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Review

Determining factors of flower coloration

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ABSTRACT

Diversity and distribution of flower coloration is a puzzling topic that has been extensively studied, with multiple hypotheses being proposed to account for the functions of coloration, such as pollinator attraction, protection against herbivory, and prevention of damage by ultraviolet light. Recent methodologies have allowed studies to consider the visual system of animals other than humans, helping to answer questions regarding the distribution of flower coloration. A survey of keywords in Web of Science shows floral color to be mainly studied in relation to macroevolutionary traits and biochemistry of pigments, focusing on pollination and anthocyanins, respectively. The present paper reviews mechanisms that determine the color of flowers. First, it is discussed how pigment, visual systems and signaling environments influence flower color; secondly, patterns of convergent evolution of flower color is debated, including evolutionary history, pollinator preference, flower color change, flowering season, and habitat. Third and last, patterns of flower coloration that have been found around the globe are addressed. In short, the aim is to contribute to ongoing research, by underlining mechanisms that lead to global patterns of coloration and indicating perspectives for future study on the topic.

Keywords: floral color, flower coloration, color vision, pollination ecology, sensory drive, flower color change, pollinator preference, color preference, flowering season

Introduction

There are an estimated 308,000 plant species in the world which depend on animals for pollination (Ollerton *et al.* 2011) and, hence, need to communicate effectively with different pollinator species to reproduce. Color is a perceptual experience characterized by the interpretation of different wavelengths of light seen by eyes and processed by the brain of an individual (Kemp *et al.* 2015; Garcia *et al.* 2020). Flowers are sexual organs of plants and contain gametes which can be sensible to the environment (Mu *et al.* 2017). Flowers use color to communicate with different organisms such as pollinators and herbivores (Lev-Yadun & Gould 2007; Schiestl & Johnson 2013). Pigments used to produce flower color may also function as stress mediators in response to environmental factors (Dalrymple *et al.* 2020). Coloration will, then, be selected by several biotic and abiotic pressures throughout the evolutionary history

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of a plant. These pressures can lead flowers to diverge or converge in their colors within the community.

In order to understand how flower color has been studied in the past, we started by searching Web of Science for flower coloration (precise search terms were "Flower colo$r*" OR "floral colo$r*"). We then inputted articles in VOSviewer to conduct a keyword analysis (Fig. 1). We found that the 40 most used keywords formed two clusters, one focused on ecological and behavioral studies and the other on biochemistry and genetics. The ecology cluster had as its main keywords "evolution", "pollination" and "bee"; and the biochemistry cluster "anthocyanin", "flavonoid" and "biosynthesis".

Based on this primary exploration, we were interested in three other questions: 1) How many articles are there on different pollinator groups?; 2) How does research on antagonists compare to that on pollination?; and 3) What is the discrepancy in the study of different kinds of pigments? To answer these questions, we ran a second search on Web of Science (all entries on the main collection over the last fifty years) adding different keywords to flower color ("Flower colo$r*" OR "floral colo$r*") (Tab. 1). Although there might be articles that appear twice (*i.e.*, an article about bees and birds), we do not consider this an issue because we are not directly comparing the literature, only showing how some terms are more common than others. We found that bees are by far the most researched pollinator (448 hits), followed by flies (113 hits) and birds (90 hits); the least researched being butterflies (70 hits), moths (51 hits) and beetles (43 hits). Studies on pollination (638 hits) outnumbered studies on antagonistic interactions (74 hits total with all keywords combined). Lastly, anthocyanin (1051 hits) was the most researched pigment, followed by flavonoid (635 hits), carotenoid (185 hits), and betalain (18 hits). Surprisingly, anthocyanin had more hits than pollination.

Moreover, according to our search outputs, the distribution of flower colors across habitats also appeared as a commonly occurring theme. Flowers can either converge or diverge in color with other flowers in their community. Having distinct coloration from neighbors helps with flower constancy, which is favorable for pollinators to consistently visit rewarding flowers, and for plants to avoid pollen wastage (Waser 1986; Chittka 1999; Schaefer *et al.* 2004). In this paper, however, we will discuss mechanisms that determine flower coloration. The review is divided in two main sections. The first, with three subsections, examines what factors give color to flowers. The first subsection (section II.a.) briefly states the importance of flower pigments for coloration and stress response. The second (section II.b.) discusses the importance of the viewer in interpreting color signals. The third (section II.c.) considers environmental conditions as an important factor for determining color and how sensory drive could be an interesting framework for the analysis of flower color. In the second section, we present different factors that can lead to flower color convergence, such as: evolutionary history (section III. a.), pollinator pressure

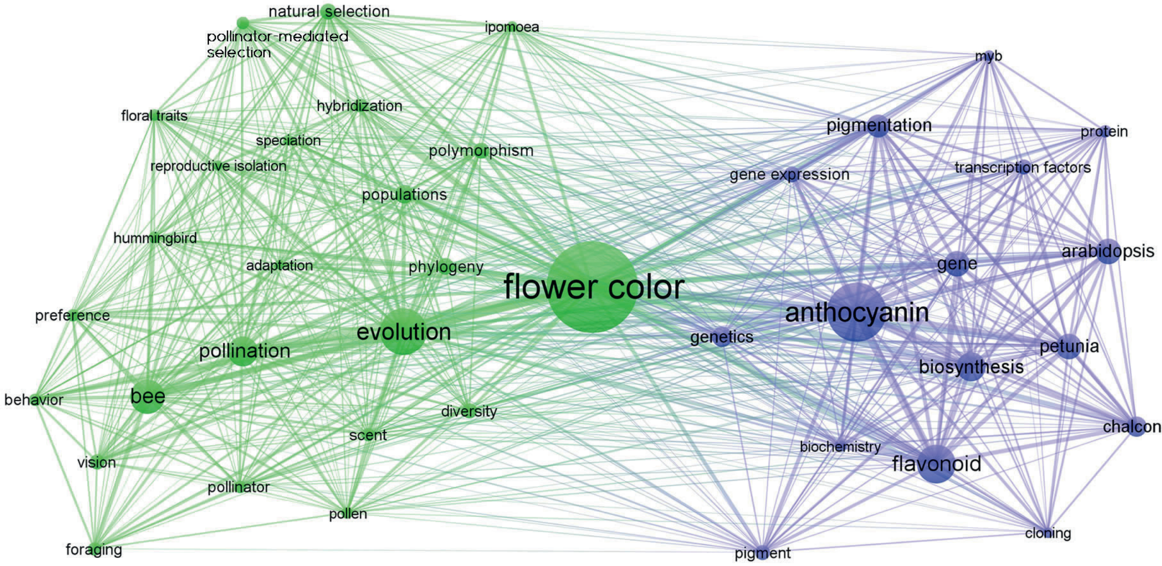

Figure 1. Word map of key-words associated with flower color. Search was conducted on web of science (21 august 2021) with the keywords: "Flower colo$r*" OR "floral colo$r*". The $ was used to include the British variation on the word color, and the * was used so color, colors, and coloration would be included. Word map was created on VOSviewer (van Eck & Waltman 2010) using author keywords and keywords plus. Keywords were manually filtered to join synonyms (*i.e.* bee, bees, *Apis*, *Bombus*, bumblebees were all joined in bee; odour, fragrance, floral scent and scent were all joined in scent) and to exclude uninformative terms (*i.e.* origin, tool, angiosperm, complex, patterns). The keyword had to appear in at least 10 entries and the 40 most used keywords were selected. Proximity of terms indicate how often they appear together and thickness of line indicated strength of links. Keywords formed two clusters; the one on the left (green) is formed of keywords related to macroevolution and behaviour such as speciation, adaptation, foraging and pollinator-mediated selection. The cluster on the right (blue) is formed of keywords related to pigment synthesis and genetics such as anthocyanin, flavonoid, gene expression and cloning.

(section III. b.), flower color change (section III. c.), flowering season and habitat (section III. d.), and what studies on flower color distribution have shown so far (section III. e.). Finally, we point out future perspectives regarding the study of floral color evolution (section IV).

