Article

DIFFERENCES IN VISITATION OF HONEYBEES AND BUMBLEBEES TO ORNAMENTAL PLANT VARIETIES CAN BE EXPLAINED BY FLORAL TRAITS

Femke Verweij[1,2]*, Jacobus C. Biesmeijer[2], Saskia G. T. Klumpers[2]

[1]*Institute of Biology Leiden, Leiden University, Sylviusweg 72, 2333 BE Leiden, The Netherlands*
[2]*NL Biodiversity and Society, Naturalis Biodiversity Centre, Darwinweg 2, 2333 CR Leiden, The Netherlands*

Journal of Pollination Ecology, 38(3), 2025, pp 36-57
DOI: 10.26786/1920-7603(2025)813

Received 10 June 2024, accepted 16 December 2024
*Corresponding author: fem.verweij@gmail.com

Abstract—Global bee populations are rapidly declining. One way of supporting bee populations is by enhancing urban green spaces with plants attractive to bees. Plant breeding has introduced a high degree of variability in floral traits, which can affect the attractiveness and usefulness of ornamental plants to bees. In this study, we investigated how variations in floral traits, including nectar sugar content, corolla tube depth, flower colour, UV-presence and the number of flowers, affected the attractiveness of 119 cultivars from eight ornamental plant genera (*Salvia nemorosa*, *Gaillardia aristata*, *Delosperma cooperi, Lavandula angustifolia, Lavandula stoechas*, *Sedum telephium*, *Perovskia atriplicifolia* and *Agastache hybrida)* to honeybees and bumblebees. Our results show that differences in bee visitation rate among cultivars were directly related to variation in floral traits. For most plant genera, cultivars of the same species varied significantly in attractiveness. Honeybees and bumblebees generally did not find the same cultivars and plant genera attractive. Nectar sugar content and flower colour were important for cultivar attractiveness to both honeybees and bumblebees, with corolla tube depth also being an important factor for honeybees. We found that flower colour was often related to the favourability of other floral traits that promote more rewarding or easily accessible flowers. However, most cultivars were considered unattractive and only a small number of cultivars were highly attractive to honeybees (6%) and bumblebees (10%). Overall, our study gives valuable insights for plant breeders, emphasising how different floral traits affect the attractiveness of ornamental plants which helps to select for floral traits that result in more attractive ornamental plants for bees.

Keywords—*Apis*, *Bombus*, Corolla tube length, Flower colour, Nectar, Plant attractiveness

INTRODUCTION

Pollinating insects, including bees, are of great commercial and ecological value (NRC 2007; Potts et al. 2016; Janousek et al. 2023), as they are responsible for 75 percent of crop pollination (FAO 2018) as well as pollination of wild plants in natural ecosystems (Aizen et al. 2009; Ollerton et al. 2011; Binkenstein et al. 2017; Katumo et al. 2022). Global bee populations are rapidly declining as a result of climate change, agricultural practices and urbanisation (Garbuzov & Ratnieks 2014b; Goras et al. 2016; Erickson et al. 2020; Kreider et al. 2020). Studies show that urban green spaces can contribute to supporting bee populations by enhancing habitats with flowering plants (Garbuzov & Ratnieks 2014a; Salisbury et al. 2015; Erickson et al. 2021). Additionally, these urban green spaces can hold a higher density of bees, a broader diversity of plant species, as well as a higher nectar availability and floral density compared to agricultural land (Salisbury et al. 2015; Baldock et al. 2019; Rollings & Goulson 2019; Tew et al. 2021, 2022). Conservation initiatives and garden centres often recommend particular ornamental plants to consumers with the claim to be beneficial to bees or pollinators (Corbet et al. 2001; Fetridge 2008; Rollings & Goulson 2019; Erickson et al. 2021). However, these recommendations are often not evidence-based (Garbuzov & Ratnieks 2014b; Garbuzov et al.

2017), and can therefore be misleading or inaccurate.

In flowering plants, floral traits relay important signals to bees, indicating how rewarding a potential flower visit will be (Latty & Trueblood 2020; Delgado et al. 2023). Floral rewards, like pollen and nectar, are of great importance to bees as it is their primary incentive while foraging and visiting flowers (Gil 2010; Binkenstein et al. 2017; Pamminger et al. 2019; Seitz et al. 2020). Visual- (e.g. Papiorek et al. 2016; Delgado et al. 2023) and olfactory traits (e.g. Dötterl & Vereecken 2010; Erickson et al. 2022; Torres Carvalho et al. 2012) also play an important role, as they attract pollinators and signal reward availability from afar. Bees can see UV, blue and green colours, with an innate preference for flowers of the colour blue, violet and yellow (Jones et al. 2015; Chittka 2022a). However, they can learn to associate flower colour with potential rewards (Jones et al. 2015; Bauer et al. 2017; Chittka 2022b; Erickson et al. 2022). Like most insects, bees cannot see the colour red, but they are not blind to the colour red as they can distinguish between green-, yellow-, orange-, and red-reflecting objects (Chittka & Waser 1997). A flower's UV-pattern acts as a nectar guide, as it generally improves the identification of the landing and/or foraging parts of flowers (Riddle 2016; Papiorek et al. 2016; Lunau et al 2017) and can make flowers more or less attractive to bees, depending on whether it increases the colour contrast (Chittka et al. 1994; Keven et al. 2001) or the spectral purity (Lunau & Maier 1995; Rhode et al. 2013). For example, UV patterns in yellow and red flowers form a high contrast pattern, making these flowers more attractive to bees (Koski and Ashman 2014; Papiorek et al. 2016; Chen et al. 2020). However, compared with UV-absorbing white flowers, UV-reflecting white flowers display a colour of low spectral purity for bees, decreasing their attractiveness (Lunau et al. 2011). Other traits, such as corolla tube depth and the number of flowers, can influence the nectar accessibility and foraging efficiency (Klumpers et al. 2019). The corolla tube, also referred to as the nectar tube, varies in shape, size, and colour (Delgado et al. 2023) and is associated with nectar production (Kaczorowski et al. 2012): a longer corolla tube is generally capable of holding more nectar (Plowright 1987; Johnson et al. 2017). However, a longer corolla tube reduces nectar accessibility for bees with shorter proboscises (Plowright 1987; Stang et al. 2007) and bees experience a longer handling time when foraging on deeper-tubed flowers (Klumpers et al. 2019). Foraging efficiency is the tradeoff of time spent foraging and amount and quality of reward. When the corolla tube is even longer than the bees proboscis, handling time increases disproportionately which may negatively affect foraging efficiency and therefore flower attractiveness (Klumpers et al. 2019). Lastly, the number of flowers can also affect plant attractiveness. The number of open flowers on a plant has a strong positive correlation to the pollinator visitation rate (Bauer et al. 2017), as this is a good indicator of nectar availability (Makino & Sakai 2007) and promotes foraging efficiency. Pollinator floral choice is mediated by combination of these floral traits; by complex multimodal floral signals (reviewed in Willmer 2011). It is assumed that ornamental flowers may be a deviation from the multi-trait, synergistic floral displays that pollinators are foraging on in co-selected plant-pollinator systems. Specifically ornamental flowers would uncouple floral traits from nutritional quality (Wright & Schiestl 2009; but see Erickson et al. 2022). Moreover, breeding can reduce nutritional resource availability in many cultivars (Comba et al. 1999). Therefore breeding may make ornamental plants less attractive to pollinators.

