Artificial light changes visual perception by pollinators in a hawkmoth-plant interaction system

Corina Vissio[1] · Eugenia M. Drewniak[1] · Andrea A. Cocucci[1] · Marcela Moré[1] · Santiago Benitez-Vieyra[1] ·
Adrián Giaquinta[1] · Florencia Soteras[1]

Abstract

Night-flying pollinators, such as hawkmoths, are particularly vulnerable to the global spread of urban artificial lighting which is changing nighttime environments worldwide, impacting organisms and their interactions. Incident light quality can alter flower and leaf color perception by insects, depending on the emission spectra of light sources and the spectral sensitivity of insects. We asked, using *Manduca sexta* visual models, whether color contrast against natural backgrounds is altered by artificial lights for flowers and leaves of 16 plant species with an estimated long history of coevolution with hawkmoth pollinators. Specifically, we compared the perception of flowers and leaves by hawkmoths under artificial lights, including light-emitting diodes (5000 K LED), mercury vapor (MV), and high-pressure sodium (HPS) artificial lights, with the perception under natural illuminations. The models we implemented estimate that LED and HPS lighting change hawkmoth perception of flowers and leaves, with color loci appearing nearer to each other in hawkmoths perceptual space than they would be under natural nighttime conditions. Receptor Noise Limited models show that under the different lighting conditions hawkmoths would still discriminate flowers from their leaves in most but not all species. Consequently, artificial lights likely alter perception by hawkmoths of floral and leaf signals possibly affecting interactions and fitness of plants and pollinators. Our results emphasize the intricate and insidious ways in which human-made environments impact species interactions. Further studies should confirm whether light pollution represents a novel selective force to nocturnal interacting partners as emerging evidence suggests. Addressing the effects of artificial lighting is crucial for designing infrastructure development strategies that minimize these far-reaching effects on ecosystem functioning.

Keywords ALAN · Visual ecology · Hawkmoth · Light pollution · Nocturnal pollination

Introduction

Worldwide increase in artificial lighting associated with urbanization has been altering natural light regimes with concomitant effects on diurnal and nocturnal species behavior (Davies et al. 2013; Owens and Lewis 2018). One of the consequences of light pollution is the alteration of the circadian clocks of plants and insects (Gaston et al. 2013; Fenske et al. 2018) causing phenological decoupling between interacting partners (Warrant 2017) and affecting the reproduction of plants that partly or exclusively rely on nocturnal insect pollination (Giavi et al. 2021). Macromoths, such as hawkmoths (Lepidoptera: Sphingidae), are regarded among nocturnal pollinators as prominent pollinators of plant species in the wild (Walton et al. 2020). Hawkmoths are particularly remarkable for their co-adaptations with plants that largely depend on them for their reproductive success (Sazatornil et al. 2016). These nocturnal insects forage for nectar on deep night-blooming flowers that often emit perfume-like scents, produce abundant and low concentrated nectar, and often appear "white" to humans (Silberbauer-Gottsberger and Gottsberger 1975). Since hawkmoths are night active, and use color vision cues for foraging at night (Stöckl and Kelber 2019), light pollution might affect their pollination efficiency and indirectly influence fitness of hawkmoth-pollinated plant species (Bariles et al. 2021).

✉ Florencia Soteras
fsoteras@imbiv.unc.edu.ar

1 Laboratorio de Ecología Evolutiva y Biología Floral,
Instituto Multidisciplinario de Biología Vegetal (IMBIV),
CONICET and Universidad Nacional de Córdoba, Vélez
Sarsfield 1611 CC 495, Córdoba, Argentina

However, the mechanisms underlying the weakening or disruption of the hawkmoth-plant pollination interaction have been seldom studied (but see Briolat et al. 2021).

Hawkmoths use floral scents and visual signals to find the flowers they pollinate (Raguso and Willis 2002; Stöckl and Kelber 2019) and use the position of the moon, and other visual cues, to orient themselves for navigation and mating behavior (Storms et al. 2022; Warrant and Dacke 2011). Because spectral properties of an illuminant contribute to the light quality reflected by a surface, light sources with emission spectra different from natural sources could potentially modify hawkmoth behavior, impacting attraction to flowers (Owens and Lewis 2018), ability to learn, and motor control when hovering towards floral resources (Deora et al. 2021). This alteration might even prevent hawkmoth from visiting flowers (Macgregor et al. 2017). Also, light pollution adds to the environment light in wavelength ranges where hawkmoths are most sensitive, i.e. ultraviolet -UV-, blue -B-, and green -G- ranges of the spectrum (White et al. 2003; Goyret et al. 2008; van Langevelde et al. 2011; Longcore 2023).

The light sources that have been widely used for street lighting are high-pressure sodium (HPS) and mercury vapor (MV) lamps. Nowadays, these lamps are being globally replaced by light-emitting diodes (LED) as an alternative technology suitable to increase energy efficiency, reduce costs, and improve visibility by humans (Davies et al. 2013). Light emission of HPS is concentrated in the yellow-to-orange region of the visible spectrum; in addition, MV lights emit in the UV region of the light spectrum (Owens and Lewis 2018). In turn, LED lights, which do not emit in the UV region, consist of a monochromatic blue light irradiant that excites single yellow or multiple yellow-to-green phosphorescent coatings to create full-spectrum white visible light (Pimputkar et al. 2009; Pawson and Bader 2014). The proportion of blue and violet emitted by the underlying blue LED is correlated to the color temperature of LED lamps, e.g., 2700 K, 3000 K, and 5000 K, (Longcore et al. 2018).

Mercury vapor lights are known to be attractive to nocturnal insects, therefore hawkmoths may congregate and fly around these light sources causing them to perish due to exhaustion or exposure to predation (Straka et al. 2021). However, conflicting evidence related to LED lights attraction of nocturnal insects has shown high (Pawson and Bader 2014) to low (Van Grunsven et al. 2014) attraction due the wide range of LED spectral composition. For instance, adjusting spectra to white light, by minimizing blue light emission, reduced nocturnal insects attraction (Longcore et al. 2015; Deichmann et al. 2021). Therefore, response of nocturnal insects to different artificial light sources does not seem straightforward.

One of the possible mechanisms by which artificial light may impact plant-pollinator interactions is the impairment of visual perception by nocturnal insects (Briolat et al. 2021), with downstream effects on both pollinator and plant fitness (Gaston et al. 2013). For instance, artificial light might alter the perception by hawkmoths of plant leaves which are the adult egg-laying and caterpillars feeding substrates (Johnsen et al. 2006; Boyes et al. 2020). Artificial light could also change the perception of adults and caterpillars by predators, increasing their susceptibility to be eaten (Moyse et al. 2023). In addition, since floral coloration plays an important role in plant-pollinator communication, alterations in the sensory perception by pollinators are likely to impact interactions with specific floral resources, potentially jeopardizing plant reproduction (Briolat et al. 2021).

Nocturnal hawkmoths critically rely on visual signals such as corolla color as short-distance cues to succeed in finding nectar sources (Goyret et al. 2007; Raguso and Willis 2002; Stöckl et al. 2016). Adults modulate innate color preferences depending on environmental light intensities, turning to blue targets under starlight, to bright UV absorbing ones under twilight, and to targets that highly contrast with the background under moonlight (Kuenzinger et al. 2019). Using the visual model of the hawkmoth *Deilephila elpenor*, Briolat et al. (2021) provided the first evidence that floral signal perception by hawkmoths changes depending on the type and intensity of artificial light as well as on flower color in numerous native and exotic plant species with various pollination syndromes that attract hawkmoths. For instance, in terms of chromatic contrast, hawkmoth perception of white and yellow flowers did not change substantially under HPS light as compared to natural lighting irrespective of light intensity. However, perception of pink and purple flowers under HPS varied with respect to light intensity since chromatic contrasts increased at the high light intensity and diminished at low light intensities as compared to natural lighting (Briolat et al. 2021).

Several Neotropical hawkmoth-pollinated plants are estimated to have a 1.4 to 7 million year long shared coevolutionary history with their partner pollinators (Aoki and Ito 2000; Reck-Kortmann et al. 2014; Moré et al. 2015; Clarkson et al. 2017; Gagnon et al. 2019; Kariñho-Betancourt et al. 2022). Therefore, since the onset of their divergence, these plants and pollinators might have engaged in specialized relationships, with reciprocally adjusted signaling and visual traits playing key roles in the success of interaction partners. For some such coevolved plant species exclusively dependent on hawkmoths for reproduction, it has been shown that pollination is indirectly affected by light intensity (Soteras et al. 2020; Bariles et al. 2021), but the ultimate mechanisms underlying this pattern remain unknown. In addition, there is a lack of information on whether flower

color discrimination by hawkmoths under light pollution is influenced by different natural background surface colors (Lind 2016; Bukovac et al. 2017), or if the discrimination of leaves can be modified under different artificial lights. The latter is relevant for egg-laying substrate detection, particularly when an herbivorous pollinator uses the same plant species as both source of nectar for adults and food source for caterpillars (Kessler et al. 2010; Balbuena et al. 2022).

In this study, we hypothesized that light pollution is altering visual perception of flowers and leaves by hawkmoths. Additionally, emission spectra of different artificial light types and reflective properties of different backgrounds may affect visual discrimination of flowers and leaves by hawkmoths. We predict that artificial lights that stimulate the three photoreceptors of hawkmoths (e.g. MV) would alter the perception of flowers and leaves by hawkmoths less than artificial lights that only stimulate some of hawkmoths photoreceptors (e.g. HPS and 5000 K LED). In order to test these hypotheses here we explored whether flowers of 16 hawkmoth-pollinated plant species could be distinguished from leaves by hawkmoths under a set of natural and artificial lighting scenarios. This comparison was performed considering different background surfaces, i.e. green, soil, sand, and gravel. We chose representative plant species from Subtropical Argentina, a region where hawkmoth pollination is widespread (Moré et al. 2014) and where urbanization is currently transforming the landscape (Bariles et al. 2021; Galfrascoli et al. 2023). In addition, we performed pairwise comparisons between natural and artificial light sources in order to assess whether perception by hawkmoths of flowers and leaves themselves would change against the different backgrounds. For all the analyses, we considered the visual system of *Manduca sexta*, a Central American hawkmoth species closely related to the main pollinators of the target plant species studied.