What colors flowers

Pigments and flower coloration

Reflected wavelengths interpreted by visual systems give color to objects. Reflectance of flowers depends on the absorption of wavelengths by pigments (molecules that absorb specific wavelengths) and light scattering that occurs by irregular structured cell complexes (van der Kooi *et al.* 2014). Consequently, pigment strongly influences the reflectance of flowers (Chittka *et al.* 1994). There are three major groups of plant pigment: flavonoids (including anthocyanins), carotenoids and betalains. Their core structures differ in light absorption properties and may also be attached to other chemical groups to form more variable flower coloration (Willmer 2011). Pigments are deposited in layers in the petals, and the efficiency of pigment filtering is dependent on the concentration and location of each layer (van der Kooi *et al.* 2016). Different concentrations of pigments may also affect most of the parameters used for studying flower coloration. These include physical parameters, such as dominant wavelength (hue) and spectral purity (saturation), as well as visual model outputs, such as green contrast (perceptual contrast of two stimuli according to green photoreceptors) and color contrast (perceptual contrast of two stimuli according to all photoreceptors) (Papiorek *et al.* 2013; van der Kooi *et al.* 2019).

Apart from contributing to flower coloration, pigments are also associated with chemical defense against herbivory, this being one of the hypotheses as to why there are different color morphs in the same species. In the wild radish, *Raphanus sativus* (Brassicaceae), pollinators prefer white and yellow morphs, which have a lower concentration of anthocyanins, in comparison to bronze and pink color morphs having higher concentrations of anthocyanins (Stanton 1987). The color morphs with lower anthocyanin concentration, however, are less resistant to herbivory, providing a selective pressure to maintain high pigment morphs (Irwin *et al.* 2003). In star-patterned petunia, *Petunia hybrida* (Solanaceae), flowers are multi-colored, having a white star pattern at the middle of the corolla, which can have multiple colors surrounding it. The colored part has a higher concentration of anthocyanins and was found to slow the development of lepidopteran larvae (Johnson *et al.* 2008). Thus, it is likely that herbivores avoid plants colored by anthocyanins because they indicate the presence of defensive compounds (Schaefer & Rolshausen 2006), a tendency that might also be regarded as aposematism (Lev-Yadun & Gould 2007; Lev-Yadun *et al.* 2018). Surprisingly, when evaluating the role of flower color on florivory, Boaventura *et al.* (2021) did not find color as factor influencing floral damage.

Environmental factors can also exert pressure in selection for pigments (Dalrymple *et al.* 2020; Sullivan & Koski 2021). Certain anthocyanins can block UV radiation and prevent DNA damage (Kootstra 1994; Mori *et al.* 2005; Koski & Ashman 2015). Accumulation of protective anthocyanins caused by UV radiation produce red to purple colors in exposed tissue (Burger & Edwards 1996), as appears to be the case in *Delachampia* (Euphorbiaceae) and *Acer* (Aceraceae) (Armbruster 2002). Plant pigments have also been associated with further functions such as drought resistance, temperature resistance, heavy metal resistance,

Table 1. Number of entries on Web of Science of keywords associated with flower color over the last 50 years. Search was conducted on 21 August 2021.

Keywords	1972-1981	1982-1991	1992-2001	2002-2011	2012-2021	Total
"Flower colo$r*" OR "floral colo$r*"	57	121	594	999	1850	3621
"Flower colo$r*" OR "floral colo$r*" AND bee	2	2	73	106	265	448
"Flower colo$r*" OR "floral colo$r*" AND beetle	0	0	8	7	28	43
"Flower colo$r*" OR "floral colo$r*" AND bird	0	0	11	18	61	90
"Flower colo$r*" OR "floral colo$r*" AND butterfly	1	0	9	16	44	70
"Flower colo$r*" OR "floral colo$r*" AND fly	0	0	13	26	74	113
"Flower colo$r*" OR "floral colo$r*" AND moth	0	0	5	15	31	51
"Flower colo$r*" OR "floral colo$r*" AND florivory	0	0	0	4	10	14
"Flower colo$r*" OR "floral colo$r*" AND herbivory	0	0	6	12	25	43
"Flower colo$r*" OR "floral colo$r*" AND nectar robb*	0	0	3	2	9	14
"Flower colo$r*" OR "floral colo$r*" AND pollen thief OR theft	0	0	0	0	3	3
"Flower colo$r*" OR "floral colo$r*" AND pollination	3	7	87	201	385	683
"Flower colo$r*" OR "floral colo$r*" AND anthocyanin$	4	13	163	270	601	1051
"Flower colo$r*" OR "floral colo$r*" AND betalain$	0	0	2	5	11	18
"Flower colo$r*" OR "floral colo$r*" AND carotenoid$	0	3	20	43	119	185
"Flower colo$r*" OR "floral colo$r*" AND flavonoid$	1	5	77	173	379	635

and antioxidative capabilities (Chalker-Scott 1999; Gould 2004; Pourcel *et al.* 2007). Indeed, solar radiation was associated with an increase in color contrast in flowers (Darlymple *et al.* 2020). Abiotic pressures could select for pigments that modify flower coloration causing convergence of colors in similar stressful environments. Interestingly, species exposed to aridity tended to increase frequency of pigmented morphs (morphs with petals other than white) over time, while species exposed to elevating temperatures tended to decrease frequency of pigmented morphs over time (Sullivan & Koski 2021). Flower coloration is linked to many characteristics other than mating, being a magic trait (Servedio *et al.* 2011).

Other kinds of color signals include iridescence, gloss, polarization and fluorescence, though there is little evidence for their biological significance (van der Kooi *et al.* 2019). The presence of pigment alone, however, does not determine flower color. Vacuolar pH and cellular architecture may also have a major role in determining flower coloration (Grotewold 2006; van der Kooi *et al.* 2019; Dyer *et al.* 2021). Varieties of *Antirrhinum majus* (Plantaginaceae) are perceived differently by their pollinators when having equal pigment concentration but differing cell shape (Glover & Martin 1998). As it is commonly known, modification of soil pH, and consequently vacuolar pH, will cause a drastic color change in the hydrangea *Hydrangea macrophylla,* from red to purple or blue (Yoshida *et al.* 2003). Likewise, purple and blue flower variants of *Ipomoea nil* (Convolvulaceae) do not differ in pigment concentration, but in sap pH (Fukada-Tanaka *et al.* 2000). More recently, Stavenga *et al.* (2021) found that changes in vacuolar pH changed the absorbance of several anthocyanins-based pigments. This reveals that flower color may be more flexible than previously thought (Stavenga *et al.* 2021).

Eye of the beholder

Communication through color requires animals to have a visual system that can perceive different wavelengths and interpret them as color. The main flower visitors are insects, mostly because of their function as pollinators, but also because they are quite vicious herbivores, florivores, nectar-robbers, pollen thieves, sapsuckers, and parasites. Hence, animals with similar visual systems can be either beneficial or harmful to the same plant. Some pollinators can even act as nectar robbers depending on the flower visited (Irwin & Brody 2000). Although plants move through growth, they do so at a slower rate than animals move, so they cannot modulate visual signals depending on who is around. Color signals are then seen by mutualist and antagonist alike (Schaefer *et al.* 2004). Through color, flowers can be conspicuous (Schaefer *et al.* 2004), camouflaged (Niu *et al.* 2018) and even aposematic (Lev-Yadum 2011), but it all depends on who is looking and their sensory capabilities.

Pollinators have different visual systems, such that signal design (comprising what wavelengths it reflects, size, shape, where flowers are located within a plant, etc.) can make flowers cryptic or conspicuous to different organism. For instance, while most humans compare information from three types of photoreceptors (cones) and hence have trichromatic color vision (the exception being color-blind individuals), and can perceive wavelengths in the blue, green, and red range of the color spectrum (Bowmaker 1981), pollinators usually have a wide range of photoreceptor types (from one to fifteen), often including UV photoreceptors (Herrera *et al.* 2008; van der Kooi *et al.* 2021).