Nowadays, urban landscapes are dominated by non-native or cultivated ornamental plants (Garbuzov & Ratnieks 2014a). Previous studies note that non-native or cultivated plant varieties are often less attractive to bees compared to native species (Garbuzov & Ratnieks 2014a, 2015; Garbuzov et al. 2017; Rollings & Goulson 2019; Seitz et al. 2020) or plants from wild populations (White 2016). This is mostly attributed to a difference in quality, availability and accessibility of food resources compared to their wild-type counterparts (Baldock et al. 2019; Seitz et al. 2020; Kovács-Hostyánszki et al. 2022). As a result, some cultivated ornamental plants have a more decorative purpose than a functional one (Erickson et al. 2020). For example, many commercially available roses and daffodils have been bred for an extra whorl of petals (Corbet et al. 2001; Wilkin & Mayo 2013; Irish 2017), which reduces nectar and pollen accessibility. This ultimately affects the usefulness of the flower and with that the overall attractiveness. Nonetheless, studies have also shown that cultivated plants can be highly attractive to bees (Garbuzov et al. 2017; Sponsler et al. 2020; Seitz et al. 2020) and in some cases even more attractive than wild-types.

Plant breeding has introduced considerable variability in floral traits and phenotypical characteristics in ornamental plants, based on selection for human preference (Garbuzov & Ratnieks 2014a, 2015; Erickson et al. 2020, 2021, 2022). Different floral trait combinations give way to plants with varying degrees of attractiveness, even among varieties of the same species or among closely related varieties attractiveness can vary significantly (Rollings & Goulson 2019; Erickson et al. 2022). Cultivated ornamental varieties are a useful tool to explore how individual floral traits and different floral trait combinations affect attractiveness among varieties of the same species (Rollings & Goulson 2019; Erickson et al. 2022).

With this study, we aim to provide insight into how attractive ornamental plants are. The plants used in this study are from the popular ornamental genera: Hyssop (*Agastache hybrida)*, Ice plant (*Delosperma cooperi), Blanket flower (Gaillardia aristata), English lavender (Lavandula angustifolia), Spanish lavender (Lavandula stoechas), Russian sage (Perovskia atriplicifolia), Woodland sage (Salvia nemorosa)* and *Stonecrop (Sedum telephium)*. We examine whether cultivars of the same plant genus differ in attractiveness to honeybees and bumblebees, and how this is related to variation in floral traits, including nectar sugar content, corolla tube depth, flower colour, UV-presence and the number of flowers. While pollen amount (Erickson et al. 2022), pollen protein content (Roulston & Cane 2000; Vaudo et al. 2016) and scent (Dötterl & Vereecken 2010; Erickson et al. 2022; Torres Carvalho et al. 2012) are known to play a role in the attraction of pollinators, these traits were not included in our study. All plant species in this study, except *D. cooperi* and *G. aristata*, are primarily nectar plants and many cultivars produce little or no pollen at all. Floral headspace volatiles are relatively difficult to measure and to identify for breeders. Moreover, these volatiles and the biosynthetic pathways that build these compounds are often located on the same chromosomes that regulate other floral traits, including colour (Raguso et al. 2015) and floral structural characteristics, such as corolla length (Smith 2016). These are also the traits that breeders select for, as they determine the attractiveness of ornamental plants to humans, which makes it more difficult for breeders to purposely select for headspace volatiles and include scent in their breeding program. Consequently, scent is less likely to play a role in the future of the breeding program of each of these plant genera. Moreover, the response of bees to scent often comes from flower-naïve bees, as more experienced bees are less attracted by odour signals and more to other floral traits (Dobson 1987; Dötterl & Vereecken 2010). Therefore, while studying the pollen and scent would provide insight on the attractiveness of cultivars, it would not directly serve the practical outcome of this study and thus were not included.

MATERIALS AND METHODS

PLANT SELECTION AND PLOT DESIGN

We studied 119 perennial ornamental cultivars from eight different plant genera (Tab. S1), based on the market share of each plant genus and their potential attractiveness to bees based on prior observation (de Haan, unpublished). All plant material was selected and provided by Dümmen Orange. The plant genera included in this study were *Salvia nemorosa*, *Gaillardia aristata*, *Delosperma cooperi, Lavandula angustifolia, Lavandula stoechas*, *Sedum telephium*, *Perovskia atriplicifolia* and *Agastache hybrida.* Of these genera, *S. nemorosa*, *S. telephium*, *L. angustifolia* and *L. stoechas* are native to Western Europe, however S. nemorosa, *L. angustifolia* and *L. stoechas* are not native to the Netherlands (POWO 2024). *A. hybrida* cultivars are considered hybrids. Fifteen cultivars were selected for each plant genus, taking into account their commercial introduction status (advanced or commercially available), findings from prior observations (de Haan, unpublished) and other commercially available cultivars on the market used for comparison. Due to the small scale of the *P. atriplicifolia* breeding program, only fourteen cultivars were studied. Cultivars were either commercially available (for commercial names, see Tab. S1) or experimental. Cultivar names specific to the breeding program have been replaced with numbered codes (e.g. SV01-SV15) in the reporting of the results to maintain confidentiality of the Dümmen Orange breeding programs. The fieldwork was conducted at an active plant breeding facility at Dümmen Orange Aalsmeer (52°17'43.66" N, 4°48'42.99" E), Noord-Holland, The Netherlands. The study site was located in a rural-urban fringe area (Nabielek et al. 2013) and was directly surrounded by greenhouses. The closest natural area which hosts a diverse range of native flowering plants and a small bee community (for overview, see Tab. S2-S3) was approximately one kilometre away.