Materials and methods

Spectral processing

To assess chromatic contrasts between flowers and leaves against four backgrounds (i.e. green, soil, sand, and gravel; Figure S1a) as perceived by *Manduca sexta* (Lepidoptera: Sphingidae) under different light sources (Figure S1b), we obtained flower and leaf spectra of 16 plant species (Fig. 1, Table S1).

Among the 16 hawkmoth-pollinated plant species studied, 14 are native to Argentina: *Mandevilla laxa* Woodson, *M. petraea* (A.St.-Hil.) Pichon (Apocynaceae), *Tillandsia xiphioides* Ker Gawl. (Bromeliaceae), *Soehrensia candicans* Gillies ex Salm-Dyck Schlumpb. (Cactaceae),

Erythrostemon gilliesii (Hook.) Klotzsch (Fabaceae), *Oenothera affinis* Cambess., *Oenothera picensis* Phil. (Onagraceae), *Petunia axillaris* (Lam.) Britton, Sterns & Poggenb., *Nicotiana longiflora* Cav., *Cestrum parqui* (Lam.) L'Hér., *Jaborosa integrifolia* Lam., *J. odonelliana* Hunz., *J. runcinata* Lam. (Solanaceae), and *Glandularia platensis* Spreng. (Verbenaceae); and two species are naturalized exotics growing spontaneously in Argentina: *Mirabilis jalapa* L. (Nyctaginaceae) -the white color morph-, and *Lonicera japonica* Thunb. (Caprifoliaceae) -the white flower stage-. All selected species exhibit flower traits associated with hawkmoth pollination and are known to be pollinated by an assemblage of long-tongued nocturnal hawkmoths, including several species closely related to *Manduca sexta* (Moré et al. 2014; Fig. 1).

Flower reflectance was measured from one to 10 individuals per species and one to three flowers per individual, the average spectrum of each species was used for further analyses. Leaf spectra were measured from one to four leaves per individual of the 16 focal species. Since focal plant species usually include herbs or lianas that may grow on a variety of backgrounds (Table S1), e.g. on exposed soil, sand or gravel or over the foliage of other plant species, the inclusion of different natural backgrounds is important to estimate pollinator-perceived color contrast in natural environments (Bukovac et al. 2017). Therefore, we included in the visual models four possible natural backgrounds: green (average spectra of leaves from all the species), soil, sand, and gravel (two to four replicates per surface type; Figure S1a).

Light reflected by flower corollas, leaves, soil, sand, and gravel was measured with an Ocean Optics USB4000 spectrophotometer equipped with a pulsed xenon light source with a light emission range between 220 and 750 nm, and a UV-visible reflection/backscatter probe that comprises high hydroxyl UV-visible fibers with a wavelength range between 300 and 1100 nm. The probe was attached to a prismatic holder at 45° to avoid specular reflectance and placed at one mm from the object surface. A white standard (WS-1-SS, Ocean Optics Inc.) was used as a 100% reflection reference and to re-calibrate the equipment after each sample measurement in order to correct for possible shifts in spectrophotometer performance (Chittka and Kevan 2005). We used SpectraSuite spectroscopy software (Ocean Optics, Inc., Dunedin, FL, USA) for data acquisition with a boxcar width set at 50 nm and an integration time at 5 s per scan. Reflectance spectra were processed and visualized using the pavo 2.2.0 package (Maia et al. 2019) of R software (R Core Team 2022). Spectra were trimmed using *as.rspec* function to the range from 300 to 700 nm, to include the hawkmoth vision range (Bennett and Brown 1985).
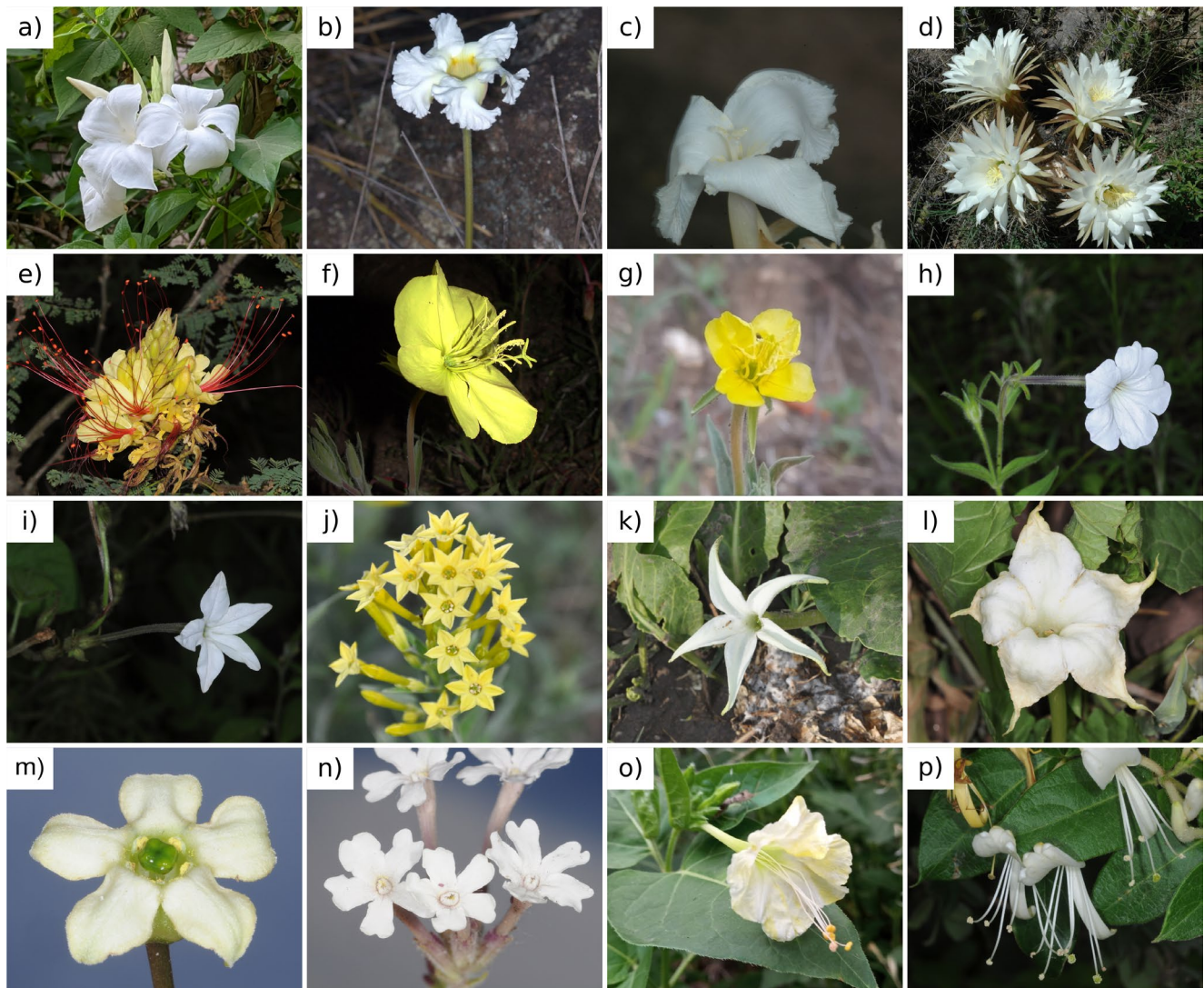
Fig. 1 Flowers of hawkmoth-pollinated plant species included in this study. (**a**) *Mandevilla laxa*, (**b**) *M. petraea*, (**c**) *Tillandsia xiphioides*, (**d**) *Soehrensia candicans*, (**e**) *Erythrostemon gilliesii*, (**f**) *Oenothera affinis*, (**g**) *Oenothera picensis*, (**h**) *Petunia axillaris*, (**i**) *Nicotiana longiflora*, (**j**) *Cestrum parqui*, (**k**) *Jaborosa integrifolia*, (**l**) *J. odonelliana*, (**m**) *J. runcinata*, (**n**) *Glandularia platensis*, (**o**) *Mirabilis jalapa* (white color morph), and (**p**) *Lonicera japonica*

Visual modeling

We modeled corolla perception in the visual system of *Manduca sexta* because most of the focal plant species are known to be pollinated in Argentina by closely related *Manduca* species. It is worth mentioning that *M. sexta* has recently been split into two species: the North and Central American *M. sexta* and the South and Central American *M. paphus* (Haxaire 2019; Kitching 2022). *Manduca sexta* is considered a model organism (Bennett and Brown 1985; Cutler et al. 1995; Goyret et al. 2007, 2008), and results from its visual system are broadly generalized to other crepuscular hawkmoth species (Goyret et al. 2008; Moré et al. 2020).

We examined variation in modeled corolla color perception by nocturnal hawkmoths under a set of natural and artificial light sources and against different backgrounds. Hawkmoths have compound eyes with three photoreceptor types, most sensitive in the ultraviolet (UV), blue (B), and green (G) ranges of the spectrum (White et al. 1994). We used *Manduca sexta* peak photoreceptor sensitivity maxima (UV = 357 nm, B = 450 nm, and G = 520 nm, Bennett and Brown 1985) to obtain sensitivity curves with the *sensmodel* function and to calculate quantum catches for each photoreceptor type using the *vismodel* function.

To depict color in perceptual spaces, quantum caches were used to place color loci in a Maxwell triangle (Renoult et al. 2017). In the thus constructed perceptual space, each corner of the triangle corresponds to a pure color that maximally excites one of the three photoreceptor types of the hawkmoth eye (Renoult et al. 2017). The location of a color locus

in the triangle represents the relative excitation of the three receptor types by a floral or leaf sample (Balkenius et al. 2004). We estimated quantum catches of each photoreceptor by incorporating a von Kries transformation. This transformation normalizes quantum catches as chromatic contrasts relative to the background, thus accounting for receptor adaptation to the background (Maia et al. 2019). Given photoreceptor adaptation, background color is assumed to excite the three photoreceptors equally thus appearing in the center of the Maxwell triangle. The role of background adaptation on stimulus discrimination has been investigated for bees, in which a wide range of natural surface colors can shift the perception of floral stimuli (Bukovac et al. 2017). Similarly, hawkmoth innate visual sensory biases can be modified by the context in which signals are perceived, depending on illuminance and background (Goyret et al. 2008; Kuenzinger et al. 2019). Therefore, considering that hawkmoth-pollinated flowers are naturally perceived against different backgrounds, the inclusion of a variety of background colors is relevant to study the influence of visual signal changes in the context of light pollution.