Most insects, including bees and moths, are trichromats with preserved photoreceptors that detect light in the UV, blue and green part of the electromagnetic spectrum (Peitish *et al.* 1992; Briscoe & Chittka 2001). The most common change in photoreceptors within insects was the addition of a red receptor, which has happened independently many times within lepidoptera (Briscoe & Chittka 2001). Butterflies may have from as few as three to as many as fifteen kinds of photoreceptors, though most butterflies have six different spectral sensitivities (Arikawa 2017). The number of photoreceptors does not necessarily mean better color vision, as they can be used for different mechanisms such as brightness perception (Cuthill *et al.* 2017). Despite usually having six photoceptors, butterflies have tetrachromatic vision using UV, blue, green and red photoreceptors (Arikawa 2017). Hawkmoths are also important pollinators and capable to perceive colors in dim light, with trichromatic vision similar to bees in the UV, blue and green range (Stöckl & Kelber 2019). Hoverflies also tend to have four photoreceptor varieties, but their color vision is still poorly studied (Lunau 2014). Among vertebrates, pollinators worth mentioning are birds and bats. Birds usually have four photoreceptors, tuned to UV, blue, green and red (Herrera *et al.* 2008), so that they are able to detect the entire color spectrum, like butterflies. Bats, despite being nocturnal, can have cones, in the UV and green range, but there are not enough behavioral test to see if their vision is dichromatic (Müller *et al.* 2009; Kries *et al.* 2018; Domingos-Melo *et al.* 2021).

Different visual systems perceive the same flower as different in color depending on their photoreceptors. This is beautifully illustrated by white flowers. For a flower to be white, it needs to activate all photoreceptors in equal proportions. That is, flowers need to reflect blue, green and red to be white for humans. To be perceived as white by bees and moths, a flower would need to reflect UV, blue and green in relatively equal proportions. Flowers need to reflect the entire color spectrum to be perceived as white by butterflies and birds. Therefore, most flowers which are white to humans are not white for any of the mentioned pollinators, because they do not reflect UV light (Kevan *et al.* 1996).

Typically, the study of flower coloration has been conducted through behavioral and ecological experiments, which are relatively time-consuming, frequently demand complex logistics, and use human perspective. Nowadays there are methods that help to avoid human perception biases. By using spectrometers or cameras that can even be adapted to UV photography, it is possible to measure how much a certain surface (*e.g.* flower petals) reflects in every wavelength (reflectance), including the UV region of the spectrum (Stevens *et al*. 2009). Reflectance of objects coupled with visual system information can be input into different computational models that allow the use of animal's point of view, and the extraction of different parameters such as color contrast, brightness, and even a standardized color category. To use these computational models properly is important to understand the visual system of the animal model, particularly by knowing photoreceptor peak sensitivity, noise and proportions in the retina (Kemp *et al.* 2015; Olsson *et al.* 2018).

Many studies refer to color as a categorical variable, but it is important to note that color categorization, that is, the capability to group distinguishable colors (Benard *et al.* 2006), might not occur in organisms other than humans (Kelber & Osorio 2010), although there is some evidence for it in bees and birds (Benard *et al.* 2006; Kelber & Osorio 2010). Even when considering human color categories (*i.e.*, blue, yellow, red), there is no consensus on how many categories are used, numbers ranging from as few as four (Warren & Billington 2005) to as many as eleven (Dyer *et al.* 2021). Furthermore, studies do not account for a clear description of categories, which might be a problem for flowers with transitional colors. If you include red and yellow categories, but not orange, how orange is categorized is a bias of the individual that categorized it. The same problem can be found with other common color descriptions, such as "cream" falling under white or yellow and "pink" falling under red or purple. This lack of concordance in methods makes it difficult to compare studies that use color as a category. It also highlights the importance of using a more standardized and replicable methodology, such as visual modeling.

In the past decade, visual modelling has been consolidated as a powerful tool (Stevens *et al.* 2009; Kemp *et al.* 2015; Renoult *et al.* 2017; Gawryszewski 2018), especially when paired with behavioral data (Dyer 2012; Olsson *et al.* 2018). While taking into account the features of any visual system that might be of interest, a visual modelling study can measure and contrast the raw reflectance of flowers and their backgrounds (Chittka *et al.* 1994; Arnold *et al.* 2009b), considering them to be illuminated by different ambient light conditions. Despite the limitation of visual information not being available for most species, visual modeling offers theoretical analyses that have potential to produce several important predictions, considering multiple kinds of pollinators and fostering future behavioral work.

The two most common models for analyses of flower coloration are the "color hexagon" and the "receptor noise limited". The "color hexagon" is a model specific for bee vision. It employs opponency of the photoreceptors to create a 2D space comprised of six regions, representing bee color categories (blue, blue-green, green, UV-green, UV and UV-blue); and the distance between flowers within the space can also be used to distinguish two stimuli (Chittka 1992). This model is the most commonly used to analyze flower coloration. The "receptor noise limited" (RNL) model is a generalist color model that can be applied to many different animals, given that proper parameters are known. It has already been validated for the visual system of bees, primates and birds (Osorio & Vorobyev 1996; Vorobyev *et al.* 1998; Vorobyev *et al.* 2001). The RNL model determines if two surfaces might be distinguishable by the visual system of the modelled receiver, according to their color distance (*i.e.*, color contrast). It may also be used to extract brightness information, though not originally design to do so (Olsson *et al.* 2018). Both models allow users to input peak photoreceptors sensitivity, ambient light and background coloration, which factors are fundamental to simulate how color is perceived in natural environments, which often vary in light and background noise. R software includes a specific package for analyzing color vision: Pavo 2.0, which can easily calculate many different color models (Maia *et al.* 2013; 2019). Color hexagon and RNL models have become the basis of other ways of analysing color (Garcia *et al.* 2020; van den Berg *et al.* 2020).

Signaling environment

Adding to the reflection of objects and the sensory capabilities of the viewer, ambient light and background noise will also shape the perception of flower coloration (Fig. 2). The same flower can be perceived as pink by reflecting pink under white light or by being a white flower under pink light (Chittka *et al.* 2014) (Fig. 2A). To solve the problem that natural illumination can vary in intensity and in spectral composition, organisms have developed color constancy, that is, the effect by which objects tend look the same color despite varying light (Foster 2011). In bees, color constancy is achieved by integrating visual information from the ocelli (Garcia *et al.* 2017); it is not, however, perfect (Dyer 1998). Indeed, bees have been shown to detect changes in ambient light and use them as contextual cues (Lotto & Chittka 2005). Furthermore, bees prefer to forage under brighter light, making it easier to distinguish flower colors (Arnold & Chittka 2012). The filtering of ambient light in areas with abundance of woody long-lived plants, in comparison to herbaceous species, might explain why some flowers appear to have lighter corollas (Hensel & Sargent 2012). Ambient light also varies across seasons, especially in deciduous or semi-deciduous forests, in which the falling of the leaves will cause a different light filtering (Endler 1993).

The background against which an object is presented can influence how we perceive certain colors, this being illustrated by several optical illusions (Fig. 2B) (Kelley & Kelley 2014). Likewise, depending on the background