Plants were propagated in a greenhouse from cuttings taken between February and early April 2023, depending on the plant genus, from the same parental plant. Subsequently, for each cultivar fifteen rooted cuttings were planted in 2-litre pots (17 cm in diameter at the top) with peat-free potting soil (Klassmann-Deilmann) and moved to outdoor plots between April and early May 2023. Plot observations for bee visitation rate and flower trait measurements were performed from mid-June to mid-September 2023. The plots were arranged in rows, each containing metal racks with a 15 cm by 15 cm grid pattern in which pots were alternatingly spaced (Fig. 1). Each plot was 75x90 cm and contained fifteen plants of the same cultivar and directly neighboured other plots of cultivars from the same plant genus. Not all plants survived outdoors until the start of observations, resulting in some plots with varying numbers of plants. We opted against replacing missing plants as growing replacements from cuttings would lead to a mismatch in flowering time between the original and replacement plants. In total, there were 50+ rows, with each row containing max. 50 cultivars and 750 pots in total (Tab. S1). At no point throughout the study were the plants treated with neonicotinoids.

Figure 1. A schematic layout of the plot design displaying a small part of a single row (50+ rows total, with each row containing max. 50 cultivars and 750 pots in total) with grid pattern in which pots are spaced alternately. Each shade of grey represents one cultivar and the numbers in the dots represent the plants of this cultivar (in total 15 plants per cultivar). The start of each plot was indicated by a label (containing plant genus and cultivar name) in the first pot (orange). All pots in a plot contained plants from the same cultivar.

BEE VISITATION RATE

Bee visitation rate per cultivar was determined by counting all bees that visited flowers within a plot, with each cultivar observed five times in total, for one minute each time, on five different days during the peak flowering period of each plant genera (Tab. S4). The number of bees was counted for all cultivars of the same plant genus within a one-hour period to ensure minimal changes brought on by time of day or fluctuation in environmental conditions on visitation rate. The time of observation varied between 11 am and 3 pm for all plant genera and took place on sunny days with low wind speed (< 20 km/h), no rain and a minimal temperature of 16°C (Kevan & Baker 1983).

All counted bees were identified to species level, except for bees belonging to the genus *Lasioglossum*. These were identified to genus level. Bumblebee species part of the *Bombus terrestris/Bombus lucorum* complex (Wignall et al. 2020), were all recorded as *B. terrestris* due to its commonality in the Netherlands (Stip et al. 2020).

We classified the level of cultivar attractiveness based on a metric from Garbuzov et al. (2015), which was adapted slightly to ensure a better fit to the results of this study. The degree of attractiveness, based on average bee visitation rate, was categorised as highly attractive (> 10 bees/plot/minute), moderately attractive (5-10 bees/plot/minute), somewhat attractive (1-5 bees/plot/minute), relatively unattractive (0.01-1 bees/plot/minute) or completely unattractive (0 bees/plot/minute).

NUMBER OF FLOWERS

The number of flowers per plot was counted once per cultivar during the peak flowering time of each plant genus. For each cultivar, only the open, fresh flowers were counted. Flower buds and old flowers were excluded, as they do not produce any nectar (Southwick & Southwick 1983). For *S. telephium* cultivars the number of flowers was not counted, as based on visual cues alone, it was nearly impossible to determine the age of a flower.

The method for counting the number of flowers depended on the inflorescence type of a plant genera. *D. cooperi* cultivars had solitary flowers, which were counted one by one per plant of five plants per cultivar and multiplied by the number of plants per plot. For *S. nemorosa*, *A. hybrida*, *P. atriplicifolia, L. stoechas* and *L. angustifolia* cultivars, the average number of flowers on an inflorescence was determined for five plants. The average number of flowers on an inflorescence was then multiplied by the number of inflorescences per plant. The number of flowers per plot was calculated by multiplying the number of flowers per plant by the number of plants per plot (Tab. S1).

Most plants species part of the Asteraceae family, like *G. aristata*, have a capitulum or head inflorescence, which is made up of an outer whorl of ray florets and numerous densely packed disc florets in the centre (Funk et al. 2009; Huang et al. 2016). This gives the appearance of a single flower (Simpson 2010). The disc florets open whorl by whorl, starting at the outside and moving to the inside (Wist & Davis 2006, 2008; Shabir et al. 2013). In most species of the Asteraceae family, only the most recently opened whorl(s) of disc florets produce nectar (Wist & Davis 2008). Different from the other plant genera in this study, first the average number of newly opened florets per head were determined across all *G. aristata* cultivars. For each cultivar the average number of heads was determined using five plants and multiplied by the average number of disc florets. The average number of disc florets per plant was then multiplied by the number of plants per plot (Tab. S1).

NECTAR MEASUREMENTS

For each cultivar, we measured the 24-hour nectar production rate (NPR). NPR gives a good indication of how much nectar plants produce (Pleasants 1983). The nectar volume and nectar sugar concentration were measured for 20 randomly selected flowers per cultivar, with a maximum of 5 flowers per measuring day. The nectar measurements were performed on the same days as the bee visitation rate counts. Depending on the flower type, an individual flower or an inflorescence was enclosed in a mesh bag for 24 hours before measurement. Bagging ensured that flowers had enough time to replenish nectar, while simultaneously restricting bees from accessing the nectar. Nectar was collected with glass microcapillary tubes (Hirschmann or Camag) of 0.5 µl, 1 µl or 2 µl, depending on the nectar quantity and flower size (width). With a digital calliper (Profi Scale Precise PS 7215), the height of the nectar column in the microcapillary tube was measured and converted to nectar volume (µl) (Klumpers et al. 2019). Nectar sugar concentration was determined by a handheld refractometer (Bellingham + Stanley 45-81, 0-50 °Brix or Bellingham + Stanley 45-82, 45-85 °Brix).