We estimated corolla conspicuousness for *M. sexta* under the Receptor Noise Limited (RNL) model of Vorobyev and Osorio (1998), in terms of chromatic contrasts against leaves (this included comparisons within species of their flowers color and leaf), against green (color averaged across all species' leaves), soil, sand, and gravel as backgrounds, and under the different light sources. The RNL model assumes that the simultaneous discrimination of colors is fundamentally limited by photoreceptor noise. Color distances under the RNL model depend on the signal-to-noise ratio and on the number of receptors per receptive field (known as the Weber fraction), as well as on photoreceptor densities (Vorobyev and Osorio 1998). In this study, we used the following parameters to model chromatic contrast: Weber fraction = 0.1, the level measured in honeybees (Olsson et al. 2018) and previously used for the tiger moth *Arctia plantaginis* (Henze et al. 2018). Photoreceptor densities were set as: UV = 0.1, B = 0.23, G = 0.67, based on data from the ratio of the three rhodopsins of ventral portion of the compound eye of *M. sexta* (White et al. 2003). Under low light intensities, hawkmoths might perceive floral resources via the achromatic aspect of signal, which is related to the "brightness" of the stimulus (van der Kooi and Kelber 2022). Achromatic vision of hawkmoths is assumed to be based only on the longest-wavelength green photoreceptor (Telles et al. 2014). Therefore, the achromatic contrast was calculated as the contrast produced in the long wavelength photoreceptor (Henze et al. 2018), considering a Weber fraction of 0.16 (Olsson et al. 2018).

It is important to caution that visual models as implemented in our study are based on measurements taken at high light intensity levels and using equations designed for vision in daylight, with receptor noise being the key source of noise (Vorobyev and Osorio 1998; Johnsen et al. 2006). There are two further sources of noise that also degrade visual discrimination by photoreceptors in dim light (i.e. "transducer noise" and "dark noise") related to the biochemical mechanisms of photoreceptors (Warrant and Somanathan 2022). Since this information is still not available for most species, our approach provides a preliminary insight into the visual discrimination of leaves and flowers by hawkmoths in nocturnal environments. As illuminant we obtained, from Briolat et al. (2021) and references therein, spectra of three natural light sources (i.e. full moon light, starlight, and twilight; Figure S1b) and three artificial lights (i.e. MV, LED 5000 K, and HPS; Figure S1b).

To assess (i) whether corollas are discriminable from leaves in the hawkmoth visual system against possible backgrounds for each light source and, (ii) whether corollas and leaves are perceived by hawkmoths as distinct in color depending on the light source, we estimated all the pairwise chromatic (Delta-S) and achromatic (Delta-L) contrasts with *coldist* function from pavo package. Two objects are predicted to be discriminable when the chromatic or achromatic contrast exceeds one distance unit or Just Noticeable Difference (i.e. > 1 JND). By using the *bootcoldist* function, we calculated the bootstrapped confidence intervals for mean distances.

Subsequently, we converted chromatic distances from Delta-S to noise-corrected Cartesian coordinates with the *jnd2xyz* function following Maia and White (2018). These coordinates were used in a multi-response permutation procedure using a PERMANOVA with the *adonis2* function of the vegan package (Oksanen et al. 2022) where each observed pairwise mean color distance was compared with a distribution obtained by randomly assigning observed colors among samples. An observed distance greater than 95% of the 1,000 pseudo-values obtained was considered significant. Before the PERMANOVA analysis, a distance-based test of homogeneity of within-group dispersions was performed using the function *betadisper*.

Finally, we performed pairwise comparisons among natural and artificial lighting scenarios, considering the configurations of color loci in the hawkmoths' visual space. This was done by comparing the corresponding matrices of noise-corrected Cartesian coordinates through a PROTEST using the *procrustes* function from the vegan package. Procrustean randomization test allows for the comparison of configurations with the same loci across different multivariate data sets. This procedure examines concordance between both matrices by scaling and rotating the configurations until maximum similarity is achieved, that is, when the minimum sum-of-squared difference between the two configurations

in a multivariate Euclidean space is reached (Peres-Neto and Jackson 2001). The significance of congruence between matrices was estimated after 999 permutations.

Results

Reflectance spectra

Overall, most studied species showed corollas with reflectance that remained almost entirely constant (30–80% of white standard) between 450 and 700 nm, i.e. perceived as white and yellow by human vision, with the exception of the yellow-flowererd *E. gilliesii*, *O. affinis*, and *O. picensis*. (Fig. 1, and 2a). Most species showed corollas reflecting relatively little in the UV-region of the spectrum (between 300 and 399 nm) except for the yellow-flowered species which had reflection peaks of 25–50% in the UV-region (Fig. 2a). Leaf reflectance spectra of most focal species showed maximum reflectance (10–30%) between 500 and 600 nm. However, *T. xiphioides* leaves showed maximum reflectance (60–70% of white standard) between 450 and 700 nm, i.e. perceived as white by humans (Fig. 2b).

Fig. 2 (**a**) Corolla and (**b**) leaf reflectance spectra of hawkmoth-pollinated native and exotic plant species spontaneously growing in central Argentina. Each spectrum is averaged from 1 to 4 samples. Symbols beside species names indicate flower color according to human vision
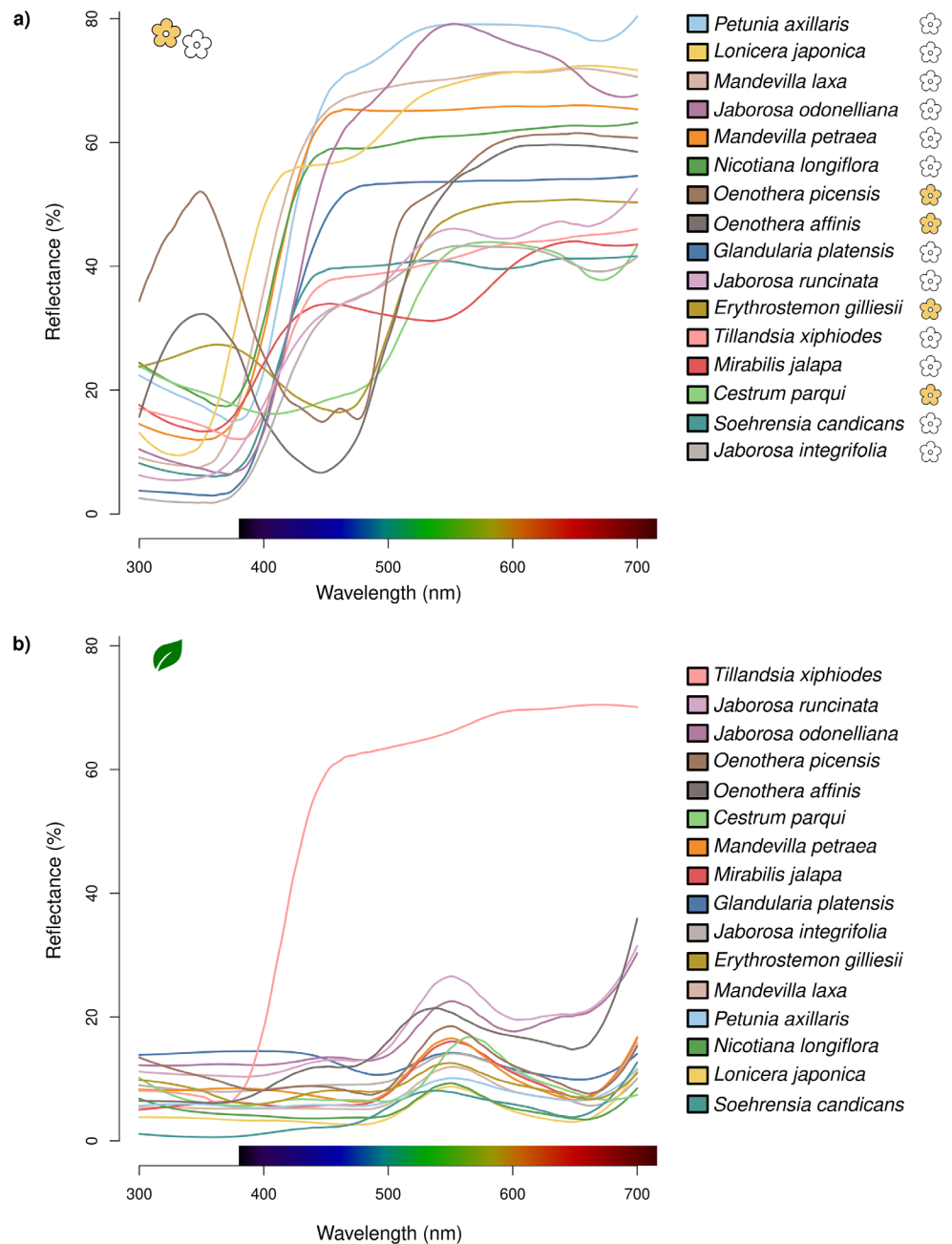
Models of color discrimination by hawkmoths

According to the flower loci configuration in the *M. sexta* perceptual space, hawkmoth-pollinated species would be perceived as colorful objects against green background under natural illumination and MV artificial lighting (Fig. 3a-c, and 3e). Under these lighting conditions, the modeled color loci of flowers perceived as white by humans were clustered together in the blue-green region, while the loci of yellow flowers and the majority of green leaves clustered around the center of the Maxwell triangle (Fig. 3a-c, and 3e). Under 5000 K LED and HPS artificial lights, floral color loci showed different locations in the hawkmoth visual space, with most of the species being clustered around the green, such that they would not differ from leaves (Fig. 3d and f). Maxwell triangles with the other three natural backgrounds broadly agreed with results of green background (Figure S2).

When analyzing color loci distribution in the Cartesian coordinates, we evidenced significant differences between flowers and leaves under every natural illumination and MV artificial light against green background, according to a PERMANOVA analyses (Fig. 4a-c, and e). Color loci distribution in the Cartesian coordinates with the other three natural backgrounds broadly agreed with results of green background (Figure S3). Therefore, flowers should be discriminable from leaves against the four backgrounds by hawkmoths under these light scenarios. However, under 5000 K LED and HPS artificial lights color loci of flower and leaves were not significantly different, suggesting that hawkmoths would not be able to discriminate flowers from leaves under these light sources (Fig. 4d and f, Figure S3).