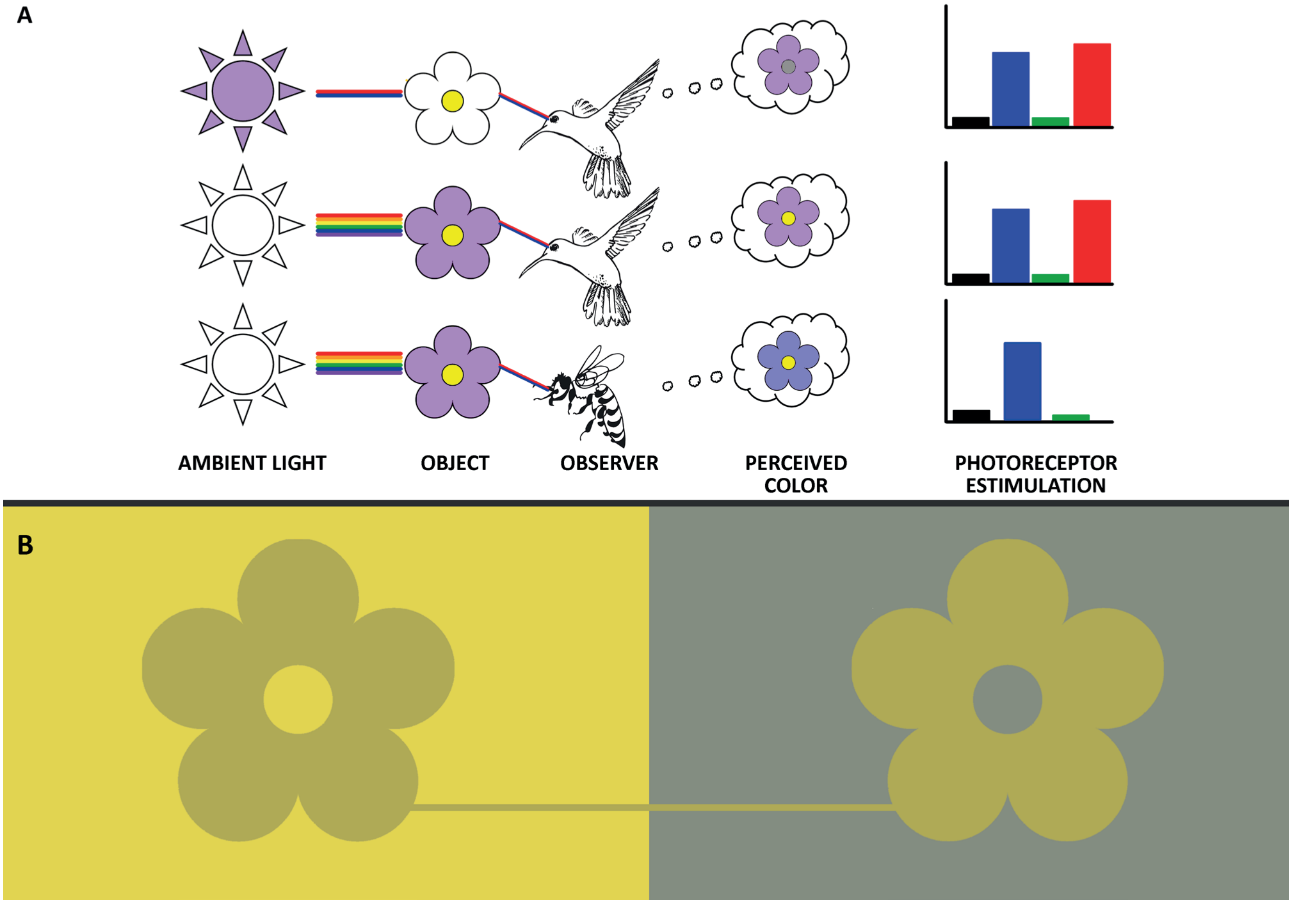

Figure 2. Factors that influence light perception. **A**) Purple is a multispectral color composed of blue and red light. A flower can be perceived as purple by viewers that are sensitive to blue and red photoreceptors, such as hummingbirds. For a flower to be perceived as purple it can be a white flower (capable of reflecting all wavelengths) under red and blue illumination; or a purple flower (capable of reflecting red and blue light) under white illumination. Viewers that cannot capture red light, such as bees, would see a purple flower under white illumination as blue. **B**) Typical optical illusion highlighting the importance of background coloration on color perception. The flower on the left appears darker than the flower on the right even though they are the same color.

contrast, the same flower may be perceived as bearing different colors, so that pressure to overcome background noise might be crucial to the development of conspicuous colors (Bukovac *et al*. 2017). Plants that develop dense foliage might overcome visual background noise (Bukovac *et al*. 2017), helping bees, for instance, forage under more visually uniform conditions (Forrest & Thomsom 2009). For flower species that occur in more than one environment (*e.g.* one with dense foliage and spread out vegetation), and/or for backgrounds that go through seasonal changes (*e.g.* falling leaves), flower signals would also have to overcome varying background noise, which could impose important selective pressure on the evolution of flower coloration on different populations. In Eastern Mediterranean flora, in order to overcome background noise, red flowers bloom before the green foliage develops, enhancing red flower contrast against sandy background (Willmer 2011).

According to Endler's theory of sensory drive, environmental bias, noise and the receiver's sensory capabilities tend to shape the evolution of signals by selecting signals and receivers that better overcome environmental noise, resulting in more conspicuous signals and more efficient receivers (Endler 1992). In pollination systems, plants emit signals via flowers and different species of pollinators receive those signals to interpret them in a foraging context. Predictively, bees prefer to forage in flowers that are more conspicuous in their background (Forrest & Thomson 2009). Since conspicuousness diminishes search time, we should expect the same for other pollinators. Pollinator receivers have a variety of visual systems that act as selective pressure for conspicuous flower coloration (Stournaras & Schaefer 2017; Koski 2020). Flowers of the same species are present in several different environments and, since they cannot relocate, are restricted to the signaling conditions of the given location. This suggests that environmental factors play a greater role in the evolution of plant signals than in that of animal signals (Koski 2020).

Sensory drive (Endler 1992) predicts that plants in the same signaling environments would converge in a conspicuous flower coloration determined by environmental signaling conditions. In the understory of a green forest, and according to the illuminant spectra registered by Endler (1993), we would expect to find many yellow flowers, as the canopy filters most of the red and blue light; while on treetops, where the broad spectrum of the sun is found, we should expect no difference in abundance of flowers of different colorations, except for green flowers, which would not contrast well against the green dappled foliage. Surprisingly, increased cloud coverage in Australia was associated with low color diversity (Dalrymple *et al.* 2020). Alternatively, in small clearings, where ambient light is shifted towards longer wavelengths (Endler 1993), red flowers would benefit, while under a woodland shade, where natural light is more bluish (Endler 1993), we would expect blue flowers to evolve. Nevertheless, in forests and grasslands of Germany (which vary in illumination and background), flowers seem to have similar colors according to the honeybee visual system (Binkenstein & Schaefer 2015). Different altitudes also vary in ambient light and background. In Colorado (USA), ambient UV light increased with altitude and different altitudes had different backgrounds (foliage or bare), which impacted the conspicuity and preference for fly and bee pollinators (Finnell & Koski 2021).

The importance of sensory drives is that it offers a distinct framework of how to integrate environmental heterogeneity and visual perception in the evolution of flower signals (Koski 2020). Signaling conditions are often overlooked when looking for patterns of color convergence in different habitats, as it is uncommon to find studies which control different background colors or light environments. The popularity of visual modeling will probably overcome this oversight in coming years. For more information on sensory drive in flower signals, we recommend the recent review published by Koski (2020).

Patterns of convergence

Evolutionary history

Flowers are dependent on their genetic make-up to determine their pigments and color possibilities (Chittka 1997). Yet some cultivated flowers, like roses, can come in a wide variety of color, such as red, pink, yellow, orange, white, violet and even green (Eugster & Märki-Fischer 1991). Plants can also produce fruits of a different color than their flowers, which exemplify that plants may allocate different pigments to serve distinct functions (Chittka 1997). Both examples show that flowers can rapidly evolve new colors given enough selective pressure (Chittka 1997). Related plants can have similar colored flowers because of their ancestral state, if there is not enough pressure to diverge from it. Some plant families tend to have similar colors. Apiaceae flowers, for example, are human white (bee blue-green) and vary mostly in brightness (in this case measured as the distance from the center of the color hexagon) rather than hue (measured as the angle from the center of the hexagon, varying from 0° to 360°) (Chittka 1997). The uncommonness of bee-white flowers has been associated with phylogenetic constraints (Chittka 1999; Koski & Ashman 2016). Other groups, however, have a tendency to preserve flower color (Chittka 1997). In Solanaceae, biochemical pathways leading to red flowers by anthocyanin, or by double production of anthocyanin and carotenoids, seem to express phylogenetic signals (Ng & Smith 2016).

Changes in flower color are common both between species and within species (polymorphism) (Roguz *et al.* 2020). This could be because in certain clades few mutations lead to new colorations. In *Antirrhinum majus* (Plantaginaceae), for example, a single gene mutation may lead to color change in flowers (Dyer *et al.* 2007). Likewise, in columbines (*Aquilegia*, Ranunculaceae), the loss of a single enzyme in the biopathway of some anthocyanins can cause blue to red transitions in flower color (Hodges & Derieg 2009). The type of mutation necessary to change flower color could explain the overrepresentation of some transitions in flower colorations (Sobel & Streisfeld 2013). Blue to red (*e.g. Ipomoea*) and pigmented to white transitions, for instance, are more common than red to blue (*e.g. Sinningia*) or white to pigmented (Raucher 2008; Ma *et al.* 2017). Despite the biochemical pathways for the production of anthocyanin being well understood (Ma *et al.* 2017), studies with other pigment groups are still needed to understand the relationship between mutations and flower color.