Using nectar volume and sugar concentration measurements, the nectar sugar content per flower (s, µg) was calculated using the formula $s = 10dvC$. In this formula d is the density of the nectar sugar concentration C (g sucrose/100g solution) and v is the nectar volume (µl), with the density defined as $d = 0.0037921C + 0.0000178C^2 + 0.9988603$ (Corbet et al. 2001).

G. aristata cultivars have a head inflorescence with disc florets that open whorl by whorl, only the disc florets of the most recently opened whorl were used to collect nectar. Based on observation, bees only collected the nectar of the most recently opened florets and through trial and error, it also became apparent that older disc florets produced little to no nectar. For *G. aristata,* we measured nectar volume and sugar concentration of a single disc floret. Similar to other plant genera, in total, we measured 20 disc florets from 20 randomly selected flower heads, with a maximum of 5 disc florets per measuring day.

Given that the bee visitation rate was determined for the entire plot, the average nectar sugar content per flower was multiplied by the average number of flowers in a plot in order to determine the average nectar sugar content per plot. The average nectar sugar content per plot was used for analyses.

Among *D. cooperi* and *S. telephium* there were four cultivars that did not produce any nectar (Tab. 2) and for other cultivars of these genera (DL11, SE03, SE06, SE07) we only managed to collect nectar between 5 to 15 times. Additionally, for *S. telephium* the nectar sugar content per flower was used as the number of flowers per plot were undetermined.

Corolla tube depth

Corolla tube depth was measured with a digital calliper (Profi Scale Precise PS 7215). We considered the corolla tube to be the part in which most larger bees, as observed in this study, can only insert their tongue (Fig. S1). The same 20 flowers per cultivar as the nectar measurements were used. Plants of the Aizoaceae and Crassulaceae family, such as *D. cooperi* and *S. telephium*, do not have a tube-shaped corolla (Simpson 2010; Haines et al. 2011) and were therefore not considered in analyses for corolla tube depth.

Flower colour and UV-presence

For all cultivars of each of the plant genera, except for *S. telephium*, the reflectance intensity and peak wavelength were measured of 5 flowers or flower petals (depending on the flower type). The flower samples were placed vertically in a UV/VIS/NIR Jasco V-770 spectrophotometer and clamped in place in front of the detector. The fragility of the *S. telephium* flowers and the set-up of the spectrophotometer did not allow for clamping without damaging the flowers, therefore *S. telephium* cultivars were not subjected to colour measurement by spectrophotometer.

The spectrum for reflectance measurements was set to 200-800 nm to include both the UV- and visible light spectrum visible to bees (Chittka 2022a). UV-presence was established for each cultivar when a wavelength with at least 10% of the total intensity was measured in the 300-400 nm range (Chittka et al. 1994; Erickson et al. 2022). A cultivar was considered to have a UV-pattern presence when three or more flowers had wavelengths in the UV spectrum (Erickson et al. 2022).

For plant genera with distinctive multicoloured flower petals, such as *G. aristata*, *D. cooperi,* each colour was measured and the primary flower colour was used for analyses. As not all *G. aristata* and *D. cooperi* cultivars were multicoloured, we also tested whether multiple flowers colours affected bee visitation rate. For *L. stoechas* the colour of the flags on an inflorescence was used for analysis instead of the flower colour, as the flags varied considerably in colour and were prominently visible from far away compared to the flowers in an inflorescence.

Data analysis

Data was analysed using R version 4.3.1 (R Core Team 2023). Differences in visitation rate of bumblebees and honeybees and how this was related to variation in floral traits among cultivars was analysed separately for each plant genus.

To test whether visitation rate and floral traits, including nectar sugar content, corolla tube depth, the number of flowers, flower colour, differed among cultivars was determined using an ANOVA with Tukey post hoc analysis. A Kruskal-Wallis rank sum test and Dunn's test for multiple comparisons with Benjamin-Hochberg correction was performed if the ANOVA residuals were not normally distributed, not even after a log10 transformation of the variable (Tab. S6-S7).

A Multiple Linear Regression (MLR) with backward selection was performed to determine how bee visitation rate was related to differences in floral traits, with nectar sugar content per plot, corolla tube depth, the number of flowers per plot and hue angle as independent variables and bee visitation rate as dependent variable. Flower colour was included as an additional independent variable for *S. nemorosa*, *D. cooperi*, *G. aristata* and *A. hybrida, with G. aristata* and *D. cooperi* also having UV-presence as an additional independent variable. How individual flower colours were related to each other within an MLR was determined by a post-hoc pairwise comparison with Tukey HSD (Tab. 4) using R package 'emmeans' (Lenth 2024). The hue angle of a colour, based on a spectrophotometer curve, was calculated with the 'pavo2' package (Maia et al.

2019) in R based on the trichromatic human colour space (Erickson et al. 2022).

Each MLR model was selected based on analysis of the residuals, with an additional check for normality of the residuals using the Shapiro-Wilk test. No model contained highly correlated variables after backward selection, which was confirmed by performing a Variance Inflation Factor (VIF) analysis with VIF < 5.0 as threshold (Kim 2019). For *S. telephium* a General Linear Model (GLM) with Gamma error structure was used to determine how bee visitation rate was related to floral traits, as the residuals of the MLR models were not normally distributed. Here, model fit was checked using R package 'DHARMa' (Hartig 2024).