When considering the theoretical threshold for color discrimination by hawkmoths (JND = 1), visual models predicted that flowers would be discriminated from leaves against the four backgrounds under the three natural illuminations and the MV and HPS lights (Fig. 5). Under the 5000 K LED artificial light, hawkmoths are also predicted to overall discriminate flowers from leaves, but the flowers of some species would not be distinguished from leaves (Fig. 5). Particularly, flowers of one of the yellow-flowered species, i.e. *C. parqui*, were not different from leaves in the hawkmoth visual models under any light sources (Fig. 5b). However, flowers of this species might be distinguished from leaves through the achromatic aspect of signal (Fig. 6). In fact, visual models for all plant species predicted that hawkmoths would distinguish flowers from leaves via the achromatic aspect of signal (Fig. 6).

Comparisons of hawkmoth perception models between lighting scenarios

Correlation in Procrustes rotation of noise-corrected Cartesian coordinates of flowers and leaves against green

Fig. 3 Floral and leaf color loci of hawkmoth-pollinated plant species in the trichromatic perceptual space of *Manduca sexta* against green foliage (black square at the center) under different natural (**a**, **b**, and **c**) and artificial (**d**, **e**, and **f**) light sources. The vertices of the Maxwell triangle represent pure color that fully excite each of the three photoreceptor types (UV = ultraviolet, G = green, and B = blue)
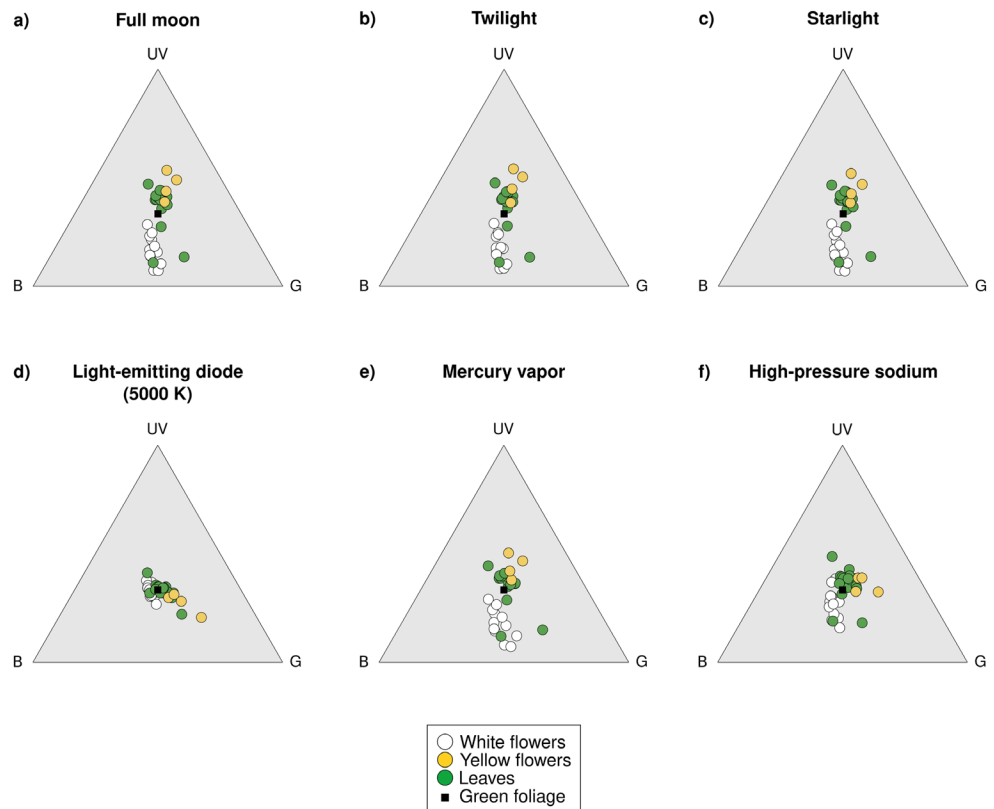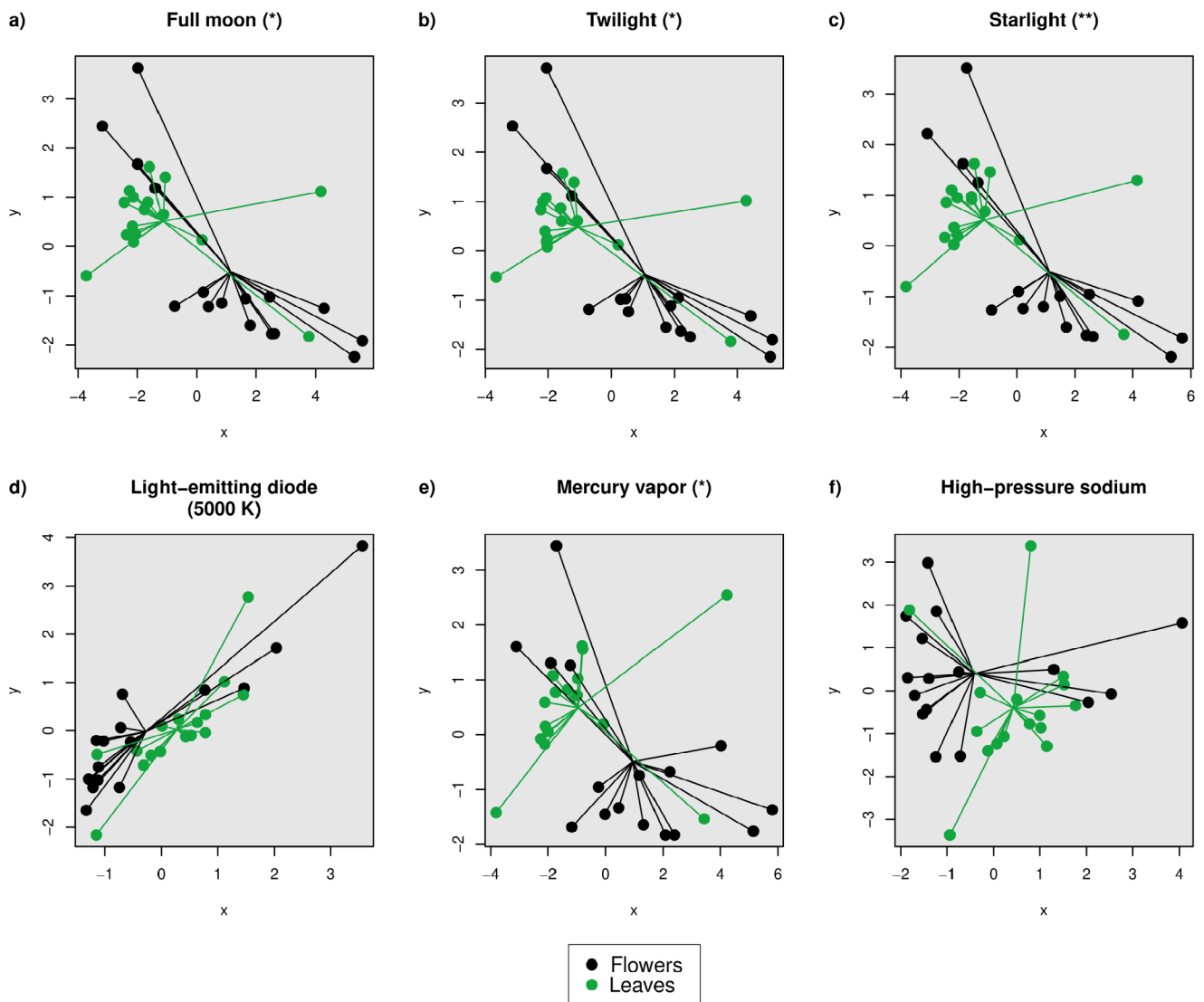
Fig. 4 Noise-corrected Cartesian coordinates of the chromatic distances between flowers (black dots linked to their group centroid) and leaves (green dots linked to their group centroid) in the hawkmoth-pollinated plant species against green foliage, under natural (**a**, **b**, and **c**) and artificial (**d**, **e**, and **f**) light sources. Significance levels estimated with PERMANOVA test (**, $P < 0.01$; *, $P < 0.05$) indicate significant difference between groups

background was higher between pairwise comparisons of natural light sources and between natural light sources and MV artificial light (Fig. 7). Contrastingly, the correlation was low when performing pairwise comparisons between natural light and 5000 K LED light sources, which might be evidence of a significant change in the perception of flowers and leaves by hawkmoths when the natural environment is illuminated by 5000 K LEDs. In the case of flowers, HPS also showed low correlation with natural light sources (Fig. 7a). These results do not change when considering the other three natural backgrounds.

The Procrustean errors for each species represent the shift in color loci distribution between two lighting scenarios; higher errors indicate greater divergence between distributions (Fig. 8). According to Procrustean errors against green background, the greatest shift in modeled hawkmoths perception was in the scenario comparison full moon vs. 5000 K LED (Fig. 8), and the smallest in the comparison full moon vs. MV (Fig. 8). The 5000 K LED and HPS artificial lights mainly changed the modeled perception by hawkmoths of white flowers (six out of the twelve white species for 5000 K LED and seven out of twelve for HPS; Fig. 8). In consistency with changes in flower perception by hawkmoths between light scenarios, the comparison between full moon and 5000 K LED, as well as the comparison between full moon and HPS scenarios, showed the highest Procrustean errors for leaf perception (Fig. 9). On the other hand, full moon vs. MV scenarios showed the

