bluebells, *Mertensia lanceolata,* whose buds are a color different from the open flowers.

Photo courtesy of Ernie Marx.

**Figure 2**

**Figure 2**. Fairy trumpets, *Ipomopsis aggregata*, exhibit white, pink, or red flowers but their main pollinators, hawkmoths and hummingbirds, do not appear to show any preference in flower color, instead visiting and cross-pollinating each variant. Left and middle photos courtesy of Ernie Marx, right photo courtesy of Mary Dubler.

**Figure 3**

**Figure 3.** Yellow stonecrop, *Sedum lanceolatum,* has red-tinged buds in sunnier areas. Photos courtesy of Jeffry Mitton.

among angiosperm groups is multifaceted, with many possible routes to generating and maintaining the diversity of colors that we see even in small communities of plants. Thus, when next marveling at the incredible array of spring wildflower colors, keep in mind the intricate underlying processes that are constantly shaping plant diversity. And, keep an eye out because if you are lucky, you might even find a familiar species with a new color variant!

**Further readings:**


Bradshaw, H. D. and Schemske, D. W. (2003) Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature.* 426: 176-178

Elam, D. R. and Linhart, Y. B. (1988) Pollination and seed production in *Ipomopsis aggregata*: Differences among and within flower color morphs. *American Journal of Botany. 75*(9): 1262-1274

Fenster, C. B., Armbruster, S., Wilson, P. Dudash, M. R., Thomson, J. D. (2004) Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics.* 35: 375-403

Waser, N. M. and Price, M. V. (1981) Pollinator choice and stabilizing selection for flower color in *Delphinium nelsonii. Evolution. 35*(2): 376-390

Whittall, J. B. and Strauss, S. 2006. Non-pollinator agents of selection on floral traits. In: *Ecology and Evolution of Flowers* (Eds. L. Harder and S. Barrett) Oxford University Press, pp.120-138



***Julienne Ng** is a postdoctoral researcher at the University of Colorado, Boulder. Her research focuses on the diversity of colorful signals that plants and animals use to communicate, and she is currently studying flower color evolution in the tomato family (Solanaceae).*

***Robert Laport** is a postdoctoral researcher at the University of Nebraska, Lincoln and the University of Colorado, Boulder. His research primarily takes place in the desert southwest, where he studies the ecological and evolutionary consequences of genome duplication (polyploidy) in the creosote bush, Larrea tridentata. This includes plant-pollinator interactions and how polyploidy may influence patterns of diversification.*


***Just Published:***

**Wildflowers and Other Plants of the Larimer County Foothills Region**

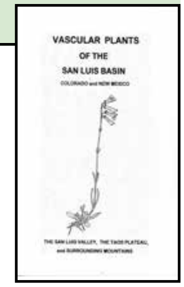

From the Introduction: "This guide focuses on the most common, showy, native plants growing in parks and open spaces in Larimer County, Colorado, between 5,000 - 8,000 feet in elevation. Key traits for identification, comparisons between similar species, and fun facts help you identify and learn about these interesting plants." CoNPS contributed funding for this guide. Available through CoNPS Bookstore.

# BOOK REVIEWS

## Vascular Plants of the San Luis Basin Colorado and New Mexico: The San Luis Valley, The Taos Plateau, and Surrounding Mountains

**Hobart Dixon** Printed by O&V Printing Inc. Alamosa, 2012.

### Review by Patrick Murphy




Those who work and play in the Rio Grande drainage will enjoy this light, functional, and quick key to the flora in this south-central pocket of Colorado. This is an excellent field manual that will slip easily into a small pack. The book is 6"x 9"x 0.5" and as I always like to report, the weight is 11.4 ounces. There are about 1,300 species in the key, so that is about 144 species per ounce.

This field key includes a map of the San Luis Basin, a review of the vegetation eco-regions within the basin, an index to the genera, index to English common names, and especially pertinent to this region of Colorado, an index to the Spanish common names.

There is also a glossary of terminology and some useful line drawings with descriptions of family or genera characteristics spread throughout the book. For example, diagrams explaining the jargon associated with Asteraceae and *Carex* are included.

The font is somewhat small but clear (even for my old eyes). There are a few exceptions to this, for example, the Family Characteristics page for Asteraceae is not as clear as the other pages.

The author explains the trials and tribulations of plant nomenclature (about which we are all aware) and has selected the PLANTS database as his nomenclature standard. That seems as reasonable as any alternative, but here is a personal comment. The PLANTS database is an old standard that was started by Dr. John T. Kartesz. He is now associated with Biota North America Program (BONAP) and has disassociated himself with PLANTS. I guess poor Dr. Dixon had to pick between Weber & Wittmann, PLANTS, BONAP, and the as yet unreleased flora by Jennifer Ackerfield, Colorado State University, Fort Collins.

I have not actually tested the keys, and keep in mind, there is no such thing as a perfect key. I did appreciate the fact that the *Salix* key allowed a branch to evaluate just vegetative characteristics of the willows. Like most quick keys, a complete description of the species is not included so you may need to find additional references to confirm your identification.

One final recommendation, immediately take the book to have the spine removed and have the book bound with a comb