RESULTS

BEE VISITATION RATE

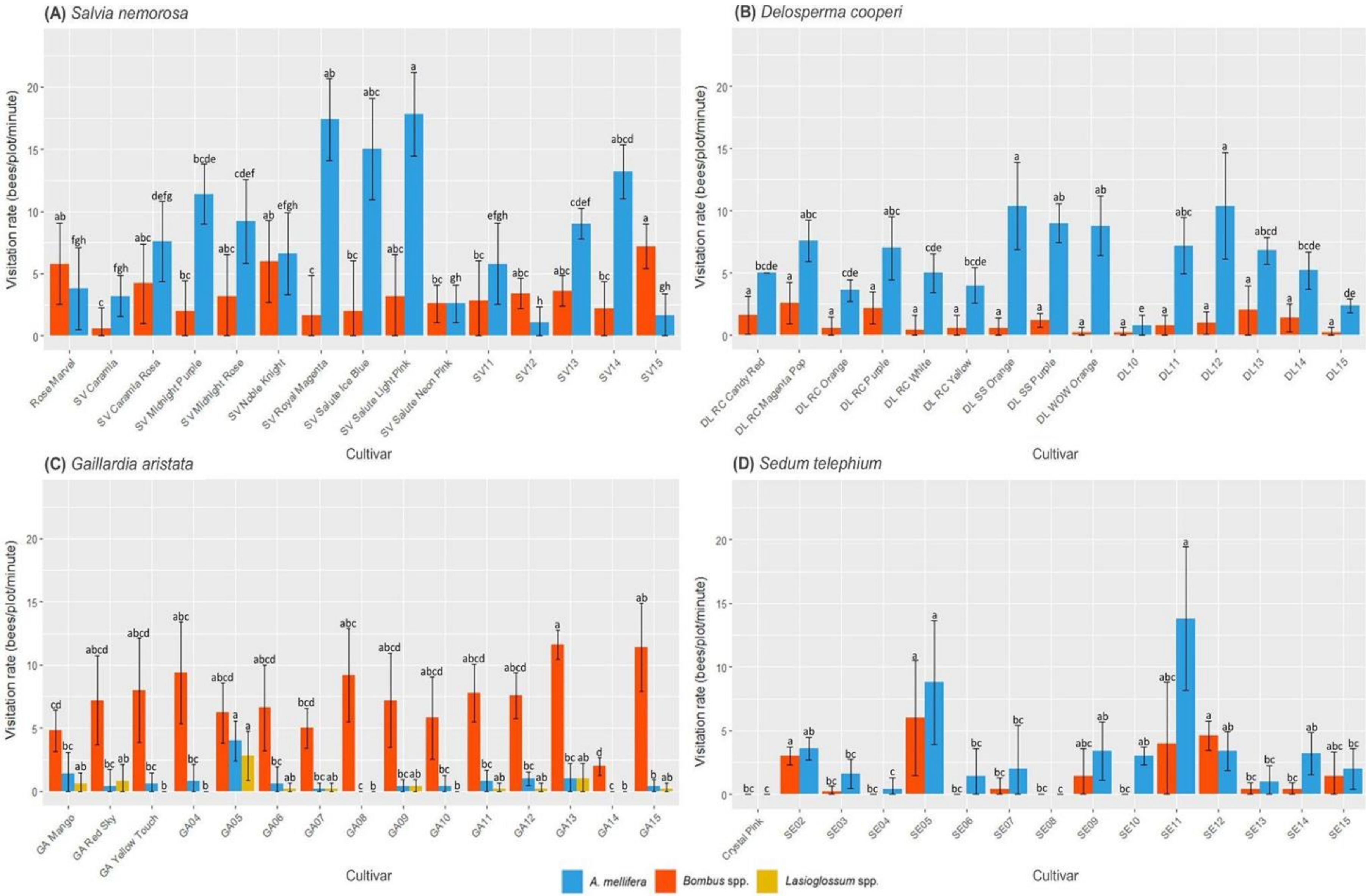
In total 5097 bees were counted, which mainly consisted of bumblebees (58%) and honeybees (41%; Tab 1). *G. aristata* was also visited by bees belonging to the genus *Lasioglossum* (Tab. 1). Of the counted bumblebees, 44% was Buff-tailed bumblebee (*Bombus terrestris*), 36% Common carder bee (*Bombus pascuorum*), 19% Red-tailed bumblebee (*Bombus lapidarius*) and the remaining 1% consisted of Tree bumblebee (*Bombus hypnorum*) and Early nesting bumblebee (*Bombus pratorum*).

Some plant genera, including *S. nemorosa*, *D. cooperi* and *S. telephium*, were primarily visited by honeybees (Fig. 2A-B, D), whereas *L. stoechas*, *L. angustifolia*, *G. aristata, A. hybrida* and *P. atriplicifolia* were primarily visited by bumblebees (Fig. 2C, E-H). To honeybees, 2% (*N* = 2) of cultivars were completely unattractive, 21% (*N* = 25) relatively unattractive, 59% (*N* = 70) somewhat attractive, 12% (*N* = 14) moderately attractive and 6% (*N* = 8) of cultivars were perceived as highly attractive. For bumblebees, the degree of attractiveness among all cultivars was distributed as 4% (*N* = 5) completely unattractive, 13% (*N* = 15) relatively unattractive, 39% (*N* = 47) somewhat attractive, 34% (*N* = 40) moderately attractive and 10% (*N* = 12) highly attractive. Most of the highly attractive cultivars to honeybees were found among *S. nemorosa*, as for instance SV Salute Light Pink, SV Royal Magenta and SV Salute Ice Blue. Alternatively, most cultivars highly attractive to bumblebees were found among *L. stoechas*, such as Forte Deep Purple, LV07 and LV09. *S. telephium* had the majority of completely unattractive cultivars, particularly Crystal Pink and SE08, as these were both not visited by honeybees or bumblebees at all.

The number of bee species varied among cultivars and plant genera, ranging from 0 to 5 species (overview per cultivar in Tab. S5). For example, all *L. angustifolia* cultivars were visited by the same four bee species, whereas the number of bee species among *S. telephium* cultivars ranged between 0 and 4. We also observed that none of the *A. hybrida* cultivars were visited by *B. lapidarius*, while this was the most frequent visitor of *D. cooperi* cultivars. *D. cooperi* cultivars were hardly visited by other bumblebee species. *Lasioglossum spp.* and *B. pratorum* individuals were only

Table 1. Overview of total number of *A. mellifera*, *Bombus* spp. and *Lasioglossum* spp. observed per plant genus.