Fig. 5 (**a**) Mean flower-leaf chromatic contrasts (Delta-S) with bootstrapped 95% confidence intervals within species comparisons and (**b**) flower-leaf chromatic contrasts (Delta-S) values per species under different natural and artificial light sources against green foliage as background. The dashed line represents the theoretical discrimination threshold of 1 JND. Flower symbols in the panel below represent the flower color of each species according to human vision
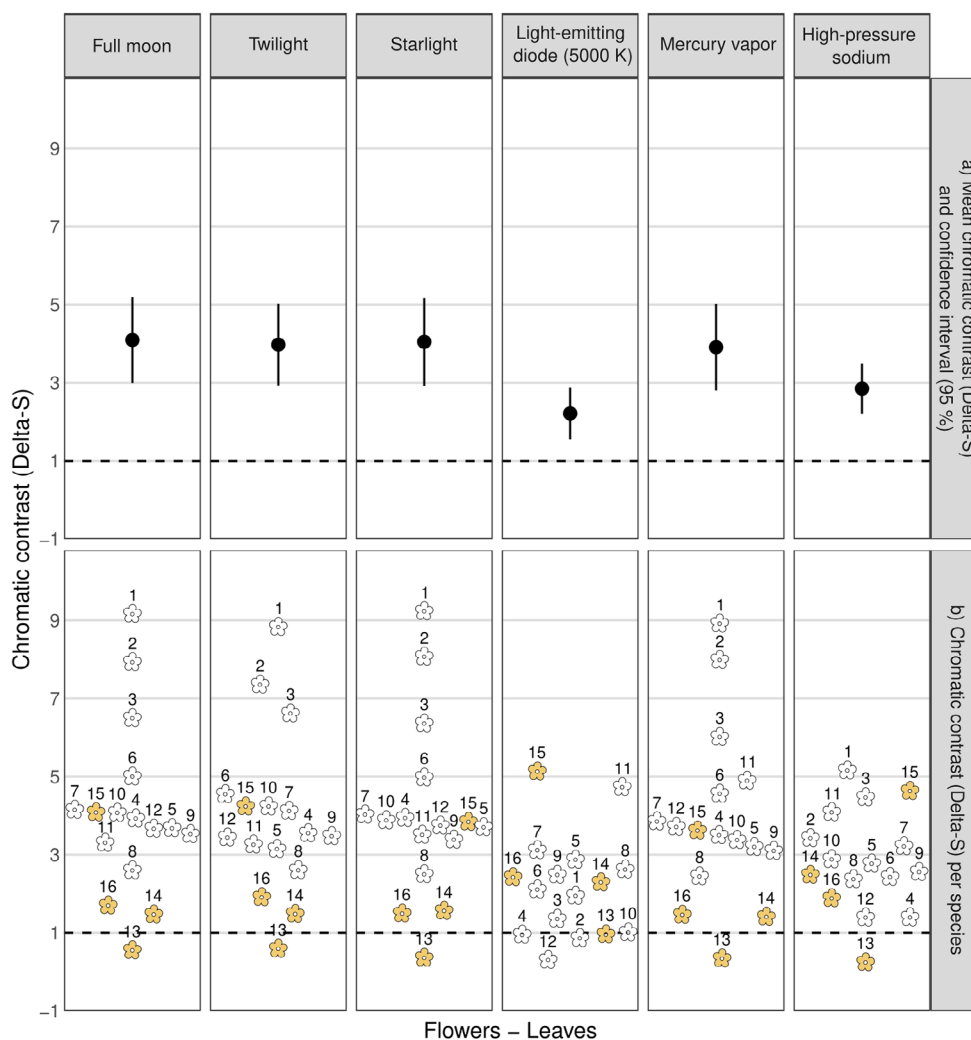
1) *Glandularia platensis*
2) *Jaborosa integrifolia*
3) *Jaborosa odonelliana*
4) *Jaborosa runcinata*
5) *Lonicera japonica*
6) *Mandevilla laxa*
7) *Mandevilla petraea*
8) *Mirabilis jalapa*
9) *Nicotiana longiflora*
10) *Petunia axillaris*
11) *Soehrensia candicans*
12) *Tillandsia xiphiodes*
13) *Cestrum parqui*
14) *Erythrostemon gilliesii*
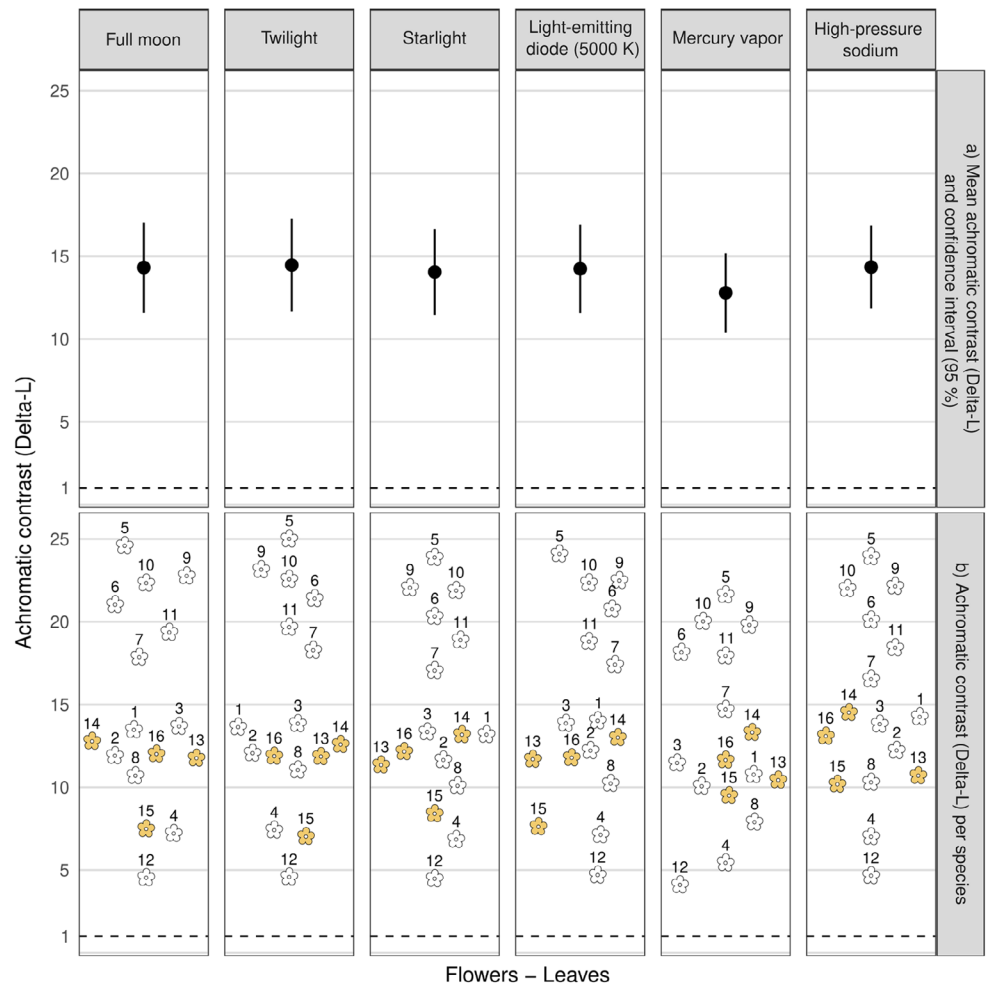15) *Oenothera affinis*
16) *Oenothera picensis*

smallest Procrustean errors (Fig. 9). These results agreed with the other pairwise comparisons between natural and artificial light sources against the other natural backgrounds.

Discussion

Our results provide evidence that artificial light may influence the visual perception by hawkmoths of flowers and leaves of species that belong to the guild of hawkmoth-pollinated plants in Subtropical Argentina, most of which are predicted to have a long history of coevolution with hawkmoths. Based on the visual models, two of the currently used artificial lights, namely 5000 K LED and HPS, have the potential to significantly alter hawkmoth perception of flowers and leaves against the four backgrounds that were tested (i.e. green, gravel, sand, and soil). Under these artificial light sources, floral color loci of most of the hawkmoth-pollinated plant species were clustered around the green background, suggesting that hawkmoths might be unable to discriminate flowers from leaves. In addition, when comparing pairwise natural and artificial lighting scenarios, we evidenced that 5000 K LED and HPS lights mainly changed hawkmoth perception of flowers that are perceived as white

Fig. 6 (**a**) Mean flower-leaf achromatic contrasts (Delta-L) with bootstrapped 95% confidence intervals within species comparisons and (**b**) flower-leaf achromatic contrasts (Delta-L) values per species under different natural and artificial light sources against green foliage as background. The dashed line represents the theoretical discrimination threshold of 1 JND. Flower symbols in the panel below represent the flower color of each species according to human vision
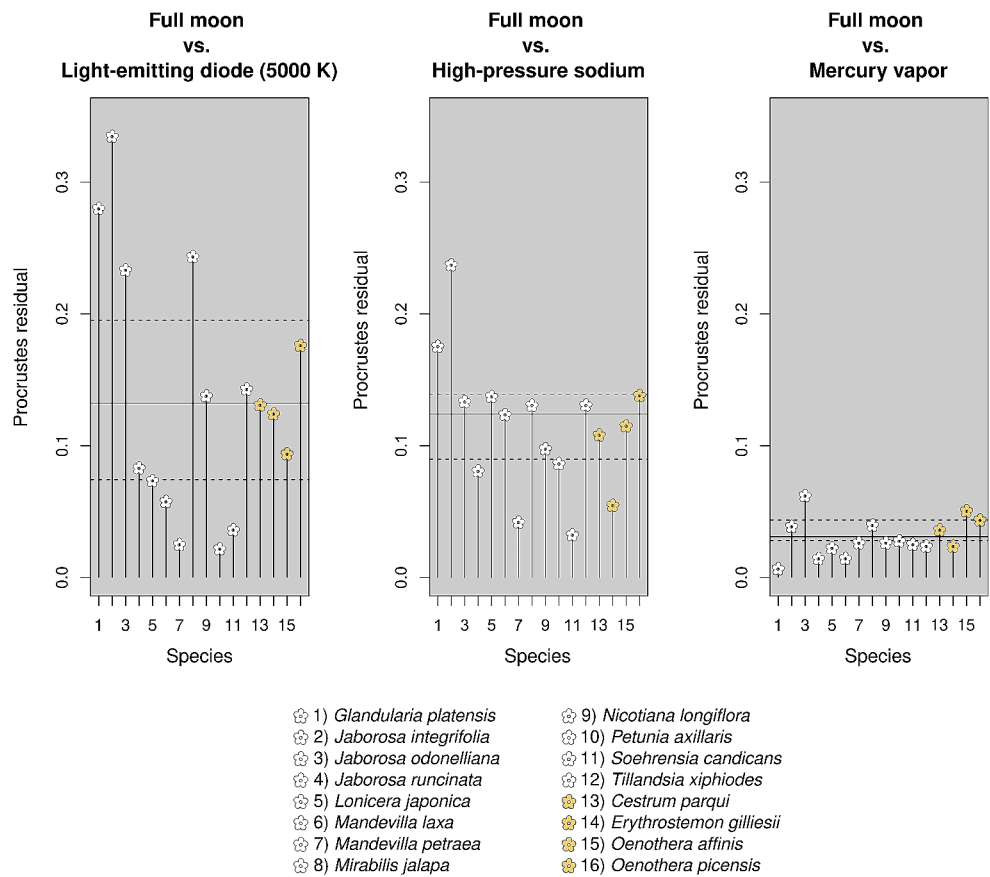