Different clades have different mutation rates and higher mutation rates can lead to higher diversification rates (Hua & Bromham 2017). Indeed, plants can accumulate mutations that will eventually lead to polymorphisms which are simply not selected against (Sapir *et al.* 2021). Adaptative radiation can exemplify how closely related flowers can easily diverge in color. The iris, *Iris lutescens* (Iridaceae), has two color morphs, with different distributions across Spain and France, different processes seeming to be in play in the two regions (Wang *et al.* 2016). Spain has monomorphic populations of either yellow or purple flowers that have little to no gene flow between them, and genetic drift seems to be the factor determining the polymorphism. In France, however, where genes flow between these populations, most populations are polymorphic and composed of both colors. Similarly, in the milk thistle *Silybum marianum* (Asteraceae), founding effect and genetic drift seem to explain the variations of color morphs along the Mediterranean (Keasar *et al.* 2016). The importance of random and neutral factors on flower color polymorphism has only recently come into light, as most studies focus on balancing selection of flower color (Sapir *et al.* 2021). Evolutionary history may also affect color because it allows for similar plants to withstand similar environmental factors, and hence to bloom close to each other (Kemp *et al.* 2019). In Nepal, monocots are more present in lower elevations, and there is more color diversity at higher elevations (Shrestha *et al.* 2013).

It is difficult to define color as a variable for phylogenetic analyses, especially to avoid bias of human vision, so several studies approach evolutionary history from alternative methods. While some studies found phylogenetic signal in flower coloration (Ng & Smith 2016; Reverté *et al.* 2016; Shrestha *et al.* 2013), others did not (Smith *et al.* 2008; Arnold et al. 2009a; McEwen & Vamosi 2010; Weber *et al.* 2018). Inasmuch as phylogenetic effect varies across groups, it is important to include phylogeny as a possible cause for patterns of flower coloration. Compiling studies on phylogenetic signal would be a welcome measure toward understanding the evolution of flower coloration.

Pollinator pressure

The diversity of flower color is often attributed to pollination pressure and sexual selection, as flowers are the sexual organs of plants, and their traits can influence plant fitness (Schiestl & Johnson 2013). This could, however, be a reflection on the overrepresentation of pollination studies (18.8 %, Tab. 1) in flower coloration literature in comparison to antagonistic interactions (2 %, Tab. 1). In this section, we will address characteristics of pollinator's behavior and visual systems that might lead flowers colors to converge.

Many pollinators display innate color preference when visiting flowers (Lunau & Maier 1995; Gumbert 2000). Bees, for instance, have innate preference towards the violet-blue color range (Briscoe & Chittka 2001), and pipevine swallowtail butterflies have innate preferences for yellow, blue and purple (Weiss 1997). Innate preferences can be overcome by learning to associate rewards with colors (Gumbert 2000; Weiss & Papaj 2003). In the pollination context, this is important because not all flowers produce equal rewards. Associative learning is important for pollinators, because it renders better foraging efficiency and fitness (Raine & Chittka 2008). Some pollinators, however, can go back to relying on innate preferences when their preferred flowers are unavailable, even after learning (Gumbert 2000). Innate preference, then, support trait convergence, because by having flower coloration that matches pollinator preference, flowers can recruit pollinators more readily.

Pollinators also exhibit flower constancy, that is, the habit of a flower visitor effectively to restrict their visits to a few flower species or morphs (Chittka *et al.* 1999). Flower constancy is important for plants because it diminishes pollen wastage (Schaefer *et al.* 2004). Having distinct coloration from neighboring plants facilitates this process (Schaefer *et al.* 2004) and is one main argument for flower color divergence. Indeed, competition for pollinators was linked to flower color diversity in hummingbird-pollinated *Iochrominae* (Solanaceae) (Muchhala *et al.* 2014). This problem could be overcome by having other morphological traits that aid distinction, such as different shape. In the *Erica* genus (Ericaceae), flowers from the same community are more likely to be similar in color when they differ in other morphological features (Coetzee *et al.* 2021).

The reproductive success of a plant is dependent on the kind of visitor it attracts (Schemske & Horvitz 1984). In *Calathea ovandensis* (Marantaceae), Hesperiidae butterflies account for 21 % of visits but for less than 1 % of seed set. *Bombus medius* (bumblebee) and *Rhathymus* sp. (bee), however, only had 5 % of visits, but were responsible for 22 % of seed set. Therefore, it is important to attract animals with the necessary behavior and morphology to pollinate properly. Some characteristics are overrepresented in flowers pollinated by certain functional groups (Fenster *et al.* 2004). Based on that, flowers are grouped by their morphological features, such as color, in pollination syndromes according to which pollinator it is supposed to attract (Willmer 2011). These morphological characteristics would have converged due to pressure by pollinators that prefer certain characteristics. Color preferences are often used in pollination syndromes (Dellinger 2020). For example, red flowers are typically associated with bird pollination and blue with bee pollination (Willmer 2011). Indeed, in Australia, bird-pollinated plants showed convergence for red-flowered plants (see the bee-avoidance hypothesis bellow) (Burd *et al.* 2014).

Floral color, however, is not always the most reliable characteristic of pollination syndromes. In fact, a recent review found that color was the most uninformative trait studied in flower syndromes in the last decade (Dellinger 2020). Results vary with the location and clade studied. In snapdragons, *Antirrhineae* (Plantaginaceae), flower morphology, including flower color, had an overall positive predictive value of 65.95 % for pollinators and flower visitors (Guzmán *et al.* 2017). Momose *et al.* (1998) associated flowers of a lowland dipterocarp forest in Sarawak (Malaysia) to pollination syndromes, and found that pollination syndromes relate to certain flower characteristics, such as reward, shape, and flowering time, but not to color. In *Erysimum* (Brassicaceae), lilac flowers were related to a pollinator niche comprised of large long-tonged bees, but it seems that the development of lilac flowers predates this pollinator preference, and is probably related to other environmental factors which eventually led to bee pollination (Gómez *et al.* 2015). Overall, it is possible that color predictability of pollinator-color interactions only plays a role in certain clades (Dellinger 2020). Interestingly, pollinators seem to prefer a certain flower color, but flower color does not determine pollinator assemblage (Reverté *et al.* 2016). Caution is necessary when interpreting these works because human vision is often used to determine the categories of flower coloration. Perhaps the use of ecologically relevant visual systems would allow for less varied results.

Schaefer *et al.* (2004) argue that the idea of pollination syndromes is outdated, because plants could have converged in flower coloration to exclude eavesdroppers just as easily as to attract pollinators. This notion fits well within the idea of private communication channels, that is, a communication system that involves a signal to which an eavesdropper is insensitive (Stevens 2013), and underlies the bee-avoidance hypothesis which explain why bird-pollinated flowers often are red. Despite common belief, birds do not have innate color preferences (Lunau *et al.* 2011). Instead, bees are generally insensitive to longer wavelengths (Peitsch *et al.* 1992), meaning that red flowers are hard for bees to detect. The red color serves to generate a private communication channel between red flowers and birds (Lunau *et al.* 2011), excluding bee visitors that can be nectar robbers in hummingbird-pollinated species (Irwin & Brody 2000). Red flowers that are pollinated by bees usually have a secondary reflectance peak in the UV range, which makes them conspicuous to bees; red flowers pollinated by birds, however, reflect only longer wavelengths which birds can easily detect, but bees cannot (Lunau *et al.* 2011; de Camargo *et al.* 2019; Chen *et al.* 2020). Interestingly, yellow flowers seem to follow the same trend, where bird-pollinated flowers absorb UV and bee-pollinated flowers reflect UV at the periphery (Papiorek *et al.* 2016). Absence of UV-reflection in the center of yellow flowers could, however, also be seen as stamen mimicry (Lunau 2005). It is noteworthy that pollinators, such as butterflies and flies, which can also detect red flowers, are usually not included in studies evaluating the bee-avoidance hypothesis. Indeed, fly-pollinated flowers also seem to tend to reflect longer wavelengths and absorb shorter wavelengths (Shrestha *et al.* 2019a). Another way to exclude unwanted visits is camouflage. Flowers of *Eucomis autumnalis* and *Eucomis comosa* (Asparagaceae) are visually cryptic by having a similar color to leaves, attracting pollinators solely by smell (Shuttleworth & Johnson 2009). Unfortunately, camouflage is a poorly studied topic in plants (Niu *et al.* 2018). Previously, dull-colored bat pollinated flowers were considered as camouflaged from other visitors (Fleming *et al.* 2009), but bats and other pollinators can use visual cues from these flowers (Domingos-Melo *et al.* 2021).