	A. mellifera	*B. terrestris*	*B. pascuorum*	*B. lapidarius*	*B. hypnorum*	*B. pratorum*	*Lasioglossum* spp.	Total
S. nemorosa	626	125	109	8	10	0	0	878
G. aristata	25	262	7	277	1	2	34	608
D. cooperi	466	1	5	74	0	0	0	546
L. angustifolia	263	280	204	116	0	0	0	863
L. stoechas	145	505	240	39	2	0	0	931
S. telephium	238	53	38	19	0	0	0	348
P. atriplicifolia	218	37	268	27	1	0	0	551
A. hybrida	105	52	215	0	0	0	0	372
Total	2086	1310	1072	566	14	2	34	5097


(A) Salvia nemorosa
(B) Delosperma cooperi
(C) Gaillardia aristata
(D) Sedum telephium
Visitation rate (bees/plot/minute)
Cultivar
Rose Marvel
SV Caramia
SV Caramia Rosa
SV Midnight Purple
SV Midnight Rose
SV Noble Knight
SV Royal Magenta
SV Salute Ice Blue
SV Salute Light Pink
SV Salute Neon Pink
SV11
SV12
SV13
SV14
SV15
DL RC Candy Red
DL RC Magenta Pop
DL RC Orange
DL RC Purple
DL RC White
DL RC Yellow
DL SS Orange
DL SS Purple
DL WOW Orange
DL10
DL11
DL12
DL13
DL14
DL15
GA Mango
GA Red Sky
GA Yellow Touch
GA04
GA05
GA06
GA07
GA08
GA09
GA10
GA11
GA12
GA13
GA14
GA15
Crystal Pink
SE02
SE03
SE04
SE05
SE06
SE07
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SE11
SE12
SE13
SE14
SE15
A. mellifera
Bombus spp.
Lasioglossum spp.

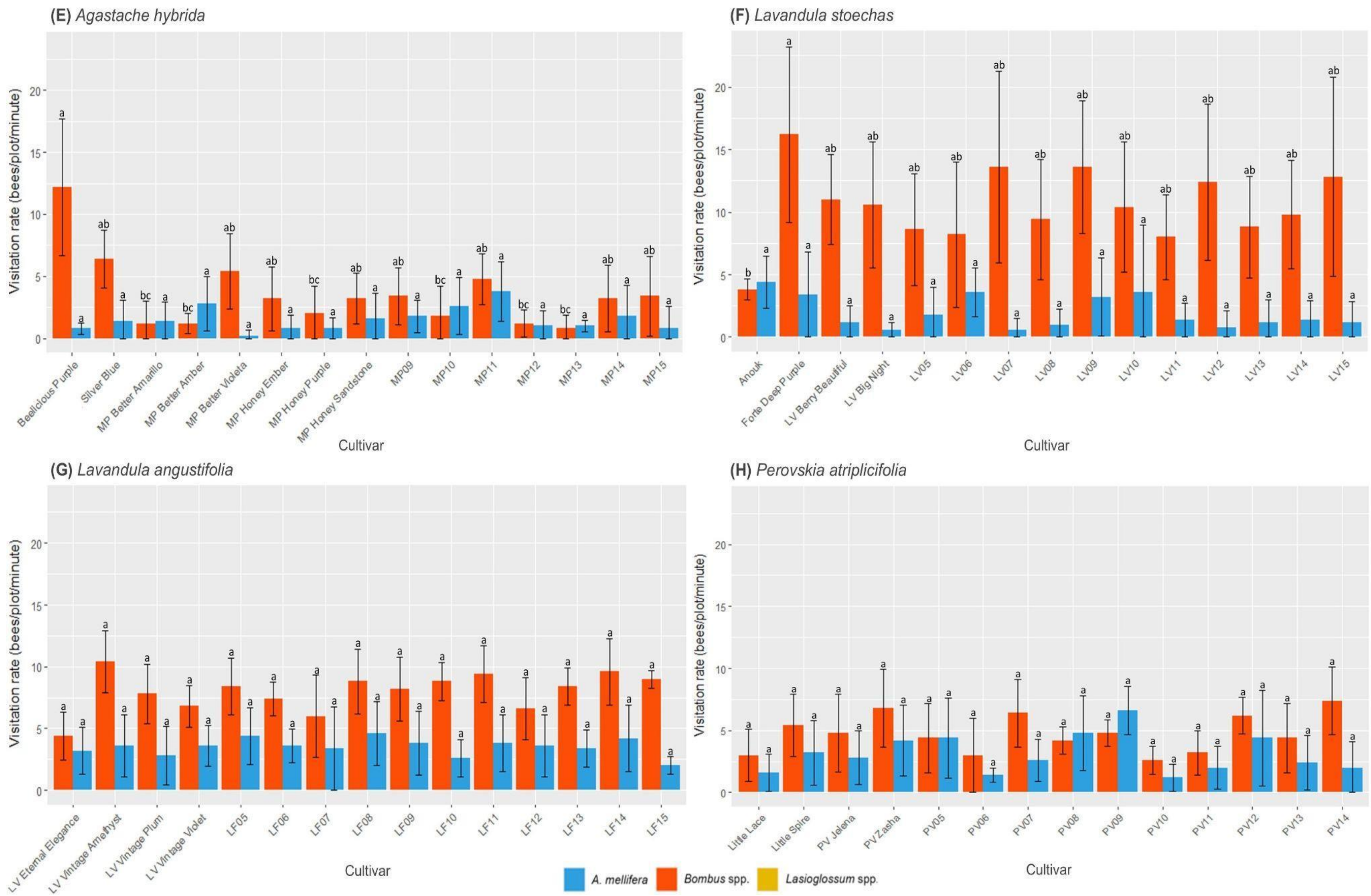

Figure 2. Bar plots for the average *A. mellifera* (Blue), *Bombus* spp. (Red) and *Lasioglossum* spp. (Yellow) visitation rate (bees/plot/minute) for (A) *S. nemorosa*, (B) *G. aristata*, (C) *D. cooperi*, (D) *S. telephium*, (E) *A. hybrida*, (F) *L. stoechas*, (G) *L. angustifolia* and (H) *P. atriplicifolia*. The error bars show the standard deviation and the letters represent the level of significance ($P < 0.05$) for each bee group. Cultivars with the same letter do not differ significantly from each other.

observed visiting *G. aristata* cultivars and *B. hypnorum* primarily *S. nemorosa* cultivars.

Across all plant genera, some cultivars varied significantly in bee visitation rate while others did not (Fig. 2). We also observed that the degree of variation in visitation rate and the degree of variation of floral traits (Tab. 2) appeared to be related for some plant genera. For example, plant genera such as *L. angustifolia*, *L. stoechas* and *P. atriplicifolia* had little to no significant variation in either honeybee or bumblebee visitation rate nor was there considerable variation in traits such as flower colour, nectar sugar content and corolla tube depth. For *S. nemorosa,* however, honeybee and bumblebee visitation rate as well as floral traits displayed a high degree of variation.