1) *Glandularia platensis*
2) *Jaborosa integrifolia*
3) *Jaborosa odonelliana*
4) *Jaborosa runcinata*
5) *Lonicera japonica*
6) *Mandevilla laxa*
7) *Mandevilla petraea*
8) *Mirabilis jalapa*
9) *Nicotiana longiflora*
10) *Petunia axillaris*
11) *Soehrensia candicans*
12) *Tillandsia xiphiodes*
13) *Cestrum parqui*
14) *Erythrostemon gilliesii*
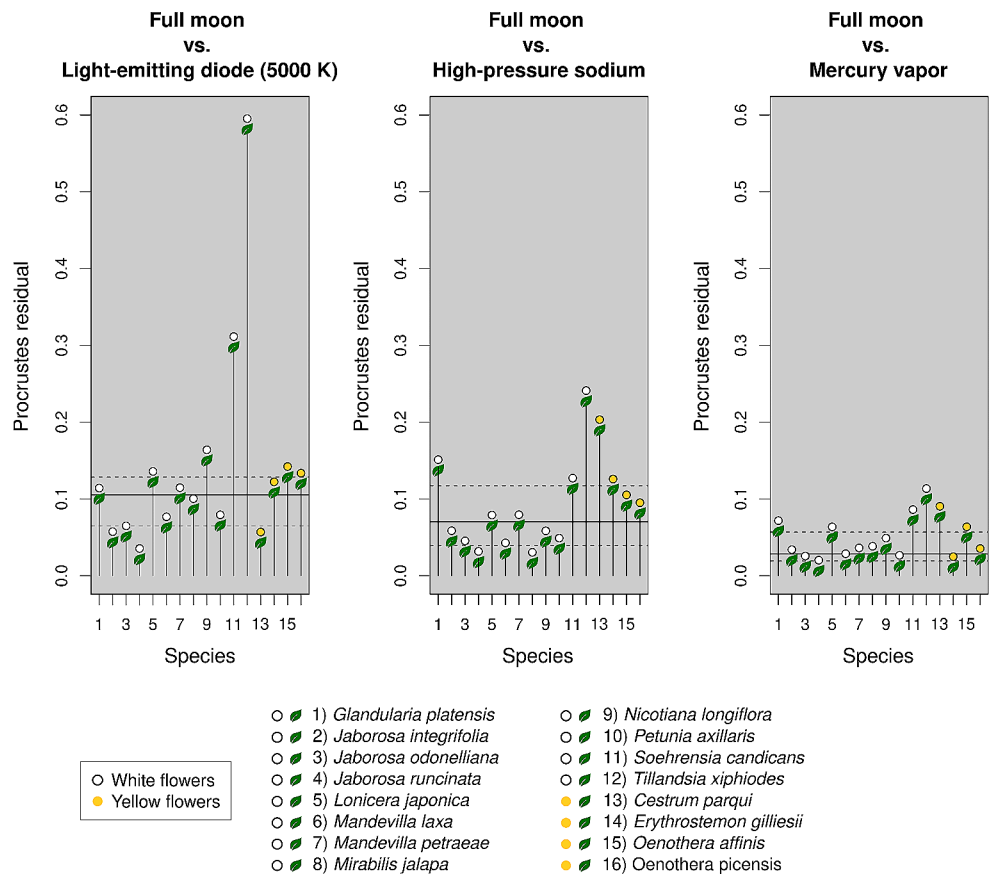15) *Oenothera affinis*
16) *Oenothera picensis*

Fig. 7 Pairwise matrix comparisons between lighting scenarios of color loci configurations with Procrustean rotation using noise-corrected Cartesian coordinates and green foliage as background for (**a**) flowers and (**b**) leaves
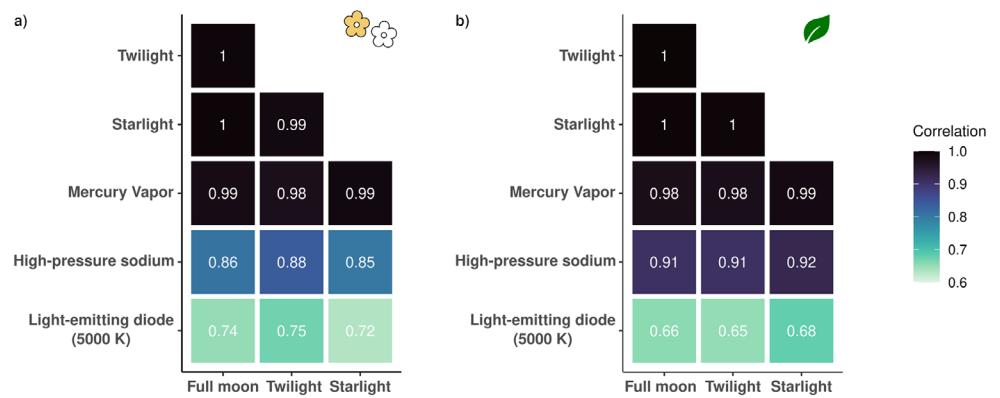
Fig. 8 Procrustean residuals of noise-corrected Cartesian coordinates of flowers in the perceptual space of *Manduca sexta* between full moon and each artificial light. Horizontal lines, from bottom to top, represent the 25% (dashed), 50% (solid), and 75% (dashed) quantiles of the residuals. Flower symbols at the top of each vertical line represent the flower color of each species

1) *Glandularia platensis*   9) *Nicotiana longiflora*
2) *Jaborosa integrifolia*   10) *Petunia axillaris*
3) *Jaborosa odonelliana*   11) *Soehrensia candicans*
4) *Jaborosa runcinata*   12) *Tillandsia xiphiodes*
5) *Lonicera japonica*   13) *Cestrum parqui*
6) *Mandevilla laxa*   14) *Erythrostemon gilliesii*
7) *Mandevilla petraea*   15) *Oenothera affinis*
8) *Mirabilis jalapa*   16) *Oenothera picensis*

Fig. 9 Procrustean residuals of noise-corrected Cartesian coordinates of leaves in the perceptual space of *Manduca sexta* between full moon and each artificial light. Horizontal lines, from bottom to top, represent the 25% (dashed), 50% (solid), and 75% (dashed) quantiles of the residuals. Dot colors at the top of each vertical line represent the flower color of each species

○ White flowers
● Yellow flowers

1) *Glandularia platensis*   9) *Nicotiana longiflora*
2) *Jaborosa integrifolia*   10) *Petunia axillaris*
3) *Jaborosa odonelliana*   11) *Soehrensia candicans*
4) *Jaborosa runcinata*   12) *Tillandsia xiphiodes*
5) *Lonicera japonica*   13) *Cestrum parqui*
6) *Mandevilla laxa*   14) *Erythrostemon gilliesii*
7) *Mandevilla petraeae*   15) *Oenothera affinis*
8) *Mirabilis jalapa*   16) Oenothera picensis

by humans. Therefore, visual signals might be modified by artificial lights which could potentially influence the interaction between hawkmoths and plants, and affect plant fitness (Macgregor et al. 2017; Bariles et al. 2021). Although MV lights might not substantially change hawkmoth perception of flowers in comparison with natural light sources, these artificial light sources which emit in the UV region of the light spectrum are particularly attractive to nocturnal insects and could be affecting the spatial orientation of hawkmoths and distracting them away from the flowers they pollinate (Gaston et al. 2013; Van Grunsven et al. 2014). Mercury vapor artificial lights have been depicted as stronger negative drivers for species richness and abundance of nocturnal macro-moths in comparison with LED lights, probably due to the effect of MV lights on nocturnal insect behavior (Straka et al. 2021).

In the case of leaves, a similar pattern of change was predicted according to the models, with primarily 5000 K LED and HPS lights changing the perception by hawkmoths of leaves against every background. Plant leaf color is relevant in hawkmoth ecology as a visual stimulus since adults use leaves as egg-laying substrate and diurnal roosting places (Boyes et al. 2020). Furthermore, hawkmoth species often are pollinators and herbivores of species belonging to the same family, and some of them are even both pollinators and herbivores of the same species. For instance, *Hyles* sp. caterpillars feed on leaves of *Oenothera* spp. and *Manduca* spp. caterpillars on *Nicotiana* spp., while simultaneously pollinating their flowers (Kessler et al. 2010; Balbuena et al. 2022). Therefore, the alteration of hawkmoth perception by light pollution might affect the ability of hawkmoths to both handle flowers they pollinate and choose suitable egg-laying substrates.

Similar to a recent study on the floral perception by hawkmoths of plant species belonging to various pollination syndromes that are visited by hawkmoths (Briolat et al. 2021), our findings provide evidence that the visual detection of hawkmoth-pollinated plants which have coevolved with hawkmoth pollinators is also influenced by artificial light. Our findings align with the observations of Briolat et al. (2021) under high light intensities when comparing artificial lights with moonlight. They evidenced that the chromatic contrast between white/yellow flowers and leaves under 5000 K LEDs is near to the theoretical threshold, in contrast to moonlight, where the chromatic contrast show higher values. In addition, similar to our results, they found that white/yellow flowers show similar chromatic contrast values under moonlight, MV and HPS lights. There is evidence that pollination by hawkmoths decreases in highly light-polluted environments and near to the brightest light source (Soteras et al. 2020; Bariles et al. 2021). Therefore, the effect of light pollution on pollinator activity through the

alteration of the visual ecology of hawkmoths could even reverberate meters away from the light source (Briolat et al. 2021).

As well as artificial lights, natural illuminations show different light intensities, increasing up to two orders of magnitude from starlight to full moonlight (Johnsen et al. 2006). Under low light intensities, hawkmoths might perceive floral resources by the "brightness" of stimulus, using the achromatic channels (van der Kooi and Kelber 2022). When comparing different light intensities, Briolat et al. (2021) evidenced that under low intensities of natural and artificial illuminations, flowers were undistinguishable from leaves by *D. elpenor* via the chromatic aspect of color (Briolat et al. 2021). However, Johnsen et al. 2006 observed that the achromatic contrast of flowers and leaves under different illuminations with varying intensities depended on the stimulus. For instance, white flowers were brighter than leaves under full moon, starlight and light pollution. Meanwhile, yellow flowers were only brighter than leaves under light pollution (Johnsen et al. 2006). Under natural and artificial light scenarios compared in our study, flowers and leaves of hawkmoth-pollinated plant species showed high achromatic contrasts. Therefore, when chromatic contrast is reduced by light pollution (e.g. some species under LED light), brightness might still help hawkmoths to recognize flowers from leaves through the achromatic aspect of signal. It would be interesting to further test the perception of flowers and leaves under different light intensities considering the achromatic aspect of color beside the chromatic contrast.