Pollinator pressure might also lead to convergence due to receiver bias in pollinators (Schaefer & Ruxton 2009). This happens when animals apply selection pressure on flowers, imposed by traits that did not evolve via interactions with flowers (Schiestl 2017). Receiver bias can be innate preference for certain flower traits. Flower guides, stingless bee nest entrances, and insectivorous pitchers, for example, tend to have dark centers, radiating striped and peripheral dots which have been linked to finding mates or nesting ground (Biesmeijer *et al.* 2005; Schiestl & Johnson 2013). Plants that do not offer any reward, but still manage to attract pollinators using pre-existing bias, are attracting pollinators via deception (Schiestl 2017). This deceit system can be the precursor of another kind of deceptive pollination, namely, mimetic flowers, because innate biases will lead flowers to converge without the need of a specific flower model (Schaefer & Ruxton 2009; Schiestl 2017). Considering the visual system of most insects evolved before flowers (Chittka 1996; van der Kooi *et al.* 2021), and most flowers are only a fraction of possible colors (Chittka *et al.* 1994), receiver bias could have had a major role shaping flower color to pollinator pre-flower preference.

Flower color change

Flower color is not static through time, something often forgotten when studying global patterns of flowering. Flower age can affect flower color, as many plants show a dramatic color change, different from senescence (Weiss 1995). This phenomenon has been found in over 70 families of plants (Weiss 1995). *Byrsonima variabilis* (Malpighiaceae), for instance, changes standard petal color during anthesis from yellow to orange and finally red, and bees preferentially visit flowers with yellow standard petals when foraging for pollen (de Melo *et al.* 2018). The retention of old flowers increases display size and, by doing so, increases attraction of pollinators (Ishii & Sakai 2001). Indeed, prolonged longevity of flowers may increase pollination even without color change (Teixido *et al.* 2019). It seems, however, that the retention of old flowers without color change might come at a cost, because it leads to plant-level avoidance by pollinators with spatial memory (Makino & Ohashi 2017). Here we aim to explore how flowers not only converge on specific colors, but also on strategy of flower color change (Weiss 1995).

Flower color change has been extensively associated with directing pollinators to rewarding flowers, inasmuch as flowers are unrewarding after color change (Weiss 1995). Indeed, at close range, flower color change can direct pollinators to rewarding flowers (Sun *et al.* 2005) and is often considered an honest signal (Schaefer *et al.* 2004; Makino & Ohashi 2017). Nevertheless, when considering long-distance attraction, it seems pollinators struggle to determine the proportion of rewarding to unrewarding flowers (Oberrath & Böhning-Gaese 1999; Kudo *et al.* 2007). Insects have poor visual acuity, and typically only use color cues at short distances, relying on green receptor contrast for long distance detection (Giurfa *et al.* 1996; Vorobyev *et al.* 1997; de Ibarra *et al.* 2015). For this reason, flower color change may attract pollinators at long distances via deception, by maintaining an increased display that includes unrewarding color-changed flowers that cannot be differentiated from rewarding flowers. Once pollinators approach, however, it provides an honest signal, regarding which flowers are rewarding (Brito *et al.* 2015). Since there might be a delay between flowers being emptied of reward and color change, flower color change might be better termed a "semi-honest" signal, that is, a signal that diminishes uncertainty, but is not completely reliable (Ruxton & Schaefer 2013).

There are other benefits from the retention of old color-changed flowers, because even without increased attraction, floral color change can decrease the amount of geitonogamous pollination (when pollen is transferred from one flower to another of the same plant) (Ida & Kudo 2003). Flower color change seems to be such an advantage that some wonder why it is not prevalent among angiosperms (Ruxton & Schaefer 2016). Flower color change is, altogether, more common than it gets credit for, and new reports of color-changing flowers are found often, even in the UV range (Ohashi *et al.* 2015). Flower color change has evolved many times (Weiss 1995), and this outcome could be due to a simple mechanism. Pollinators have been shown to recognize old flowers, as is the case in *Rosa virginiana* (Rosaceae), where second day flowers are paler, and bees preferentially visit younger flowers (MacPhail *et al.* 2007). Pigments, especially anthocyanins, are altered by sunlight (Grotewold 2006). Though color change may happen in any pigment, most color changes seem to be associated with variation in anthocyanins (Weiss 1995; Lippi *et al.* 2011). In *Viola cornuta* (Violaceae) flowers, changes in color are due to anthocyanins; when flowers are grown in the dark, they do not show color change, as opposed to a white to purple change that occurs under light conditions (Farzad *et al.* 2002). Thus, the first color changing in flowers would be brought upon by senescence. Natural selection would refine this natural change, inasmuch as flower color change benefits plants by attracting more pollinators (Ishii & Sakai 2001; Ida & Kudo 2010) and by diminishing geitonogamous pollination (Ida & Kudo 2003; Sun *et al.* 2005); while it benefits pollinators by diminishing foraging time (Kudo *et al.* 2007). The first step into flower color change would be to retain older flowers (as flowers that fall from the plant do not go through color change), and such retention does not happen in multiple species. The cost of flower maintenance is, then, crucial to better understand this phenomenon.

There are other hypotheses that could explain flower color change. A pollinator may learn to visit plants that have honest signals regarding rewarding flowers, so a plant could evolve color change in response to that (Makino & Ohashi 2017; Ohashi *et al.* 2015). Another fascinating explanation is that flower color change is a step toward transitioning flowers from one pollinator to another, being ephemeral in evolutionary time (Ruxton & Schaefer 2016). In *Combretum indicum* (Combretaceae), white flowers are mostly visited by moths, while red ones are visited by butterflies (Yan *et al.* 2016). Of course, different explanations could apply to different groups presenting flower color change, as there is a predisposition for flower color to change in some families (Ohashi *et al.* 2015).

Flowering season and habitat

Another recurring theme in the literature is that plants with flowers of certain colors bloom at certain seasons (Willmer 2011). Insects can change their color preference over time through learning (Gumbert 2000; Weiss & Papaj 2003). Sharp & James (1979) found that yellowjackets were most attracted to traps painted buttercup yellow during spring and summer, and traps painted Saturn yellow during fall and winter. This move could be triggered by the blooming of abundant species. Aydin (2011) found that the beetle *Tropinota hirta* (Scarabaeidae) alternated color preference during blooming of cherry trees, preferring light blue traps when flowers were in bloom and white traps before and after cherry blooming. Although blooming time is important for pollinator attraction, there are too few papers evaluating pollinator preference over seasons to be able to access how this affects flower communities.

The abundance of insects with color preference can also change throughout the year (Kevan 1983). In Australia, *Epacris impressa* (Ericaceae) has different color morphs, which vary across seasons. The white morph is found in spring and the red in winter. This pattern of occurrence seems to be related to abundance of pollinators, because birds are present in winter, when the red morph blooms, and white morphs occur in spring, when insects are more plentiful (Stace & Fripp 1977). Similar patterns were also found in the Tibetan flower *Gentiana leucomelaena* (Gentianaceae), where white morphs are more abundant when ambient temperature is higher and there are more fly pollinators available, but blue morphs are more common when it is colder and bee pollinators prevail (Mu *et al.* 2010; Mu *et al.* 2017).

Another hypothesis that could explain color differences due to ambient temperature is related to flower heat. Flowers of darker color will be warmer than light colored flowers, as they absorb more heat (Koski & Galloway 2021). Warmer flowers can bring advantages to plants under cold environments, because warmer flowers speed the development of floral organs (Whitney *et al.* 2011; Koski & Galloway 2021), and in warm environments lighter colors dissipate heat (Sullivan & Koski 2021). Different color morphs also affect anther temperature (Mu *et al.* 2017). Pollen is sensitive to temperature variations, so when flowers are too warm or too cold, there is loss of pollen viability (Mu *et al.* 2017). In *Campanulastrum americanum* (Campanulaceae) temperature explains flower color better than pollinator assemblage (Koski & Galloway 2021).