Variation in floral traits among cultivars

Across each plant genus we found cultivars with significant variation in floral traits, though some traits varied more than others (Tab. 2). For example, *S. nemorosa* and *A. hybrida* varied considerably across all floral traits, whereas *L. angustifolia*, *L. stoechas* and *P. atriplicifolia* only varied considerably in the number of flowers per plot.

The degree of variation of flower colour varied across all plant genera. *D. cooperi* and *A. hybrida* cultivars varied most in colour, while *P. atriplicifolia, L. angustifolia* and most *L. stoechas* cultivars were limited to various shades of purple. A UV-pattern was only detected among *D. cooperi* and *G. aristata* cultivars, but not all. The corolla tube depth varied significantly among cultivars of all plant genera. *A. hybrida* was the plant genus with the longest corolla tube, with corolla tube depth ranging from 7.37 mm to 20.64 mm among cultivars. The shortest corolla tube of 4.12 mm was found in *S. nemorosa*, though corolla tube depth among cultivars ranged up to 7.47 mm. The nectar sugar content was the lowest among *D. cooperi* cultivars with an average of 43.76 ± 17.66 μg (mean ± S.D.) ranging from 0 μg to 67.30 μg, whereas the highest nectar sugar content of 318.18 ± 219.55 μg (mean ± S.D.) ranging from 106.06 μg to 906.48 μg was measured among *A. hybrida* cultivars. The number of flowers in a cultivar plot varied considerably between plant genera and among cultivars, with cultivar averages ranging from 150 to 3,990 and 8,073 to 29,571 for *D. cooperi* and *L. stoechas*, respectively.

Relationship between floral traits and visitation rate

Honeybee visitation rate was positively related to a higher nectar sugar content for *D. cooperi* ($t = 5.715$, $P < 0.001$) and *A. hybrida* ($t = 2.341$, $P < 0.05$), whereas the nectar sugar content was negatively related for *S. nemorosa* ($t = -2.687$, $P < 0.05$) and *S. telephium* ($t = -2.498$, $P < 0.05$; Tab 2). While not significant, we found the same relationship to play a role positively for *P. atriplicifolia* ($t = 1.958$, $P < 0.1$) and negatively for *G. aristata* ($t = -2.095$, $P < 0.1$). There was also a significant decrease in honeybee visitation with an increase in corolla tube depth among *S. nemorosa* ($t = -3.375$, $P < 0.001$) cultivars and the same relationship, although not significant, was observed for *P. atriplicifolia* ($t = -1.839$, $P < 0.1$) and *L. stoechas* ($t = -1.880$, $P < 0.1$; Tab 2). Interestingly, honeybees visited *A. hybrida* ($t = 3.974$, $P < 0.01$; Tab 2) cultivars with a long corolla tube more often than cultivars with a short corolla tube. Among *G. aristata* cultivars red (mean = 0.38, S.D. = 0.27; $P < 0.01$) and yellow (mean = 0.73, S.D. = 0.31; $P < 0.05$) flowers were visited significantly less by honeybees than orange (mean = 2.13, S.D. = 1.63) flowers (Tab. 4). Honeybee visitation rate was also significantly lower for *G. aristata* cultivars with a UV-pattern ($t = -2.472$, $P < 0.05$; Tab. 3). For *S. nemorosa,* cultivars with pink (mean = 10.02, S.D. = 5.21; $P < 0.001$) or white (mean = 9.00, S.D. = 1.22; $P < 0.05$) flowers were visited significantly more by honeybees than purple flowers (mean = 4.03, S.D. = 3.56; Tab. 4). The number of flowers was not related to honeybee visitation rate for any plant genera.

Bumblebee visitation rate was positively related to a higher nectar sugar content among cultivars of *L. stoechas* ($t = 4.549$, $P < 0.001$) and *G. aristata* ($t = 2.694$, $P < 0.05$), while for *S. telephium* cultivars this relationship was negative ($t = -2.708$, $P < 0.05$; Tab. 3). The same relationship was found for *S. nemorosa*, although it was not significant ($t = 1.860$, $P < 0.1$; Tab. 3). Only for *A. hybrida* was corolla tube depth related to bumblebee visitation, with shorter corolla tubes being visited more often ($t = -5.180$, $P < 0.001$; Tab. 3). The number of flowers per plot had a significant positive relation to bumblebee visitation for *P. atriplicifolia* ($t = 3.607$, $P < 0.01$; Tab. 3) cultivars. In contrast, the number of flowers per plot were negatively related to bumblebee visitation rate for *G. aristata* ($t = -1.897$, $P < 0.1$), although this relationship was not