Manduca sexta adults have spectral sensitivity between 10 and 100 times higher for blue light than for lights of longer wavelengths in the context of feeding and show an innate preference towards blue (Cutler et al. 1995). These sensory biases are innate, but can be modified by the context in which signals are perceived, depending on illuminance and background (Goyret et al. 2008; Kuenzinger et al. 2019). As is expected for insects that are active during different natural light conditions such as dawn and dusk, hawkmoths are able to recognize the same flower color under changing illumination spectra (Balkenius et al. 2004). However, the ability of finding flowers is known to be impaired when the illumination changes even though flowers can still be correctly chosen (Balkenius et al. 2004). It is important to consider that after discriminating flowers from the background hawkmoths have to cope with the visual guides of within-flower nectar localization, which involves visual in addition to mechanical senses (Goyret and Raguso 2006; Deora et al. 2021). Consequently, light pollution might influence hawkmoths ability to efficiently handle and pollinate flowers, influencing fitness of both hawkmoths and hawkmoth-pollinated plant species. It should be further explored whether

new selective forces are being imposed to both hawkmoths and hawkmoth-pollinated plants by artificial lighting.

High pressure sodium and MV lamps widely used for street lighting, are being progressively replaced by more energy-efficient and more affordable LED technologies (Gaston et al. 2013). Currently, particularly in Argentina, artificially illuminated environments include both new and older technologies, such as LED and MV. Although hawkmoths might learn to recognize visually-changed floral signals (Goyret et al. 2008), they might have to process contrasting visual signals every night of their lives. Therefore, a modified anthropic environment with a mixture of new and older technologies is probably altering hawkmoth activity. Searching images learned under one lighting scenario may negatively condition the search of plant sources under another scenario, thus likely affecting both insect and plant fitness. Further testing is needed to assess whether mixed artificial illuminations impair the search of floral resources more than a single kind of artificial light source.

Some recommendations can be considered in the light of the present findings. To reduce the impact on the visual ecology of nocturnal insects, such as hawkmoths, the planning of artificial lighting should aim to minimize the use of any artificial light. When its use is inevitable, different types of light sources at the same time and place should be avoided. With regard to the reduction in the use of artificial lighting, several measures to assure "dark" habitats for nocturnal pollinators could be taken such as limiting the density, distribution, intensity, and duration of artificial lighting (Gaston et al. 2013; Longcore et al. 2018). It is important to consider that while one light source might have moderate effects on one organism, it could be highly disruptive to another. For instance, the short wavelengths of white LEDs are suppressors of melatonin of nocturnal marsupials, among other taxa, and this effect might be mitigated when shifting to long-wavelength amber LEDs (Dimovski and Robert 2018). In addition, traditional broad-spectrum LEDs have been evidenced to disrupt predator-prey relationships while customized LEDs, with blue wavelengths filtered, removed this effect (Moyse et al. 2023). However, orange LEDs, without blue wavelength emission, avoid flower detection by hawkmoths (Briolat et al. 2021). Therefore, the impact of light pollution on organisms and their interactions should be evaluated globally in order to implement the least harmful artificial sources for natural ecosystems.

Another potential solution to prevent some of the negative impacts of light pollution is to generate "islands of shade" (Straka et al. 2021). High tree cover in artificially-lighted environments seems to mitigate the decrease in macro-moths species richness and abundance (Straka et al. 2021), as well as to favor hawkmoth pollination activity (Bariles et al. 2021). Tree cover might help to prevent

light impact on nocturnal insects but also to provide shelter to exhausted individuals affected by light pollution (Straka et al. 2021). In addition, the health of the natural habitat is crucial for pollination and fitness of hawkmoth-pollinated plant species (Martins and Johnson 2009), co-flowering neighbor plants may attract more pollinators, thus promoting interspecies and interplant visits. In consistency, it has been previously evidenced that plant fitness and pollen load of the hawkmoth-pollinated *E. gilliesii* was promoted under high tree-covered sites, despite the influence of light pollution (Bariles et al. 2021).

Increasing evidence about the impact of light pollution on the visual ecology of different organisms, including hawkmoths (Briolat et al. 2021), has highlighted the insidious ways in which artificial lights might differentially affect visual perception depending on spectral sensitivity of ecological actors and light source spectra. Our results support such assertions for hawkmoth-pollinated species that likely have a long history of coevolution with hawkmoths and provide new evidence about the differential hawkmoth perception of flower and leaf signals depending on the color of visual signal when comparing natural with artificial illumination. Further studies should evaluate whether artificial illumination is imposing new selective forces on both hawkmoths and hawkmoth-pollinated plants. In addition, other mechanisms, apart from changes in visual perception, through which light pollution may impact pollination ecosystem services should be further evaluated. These mechanisms could include the effects of light pollution on the circadian clocks of hawkmoths and the phenology of plants (Gaston et al. 2013).

Declarations

Competing interests The authors declare no competing interests.

References

Aoki S, Ito M (2000) Molecular phylogeny of *Nicotiana* (Solanaceae) based on the nucleotide sequence of the matK gene. Plant Biol 2:316–324. https://doi.org/10.1055/s-2000-3710

Balbuena MS, Broadhead GT, Dahake A et al (2022) Mutualism has its limits: consequences of asymmetric interactions between a well-defended plant and its herbivorous pollinator. Philos Trans R Soc B Biol Sci 377:20210166. https://doi.org/10.1098/rstb.2021.0166

Balkenius A, Kelber A, Balkenius C (2004) A model of selection between stimulus and place strategy in a hawkmoth. Adapt Behav 12:21–35. https://doi.org/10.1177/105971230401200101

Bariles JB, Cocucci AA, Soteras F (2021) Pollination and fitness of a hawkmoth-pollinated plant are related to light pollution and tree cover. Biol J Linn Soc 134:815–822. https://doi.org/10.1093/biolinnean/blab114/6377657

Bennett RR, Brown PK (1985) Properties of the visual pigments of the moth *Manduca sexta* and the effects of two detergents, digitonin and CHAPS. Vis Res 25:1771–1781. https://doi.org/10.1016/0042-6989(85)90002-1

Boyes DH, Evans DM, Fox R et al (2020) Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle. Insect Conserv Divers 14:167–187. https://doi.org/10.1111/icad.12447

Briolat ES, Gaston KJ, Bennie J et al (2021) Artificial nighttime lighting impacts visual ecology links between flowers, pollinators and predators. Nat Commun 12:4163. https://doi.org/10.1038/s41467-021-24394-0

Bukovac Z, Shrestha M, Garcia JE et al (2017) Why background colour matters to bees and flowers. J Comp Physiol A 203:369–380. https://doi.org/10.1007/s00359-017-1175-7

Chittka L, Kevan PG (2005) Flower colors as advertisement. In Practical pollination biology. Enviroquest

Clarkson JJ, Dodsworth S, Chase MW (2017) Time-calibrated phylogenetic trees establish a lag between polyploidisation and diversification in *Nicotiana* (Solanaceae). Plant Syst Evol 303:1001–1012. https://doi.org/10.1007/s00606-017-1416-9

R Core Team (2022) R: A language and environment for statistical computing

Cutler D, Bennett R, Stevenson R, White R (1995) Feeding behavior in the nocturnal moth *Manduca sexta* is mediated mainly by blue receptors, but where are they located in the retina? J Exp Biol 198:1909–1917. https://doi.org/10.1242/jeb.198.9.1909

Davies TW, Bennie J, Inger R, Gaston KJ (2013) Artificial light alters natural regimes of night-time sky brightness. Sci Rep 3:1–6. https://doi.org/10.1038/srep01722

Deichmann JL, Ampudia Gatty C, Andía Navarro JM et al (2021) Reducing the blue spectrum of artificial light at night minimises insect attraction in a tropical lowland forest. Insect Conserv Divers 14:247–259. https://doi.org/10.1111/icad.12479

Deora T, Ahmed MA, Brunton BW, Daniel TL (2021) Learning to feed in the dark: how light level influences feeding in the Hawkmoth *Manduca sexta*. Biol Lett 17:20210320. https://doi.org/10.1098/rsbl.2021.0320

Dimovski AM, Robert KA (2018) Artificial light pollution: shifting spectral wavelengths to mitigate physiological and health consequences in a nocturnal marsupial mammal. J Exp Zool Part Ecol Integr Physiol 329:497–505. https://doi.org/10.1002/jez.2163

Fenske MP, Nguyen LAP, Horn EK et al (2018) Circadian clocks of both plants and pollinators influence flower seeking behavior of the pollinator hawkmoth *Manduca sexta*. Sci Rep 8:1–13. https://doi.org/10.1038/s41598-018-21251-x

Gagnon E, Ringelberg JJ, Bruneau A et al (2019) Global succulent biome phylogenetic conservatism across the pantropical *Caesalpinia* Group (Leguminosae). New Phytol 222:1994–2008. https://doi.org/10.1111/nph.15633

Galfrascoli GM, Calviño A, Chiapero AL, Fenoglio MS (2023) Living in an urban pod: seed predation and parasitism of bruchid beetles in a native tree species. Ecol Entomol 48:31–39. https://doi.org/10.1111/een.13199

Gaston KJ, Bennie J, Davies TW, Hopkins J (2013) The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biol Rev 88:912–927. https://doi.org/10.1111/brv.12036

Giavi S, Fontaine C, Knop E (2021) Impact of artificial light at night on diurnal plant-pollinator interactions. Nat Commun 12:8–13. https://doi.org/10.1038/s41467-021-22011-8

Goyret J, Raguso RA (2006) The role of mechanosensory input in flower handling efficiency and learning by *Manduca sexta*. J Exp Biol 209:1585–1593. https://doi.org/10.1242/jeb.02169

Goyret J, Markwell PM, Raguso RA (2007) The effect of decoupling olfactory and visual stimuli on the foraging behavior of *Manduca sexta*. J Exp Biol 210:1398–1405. https://doi.org/10.1242/jeb.02752