Additionally, some pollinators, such as bees, can associate color difference with warmer flowers and preferentially forage on warmer artificial feeders (Dyer *et al.* 2006). This makes for a pollination system in which heat is offered as a reward (Whitney *et al.* 2011). In three species of *iris* (Iridaceae), *I. atrofusca* (dark purple to brown), *I. atropurpurea* (dark purple to brown), and *I. hermona* (dark spotted inner petter and blue outer petal), pollinators do not get any nectar or pollen reward; instead, flowers warm up quicker than ambient temperature in the early morning, so that male bees, who sleep inside flowers, will start foraging earlier the next day (Sapir *et al.* 2006). Ambient temperature could be acting as a selective pressure for flowers to converge to darker morphs in colder environments, and to lighter morphs in warmer environments. The literature on flower temperature is, however, biased towards the heating effect of flower color, with most studies being conducted on alpine or artic species (van der Kooi 2019).

Another influence of phenology on flower color ensues from synchronous flowering, that is, overlap between flowering species of a community (Wolowski *et al.* 2017). Flowering together with other members of the same community can lead to convergence of colors because of joined attraction to pollinators (Wolowski *et al.* 2017; Bergamo *et al.* 2020). This particularly aids rare flowers that might not be numerous enough to attract pollinators alone (Bergamo *et al.* 2020). There is some evidence of a convergence of flower color according to season. Initially spring flowers were thought to be predominantly white, based on a study done by Motten (1986) in North Carolina, USA. A posterior study showed that, instead, the corolla color of spring flowers in temperate deciduous forests are lighter than non-spring flowers, but not necessarily white (Hensel & Sargent 2012). In the Brazilian Savanna, yellow flowers were abundant year around, but white flowers peaked in the dry season, and pink flowers in the wet season (Martins *et al.* 2021). Indeed, in Itatiaia National Park (Brazil), community level fitness increased with synchronous flowering and color similarities, using visual systems of bees, flies and birds (Bergamo *et al.* 2020). In Germany, however, flower color was studied across a year period, and there was no relationship between floral color and blooming time when considering the bee visual system; but there was a difference when considering human vision, which exemplifies the importance of using an ecologically relevant visual model to study flower coloration (Arnold *et al.* 2009b). Further research, emphasizing pollinator perspective and accessing different populations, is essential to reach a better understanding of the effects of seasonality on flower coloration.

Similar to flowering season, different environments exert different selective pressures for plant communities, so it is important to take locality under consideration when analyzing flower color patterns. Abiotic factors, such as temperature (discussed in the previous section), rainfall, and ambient light, can vary between environments. Warren & Mackenzie (2001) found that in polymorphic flowers, none-white morphs performed better under drought conditions and white morphs performed better on well-watered conditions. Koski & Ashman (2016) found that habitats with high UV-B irradiance were more likely to have UV-absorbing flowers. Abiotic conditions are, however understudied compared to biotic pressures on flower color (Darlymple *et al.* 2020).

Biotic interactions may also affect flower color either to defend from antagonists or to better attract pollinators. Despite lack of studies relating antagonistic interactions and flower color, Boaventura *et al.* (2021) found that florivory is twice as high on tropical plants. This could suggest a tendency for less conspicuous flowers in the tropics. Indeed, a comparison of flower coloration between different latitudes in Australia showed that colors are more saturated, contrasting and diverse farther from the tropics (Dalrymple *et al.* 2015).

Locality can influence pollinators in three ways. First, pollinators can have differential color preferences between habitats. Bumblebees usually have a UV-violet preference, but some populations have an additional red preference (Raine *et al.* 2006). Hence, plants can have local adaptations depending on pollinator's preference. The mimetic orchid *Disa ferruginea* (Orchidaceae) is pollinated by a single species of butterfly. This orchid has two color morphs occurring in different mountains in South Africa (Newman *et al.* 2012). The red morph occurs when there are red rewarding flowers around, and butterflies show preference for red flowers, and the orange morph occurs when there are orange rewarding flowers and butterflies show orange preference (Newman *et al.* 2012).

Second, the abundance of different kinds of pollinators varies across habitats. Ellis *et al.* (2021) found that pollinator density predicted the distribution of white and orange daisies, with white daisies flowering where the dominant fly species had an innate preference for white flowers and orange daisies flowering where the dominant fly species had an innate preference for orange. Flower coloration in Australia (Dyer *et al.* 2012) and Israel (Chittka & Menzel 1992) seems to be shaped by Hymenoptera vision, while the abundance of red flowers in the tropics is often attributed to hummingbird pollination (Willmer 2011). Red flowers from the New World, where birds are important pollinators, are more conspicuous to birds than red flowers from the Old World (Chen *et al.* 2020). Blue-purple flowers in the Arctic seem to be related to species richness of bumblebees showing a coevolution between flower color and pollinator species (Eidesen *et al.* 2017). Likewise, New Zealand flora is mostly comprised of white flowers well suited for bee detection (Bischoff *et al.* 2013). In Macquarie Island (Australia), where there are no birds and bee pollinators, flowers are predominantly cream-green and white colored, a circumstance that could be due to fly pollination, either by allowing migrants with these colors to persist or by flowers converging to these colors due to pollinator pressure (Shrestha *et al.* 2016).

Convergence of flower coloration within communities can increase misidentification from pollinators, and with that, pollen loss between similar species (Coetzee *et al.* 2021). The effect of color convergence depends on community structure. Competition would result in loss of fitness for the whole community (Bergamo *et al.* 2020), but another possibility is that color similarities can cause a gain of fitness in communities through facilitation (Bergamo *et al.* 2020). Under the facilitation scenario, flowers blooming together with the same coloration would attract more pollinators, creating a rewarding mimicry ring (Jamie 2017; Coetzee *et al.* 2021). *Turnera sidoides* (Turneracea) occurs in two varieties in different locations, color closely resembling other abundant Malvacea species of the flowering region (Benitez-Vieyra *et al.* 2007). Additionally, reproductive success of one of the *T. sidoides* phenotypes increased when the model Malvacea species was more abundant (Benitez-Vieyra *et al.* 2007). Facilitation leads to flower color convergence, as shown in some communities. In South African *Erica* (Ericaceae) communities, birds vary in preference between sites. Visitation of less preferred *Erica* flower species increased when they were similar in color to preferred species by local birds (Coetzee *et al.* 2021). Community flower abundancy was related to lower trait (including color) diversity in Brazil (Bergamo *et al.* 2020). In Australia, flower communities with higher diversity tended to converge to less contrasting colors (Dalrymple *et al.* 2020).

Higher altitude gradients are an interesting study system because they vary in biotic and abiotic factors such as ambient light, with higher altitudes having higher UV (Gray *et al.* 2018); and in pollinator assemblage (Shrestha *et al.* 2013). At first, a study in Norway (Arnold *et al.* 2009a), with altitudes varying from 700-1600 m above sea level (*a.s.l.*), found no effect of altitude on flower color. The same data was re-evaluated latter and found within community convergence of flower colors in higher elevations (Bergamo *et al.* 2018). By contrast, in Nepal (900-4100 m *a.s.l.*), flowers found in higher altitudes show more diversity of colors than in lower ones (Shrestha *et al.* 2013). In Colorado (2,700-4,000 m *a.s.l.*), there was a decrease of short wavelength reflection and bee-blue species, along with an increase in saturation with higher elevations (Gray *et al.* 2018). The same study found a hump-shaped pattern for longer wavelengths and green receptor contrast throughout elevation gradients. In Japan and New Zealand (sites varying from 1500-1630 m to 2200-2850 m *a.s.l.*), there was an increase of the likelihood of bee-blue or UV-blue flowers occurring in higher altitudes. Finally, in Taiwan (sites varying from 0-900 m to 2800-3300 m *a.s.l.*), lower altitudes had more diversity in flower color than higher altitudes (Tai *et al.* 2020). Although metrics of diversity and altitudes varied between studies, overall four out of six studies found that flowers in higher altitudes were less diverse in color than in lower altitudes. Though many studies relate altitude patterns to pollination, it is possible that abiotic factors, though understudied, also play a crucial role (Dalrymple *et al.* 2020). The studies mentioned are still not enough to identify a clear altitudinal pattern, and changes in color diversity could be due to other factors.

Global patterns

We have looked so far at mechanisms that might lead flowers to converge, and in this section, we will look at studies done around the world to see whether these mechanisms lead to an overabundance of certain colors categories (refer to section II.b for a discussion on limitations of using color categories) in flower communities around the world. We will first address studies using human vision, and then using bee vision.