Goyret J, Pfaff M, Raguso RA, Kelber A (2008) Why do *Manduca sexta* feed from white flowers? Innate and learnt colour preferences in a hawkmoth. Naturwissenschaften 95:569–576. https://doi.org/10.1007/s00114-008-0350-7

Haxaire J (2019) A revised and annotated checklist of the Brazilian Sphingidae with new records, taxonomical notes, and description of one new species (Lepidoptera Sphingidae). Eur Entomol 11:101–187

Henze MJ, Lind O, Mappes J et al (2018) An aposematic colour-polymorphic moth seen through the eyes of conspecifics and predators – sensitivity and colour discrimination in a tiger moth. Funct Ecol 32:1797–1809. https://doi.org/10.1111/1365-2435.13100

Johnsen S, Kelber A, Eric Warrant et al (2006) Crepuscular and nocturnal illumination and its effects on color perception by the nocturnal hawkmoth *Deilephila elpenor*. J Exp Biol 209:789–800

Kariñho-Betancourt E, Carlson D, Hollister J et al (2022) The evolution of multi-gene families and metabolic pathways in the evening primroses (*Oenothera*: Onagraceae): a comparative transcriptomics approach. PLoS ONE 17:e0269307. https://doi.org/10.1371/journal.pone.0269307

Kessler D, Diezel C, Baldwin IT (2010) Changing pollinators as a means of escaping herbivores. Curr Biol 20:237–242. https://doi.org/10.1016/j.cub.2009.11.071

Kitching IJ (2022) Sphingidae Taxonomic Inventory. Accessed 9 Mar 2023

Kuenzinger W, Kelber A, Weesner J et al (2019) Innate colour preferences of a hawkmoth depend on visual context. Biol Lett 15:20180886. https://doi.org/10.1098/rsbl.2018.0886

Lind O (2016) Colour vision and background adaptation in a passerine bird, the zebra finch (*Taeniopygia guttata*). R Soc Open Sci 3:160383. https://doi.org/10.1098/rsos.160383

Longcore T (2023) A compendium of photopigment peak sensitivities and visual spectral response curves of terrestrial wildlife to guide design of outdoor nighttime lighting. Basic Appl Ecol 73:40–50. https://doi.org/10.1016/j.baae.2023.09.002

Longcore T, Aldern HL, Eggers JF et al (2015) Tuning the white light spectrum of light emitting diode lamps to reduce attraction of nocturnal arthropods. Philos Trans R Soc B Biol Sci 370:20140125. https://doi.org/10.1098/rstb.2014.0125

Longcore T, Rodríguez A, Witherington B et al (2018) Rapid assessment of lamp spectrum to quantify ecological effects of light at

night. J Exp Zool Part Ecol Integr Physiol 329:511–521. https://doi.org/10.1002/jez.2184

Macgregor CJ, Evans DM, Fox R, Pocock MJOO (2017) The dark side of street lighting: impacts on moths and evidence for the disruption of nocturnal pollen transport. Glob Change Biol 23:697–707. https://doi.org/10.1111/gcb.13371

Maia R, White TE (2018) Comparing colors using visual models. Behav Ecol 29:649–659. https://doi.org/10.1093/beheco/ary017

Maia R, Gruson H, Endler JA, White TE (2019) pavo 2: New tools for the spectral and spatial analysis of colour in r. Methods Ecol Evol 10:1097–1107. https://doi.org/10.1111/2041-210X.13174

Martins DJ, Johnson SD (2009) Distance and quality of natural habitat influence hawkmoth pollination of cultivated papaya. Int J Trop Insect Sci 29:114–123. https://doi.org/10.1017/S1742758409990208

Moré M, Benitez-vieyra S, Sérsic AN, Cocucci AA (2014) Patrones De depósito De Polen Sobre El Cuerpo De Los polinizadores en comunidades esfingófilas de Argentina subtropical. Darwiniana 2:174–196. https://doi.org/10.14522/darwiniana.2014.21.568

Moré M, Cocucci AA, Sérsic AN, Barboza GE (2015) Phylogeny and floral trait evolution in *Jaborosa* (Solanaceae). Taxon 64:523–534. https://doi.org/10.12705/643.8

Moré M, Ibañez AC, Drewniak ME et al (2020) Flower diversification across pollinator climates: sensory aspects of corolla color evolution in the florally diverse south American genus *Jaborosa* (Solanaceae). Front Plant Sci 11:601975. https://doi.org/10.3389/fpls.2020.601975

Moyse E, Firth LB, Smyth T et al (2023) Artificial light at night alters predation on colour-polymorphic camouflaged prey. Basic Appl Ecol 73:88–93. https://doi.org/10.1016/j.baae.2023.11.002

Oksanen J, Simpson G, Blanchet F et al (2022) _vegan: Community Ecology Package_. R package version 2.6–4, https://CRAN.R-project.org/package=vegan

Olsson P, Lind O, Kelber A (2018) Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. Behav Ecol 29:273–282. https://doi.org/10.1093/beheco/arx133

Owens ACS, Lewis SM (2018) The impact of artificial light at night on nocturnal insects: a review and synthesis. Ecol Evol 8:11337–11358. https://doi.org/10.1002/ece3.4557

Pawson SM, Bader MK-F (2014) LED lighting increases the ecological impact of light pollution irrespective of color temperature. Ecol Appl 24:1561–1568. https://doi.org/10.1890/14-0468.1

Peres-Neto P, Jackson D (2001) How well do multivariate data sets match? The advantages of a procrustean superimposition approach over the Mantel test. Oecologia 129:169–178. https://doi.org/10.1007/s004420100720

Pimputkar S, Speck JS, Denbaars SP, Nakamura S (2009) Prospects for LED lighting. Nat Photonics 3:180–182. https://doi.org/10.1038/nphoton.2009.32

Raguso RA, Willis MA (2002) Synergy between visual and olfactory cues in nectar feeding by naïve hawkmoths, *Manduca sexta*. Anim Behav 64:685–695. https://doi.org/10.1006/anbe.2002.4010

Reck-Kortmann M, Silva-Arias GA, Segatto ALA et al (2014) Multilocus phylogeny reconstruction: new insights into the evolutionary history of the genus *Petunia*. Mol Phylogenet Evol 81:19–28. https://doi.org/10.1016/j.ympev.2014.08.022

Renoult JP, Kelber A, Schaefer HM (2017) Colour spaces in ecology and evolutionary biology. Biol Rev Camb Philos Soc 92:292–315. https://doi.org/10.1111/brv.12230

Sazatornil FD, Moré M, Benitez-Vieyra S et al (2016) Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth–plant networks. J Anim Ecol 85:1586–1594. https://doi.org/10.1111/1365-2656.12509

Silberbauer-Gottsberger I, Gottsberger G (1975) Über Sphingophile Angiospermen Brasiliens. Plant Syst Evol 123:157–184. https://doi.org/10.1007/BF00989402

Soteras F, Rubini Pisano MA, Bariles JB et al (2020) Phenotypic selection mosaic for flower length influenced by geographically varying hawkmoth pollinator proboscis length and abiotic environment. New Phytol 225:985–998. https://doi.org/10.1111/nph.16192

Stöckl AL, Kelber A (2019) Fuelling on the wing: sensory ecology of hawkmoth foraging. J Comp Physiol A 205:399–413. https://doi.org/10.1007/s00359-019-01328-2

Stöckl A, Heinze S, Charalabidis A et al (2016) Differential investment in visual and olfactory brain areas reflects behavioural choices in hawk moths. Sci Rep 6:26041. https://doi.org/10.1038/srep26041

Storms M, Mitesser O, Degen T et al (2022) The rising moon promotes mate finding in moths. Commun Biol 5:393. https://doi.org/10.1038/s42003-022-03331-x

Straka TM, von der Lippe M, Voigt CC et al (2021) Light pollution impairs urban nocturnal pollinators but less so in areas with high tree cover. Sci Total Environ 778:146244. https://doi.org/10.1016/j.scitotenv.2021.146244

Telles FJ, Lind O, Henze MJ et al (2014) Out of the blue: the spectral sensitivity of hummingbird hawkmoths. J Comp Physiol A 200:537–546. https://doi.org/10.1007/s00359-014-0888-0

van der Kooi CJ, Kelber A (2022) Achromatic cues are important for flower visibility to hawkmoths and other insects. Front Ecol Evol 10:819436. https://doi.org/10.3389/fevo.2022.819436

van Grunsven RHA, Lham D, Van Geffen KG, Veenendaa EM (2014) Range of attraction of a 6-W moth light trap. Entomol Exp Appl 152:87–90. https://doi.org/10.1111/eea.12196

van Langevelde F, Ettema JA, Donners M et al (2011) Effect of spectral composition of artificial light on the attraction of moths. Biol Conserv 144:2274–2281. https://doi.org/10.1016/j.biocon.2011.06.004

Vorobyev M, Osorio D (1998) Receptor noise as a determinant of colour thresholds. Proc R Soc Lond B Biol Sci 265:351–358. https://doi.org/10.1098/rspb.1998.0302

Walton RE, Sayer CD, Bennion H, Axmacher JC (2020) Nocturnal pollinators strongly contribute to pollen transport of wild flowers in an agricultural landscape. Biol Lett 16:20190877. https://doi.org/10.1098/rsbl.2019.0877

Warrant EJ (2017) The remarkable visual capacities of nocturnal insects: vision at the limits with small eyes and tiny brains. Philos Trans R Soc B Biol Sci 372:20160063. https://doi.org/10.1098/rstb.2016.0063

Warrant E, Dacke M (2011) Vision and visual navigation in nocturnal insects. Annu Rev Entomol 56:239–254. https://doi.org/10.1146/annurev-ento-120709-144852

Warrant E, Somanathan H (2022) Colour vision in nocturnal insects. Philos Trans R Soc B Biol Sci 377:20210285. https://doi.org/10.1098/rstb.2021.0285

White RH, Stevenson RD, Bennett RR et al (1994) Wavelength discrimination and the role of ultraviolet vision in the feeding behavior of Hawkmoths. Biotropica 26:427. https://doi.org/10.2307/2389237

White RH, Xu H, Münch TA et al (2003) The retina of *Manduca sexta*: rhodopsin expression, the mosaic of green-, blue- and UV-sensitive photoreceptors, and regional specialization. J Exp Biol 206:3337–3348. https://doi.org/10.1242/jeb.00571