A survey of the Plant Trait Database (www.try-db.org; Kattge *et al.* 2019), conducted by Dyer *et al.* (2021), found that the majority of flower colors recorded were white and yellow (24 % and 20 % respectively). When considering only animal-pollinated species, most of the flowers remained white and yellow (35 % and 22 % respectively). Interestingly, when only considering abiotic pollinated plants, green (41 %) was the most abundant color, followed by white (20 %) and brown (20 %). This aligns with other studies in the Brazilian sandbank and seasonally dry forest (Machado & Lopes 2004), mountainous landscapes in central Europe (Dyer *et al.* 2021), and Taiwan (Tai *et al.* 2020). Other studies describe a different pattern. In the Brazilian savanna, the main flower color was white, followed by pink, and then yellow, but color category abundancy changed over seasons (Martins *et al.* 2021). In British grasslands, yellow was the most common color followed by pink and white (Warren & Billington 2005). In Macquarie Island (Australia), frequently blooming flowers are predominantly pale cream to dull green (Shrestha *et al.* 2016), a category which is missing from other studies, where these flowers could likely be considered either yellow, green or white. Hence, even studies that did not find a white and yellow prevalence found a white or yellow prevalence in flower categories. When using human vision to categorize, then, flowers seem to converge towards white and yellow across habitats, and pink flowers are also common. This pattern must be considered with caution, because many places in the world remain unsampled.

White flowers are typically blue-green in a bee color space and yellow flowers are typically UV-green (Tai *et al.* 2020). Actually, studies using the flower hexagon have shown an overwhelming majority of bee blue-green flowers and a scarcity of purely UV reflecting flowers Chittka (1997). Prevalence of blue-green flowers has been found in various environments such as the Rocky Mountains (Gray *et al.* 2018), Brazilian Savanna (Martins *et al.* 2021), Japan and New Zealand (Ishii *et al.* 2019); Taiwan (Tai *et al.* 2020); Macquarie Island (Shrestha *et al.* 2016); Australia, Nepal and Israel (Shrestha *et al.* 2019b). The second most abundant color varies among studies. This prevalence of blue-green color could be due to bee's innate preference for blue-reflecting flowers, coupled with the easily detectability of green-reflecting flowers by green-contrast (Dyer *et al.* 2021).

When looking for patterns of convergence other than using color categories, results widely differ between studies. Chittka (1997) has shown that the color distribution of flowers in a German grassland was found not to differ from chance, but in the Brazilian rainforest, flowers seemed convergent towards bee-blue. Gumbert *et al.* (1999) analyzed five different habitats within Germany for trends in flower color. When considering common flowers only, they did not find any color to prevail; but when rare flowers were included, results varied across communities studied, with two showing divergent distribution, another showing convergent distribution and two finding random distribution (Gumbert *et al*. 1999). Subalpine communities in Canada show evidence for divergent evolution of floral color (McEwen & Vamosi 2010). Daisy communities in South Africa showed evidence for convergent evolution in flower coloration (Kemp *et al*. 2019). Shrestha *et al*. (2019b) analyzed flower communities in the perspective of different species of bees in the state of Victoria (Australia) and found that flower color structure varied according to the visual system used, some showing convergence, others divergence, but most showing a random distribution of flower coloration. These results highlight the importance of using the visual system of local pollinators or antagonists for analyzing patterns.

Using color categories, most flowers worldwide seem to follow a pattern of white and yellow flowers according to human vision and blue-green flowers according to bee vision. It is also important to note that there is publication bias towards studies that find differences between habitats which could be influencing this pattern. Patterns of convergence independent of flower categories depend on the habitat, and can vary relative to the visual system used to analyze these patterns. Even though most species of bees have similar visual systems (Peitsch *et al*. 1992), Shrestha *et al*. (2019b) showed that demonstrating color divergence or convergence of the same set of flowers is possible when utilizing different bee species as models. We encourage future work to take this matter into consideration, preferentially adopting species which naturally occur in the studied environment, better to understand biogeographic patterning of flower color. Here we only addressed studies using human and bee perspectives, partly because studies using other pollinators are relatively scarce and also because the bee-hexagon model can provide clear color categories (Chittka 1992) and such models are not available for most pollinators. Greater appreciation of other visual systems is important so that similar analyses can be conducted using perspectives of other pollinators and herbivores.

Summary and prospects

Research on flower coloration has increased in the past decades, but there are still many topics to be studied. So far, inquiries into this topic have focused on two areas: ecology and evolution, and biochemistry of pigments. Most ecological research has been focused on pollinator pressures, specifically on bee pollination. Biochemical research has focused mainly on anthocyanin biosynthesis.

The biochemistry of flower coloration is determined by the synergy of pigments, pH and cellular structure, and is influenced by environment. Flower pigments are selected via a balance between pollinator attraction, defense against herbivores and resistance to environmental factors. Regarding mechanisms of flower coloration, the impact of iridescence, fluorescence and polarization regarding communication with pollinators and antagonists still remains to be explored.

The study of biochemical pathways which lead to flower coloration, particularly betalains and carotenoids, and what genes are associated with them would help determine how frequently new colors evolve within different clades. New colorations can be fixed by selective pressure or lack thereof, and the effect of random and neutral processes on coloration is still in its infancy and has much space to grow. It is important to consider phylogenetic history when interpreting flower coloration data. A global analysis or metanalyses of phylogenetic signal of flower color is still lacking. Quantifying coloration on a global level can be difficult because coloration varies according to the receiver, and there are few species of which there is enough information of their visual systems to make robust analyses. Using purely physical data to analyze coloration often does not translate into realistic models. Since most pollinators see UV light, it can be costly to purchase equipment proper to study flower color, especially where government investment in science is lacking, so collaboration among research groups is recommended to help overcome the impeding costs of this kind of research. A good example is the Flower Reflectance Database (www.reflectance.co.uk) that provides reflectance data on many different flowers in an accessible way (Arnold *et al*. 2010). The good news is that methods for analyzing coloration using animal perspective are becoming more refined and widespread.

Biochemical studies of flower pigments can also help to understand how flower color change evolved. In particular, the degradation of anthocyanins by sunlight could be a key precursor of flower color change. Likewise, studying the cost of maintaining color changed flowers would help explain why flower color change is not more common. Finding a model that only presents color-changed flowers under certain environmental conditions would greatly assist in this matter.

There are many pressures in each habitat that will make for flower color patterning. Most studies on biotic factors are about pollination; among pollinators and regarding flower color, bees are the most and beetles are the least studied. An interesting abiotic factor to consider would be the impact of temperature on blooming of polymorphic flowers. This is particularly intriguing because, aside from providing heat for pollinators as a reward, overheating of flowers could damage pollen and impact male fitness of flowers. Climate change makes it pressing to better understand how color impacts temperature of flowers and how temperature affects color in flowers. Ambient light and background contrast in flower coloration are promising topics, especially coupled with the sensory drive hypothesis. An interesting way to study this topic would be to compare flower colors between the canopy and understory of forests, where light variation (blue sky and forest shade) and background variations (green leaves in the canopy and leaf litter in the understory) occur. Another promising model system would be to analyze patterns of flower coloration on deciduous environments, comparing flower colors of forests which lose their leaves in winter against those which lose leaves in summer. This model could also assist to understand the trade-off between conspicuity and resistance to extreme temperature.

Overall patterns of flower coloration across different habitats remain to be studied in many biomes and using pollinators other than bees as a visual model. Current studies show a prevalence of white and yellow flowers according to human vision and blue-green flowers according to bee vision. A coordinated studied (standardizing environmental variables such as biome, altitude, latitude), with replicable methodology around the world is still lacking and would add to our comprehension of the evolution of flower color. Studying how pollinators preference can change across seasons could also aid understanding the global pattern of flower coloration. Use of eavesdropper perspective on flower coloration is rare and could foster interesting findings in plant biology. Herbivores and other antagonists can also employ flower coloration to identify food sources. Several interesting questions can come from bringing herbivores to the spotlight of flower color evolution. How does the presence of flowers influence egg-laying in herbivore insects (such as Lepidoptera)? Are blooming plants more parasitized (*e.g.* have more galls) than non-blooming plants? Are plants with flowers of certain color more damaged by herbivores (or florivores) from a specific group (ie. grasshoppers prefer to eat plants with blue flowers)?

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