Plant species	Cultivar	Flower colour and UV-presence	Corolla tube depth (mm)	Nectar sugar content (µg)	Nr of flowers per plot
S. nemorosa	Rose Marvel	Dk. Pink	A	BC	EF
S. nemorosa	SV Caramia	Purple	CD	CD	G
S. nemorosa	SV Caramia Rose	Lt. Pink	E	DE	B
S. nemorosa	SV Midnight Purple	Purple	F	CD	A
S. nemorosa	SV Midnight Rose	Pink	E	CDE	DE
S. nemorosa	SV Noble Knight	Purple	AB	CD	A
S. nemorosa	SV Royal Magenta	Dk. Pink	CD	CD	CD
S. nemorosa	SV Salute Ice Blue	Lt. Purple	EF	AB	B
S. nemorosa	SV Salute Light Pink	Lt. Pink	EF	AB	G
S. nemorosa	SV Salute Neon Pink	Pink	CD	C	FG
S. nemorosa	SV11	Pink	EF	E	DE
S. nemorosa	SV12	Purple	A	AB	G
S. nemorosa	SV13	White	BC	A	CD
S. nemorosa	SV14	Dk. Pink	DE	CD	DE
S. nemorosa	SV15	Pink	A	CD	BC
G. aristata	GA Mango	✪ Orange	DEF	B	BCD
G. aristata	GA Red Sky	✪ Red	CDEF	B	DEF
G. aristata	GA Yellow Touch	✪ Red	BCD	B	BC
G. aristata	GA04	Red/Yellow	DEF	B	EFG
G. aristata	GA05	Orange	BCD	AB	G
G. aristata	GA06	✪ Yellow/Red	A	B	BC
G. aristata	GA07	✪ Red/Yellow	CDE	B	BCDE
G. aristata	GA08	Red	DEF	A	BCDE
G. aristata	GA09	✪ Yellow/Red	BCD	B	B
G. aristata	GA10	✪ Red	AB	B	FG
G. aristata	GA11	✪ Yellow	G	AB	BCD
G. aristata	GA12	✪ Orange/Yellow	EF	B	A
G. aristata	GA13	✪ Yellow/Red	A	B	CDE
G. aristata	GA14	✪ Red	FG	B	H
G. aristata	GA15	✪ Red/Yellow	ABC	AB	BCDE
D. cooperi	DL RC Candy Red	Red/Pink	NA	BC	E
D. cooperi	DL RC Magenta Pop	Purple/White	NA	D	D
D. cooperi	DL RC Orange	Orange/White	NA	CD	FG
D. cooperi	DL RC Purple	Purple	NA	AB	CD
D. cooperi	DL RC Yellow	Yellow/White	NA	A	EF
D. cooperi	DL RC White	White	NA	ABC	FG
D. cooperi	DL SS Orange	✪ Orange/Yellow	NA	ABC	B
D. cooperi	DL SS Purple	Purple/White	NA	AB	B
D. cooperi	DL WOW Orange	✪ Orange/Yellow	NA	ABC	AB
D. cooperi	DL10	✪ Purple/White	NA	E	EF
D. cooperi	DL11	✪ Purple/White	NA	DE	A
D. cooperi	DL12	✪ Purple/White	NA	ABC	AB
D. cooperi	DL13	Red/White	NA	BCD	C
D. cooperi	DL14	Red/White	NA	ABC	EF
D. cooperi	DL15	Dk. Orange/White	NA	ABC	G
S. telephium	Crystal Pink	Lt. Pink	NA	NA	NA
S. telephium	SE02	Yellow	NA	AB	NA
S. telephium	SE03	Dk. Red	NA	D	NA
S. telephium	SE04	DK. Red	NA	NA	NA
S. telephium	SE05	Dk. Pink	NA	A	NA
S. telephium	SE06	Yellow Mix	NA	ABCD	NA
S. telephium	SE07	Pink	NA	ABC	NA
S. telephium	SE08	Pink	NA	ABCD	NA
S. telephium	SE09	Yellow	NA	CD	NA
S. telephium	SE10	Yellow Mix	NA	D	NA
S. telephium	SE11	Yellow Mix	NA	ABC	NA
S. telephium	SE12	Yellow Mix	NA	ABC	NA
S. telephium	SE13	Yellow	NA	NA	NA
S. telephium	SE14	Pink	NA	BC	NA
S. telephium	SE15	Pink	NA	ABC	NA
			0 – 21	0 – 906	0 – 30,000

Table 2. Overview of average flower trait measurements, including colour and UV presence, corolla tube depth, nectar sugar content per flower or floret (for *G. aristata*) and the number of flowers per plot for each cultivar. Cultivars with a star in the colour dot have an identified UV-presence. For *G. aristata* and *D. cooperi*, multicoloured flowers are mentioned with the main colour noted first. The letters represent the level of significance ($P < 0.05$). Cultivars with the same letter do not differ significantly from each other.

Table 2 continued

Plant species	Cultivar	Flower colour and UV-presence	Corolla tube depth (mm)	Nectar sugar content (µg)	Nr of flowers per plot
A. hyrbida	Silver Blue	Lt. Purple	GH	AB	BC
A. hyrbida	Beelicious Purple	Purple	I	EFG	CD
A. hyrbida	MP Better Amarillo	Yellow	AB	FG	CD
A. hyrbida	MP Better Amber	Orange	A	BC	D
A. hyrbida	MP Better Violeta	Purple	GHI	CD	F
A. hyrbida	MP Honey Ember	Lt. Orange	EFG	DEF	B
A. hyrbida	MP Honey Purple	Purple	DEF	BCD	DE
A. hyrbida	MP Honey Sandstone	Lt. Orange	FG	CDE	A
A. hyrbida	MP09	Pink	A	ABC	D
A. hyrbida	MP10	Purple	BC	DE	DE
A. hyrbida	MP11	Pink	ABC	A	D
A. hyrbida	MP12	Yellow	BCD	FG	EF
A. hyrbida	MP13	Yellow	CDE	G	A
A. hyrbida	MP14	Dk. Pink	A	DEF	B
A. hyrbida	MP15	Purple	GHI	BCD	B
L. stoechas	Anouk	Purple	E	A	FG
L. stoechas	Forte Deep Purple	Purple	E	A	B
L. stoechas	LV Berry Beautiful	Purple	B	A	F
L. stoechas	LV Big Bight	Purple	C	A	A
L. stoechas	LV05	Purple	CD	A	E
L. stoechas	LV06	Purple	E	B	DE
L. stoechas	LV07	Purple	CD	AB	BC
L. stoechas	LV08	Pink	A	AB	CD
L. stoechas	LV09	Purple	ABC	A	A
L. stoechas	LV10	White	BC	A	B
L. stoechas	LV11	Pink	E	AB	CD
L. stoechas	LV12	Purple	BC	A	CD
L. stoechas	LV13	Lt. Pink	AB	AB	G
L. stoechas	LV14	Purple	BC	AB	BC
L. stoechas	LV15	Purple	BC	AB	A
L. angustifolia	LV Eternal Elegance	Purple	D	BCDE	CD
L. angustifolia	LV Vintage Amethyst	Purple	B	E	A
L. angustifolia	LV Vintage Plum	Purple	BC	AB	D
L. angustifolia	LV Vintage Violet	Purple	BC	DE	CD
L. angustifolia	LF05	Purple	BC	BC	BC
L. angustifolia	LF06	Purple	CD	AB	BC
L. angustifolia	LF07	Purple	CD	CDE	G
L. angustifolia	LF08	Purple	BC	BCDE	AB
L. angustifolia	LF09	Purple	BC	ABC	D
L. angustifolia	LF10	Purple	CD	AB	EF
L. angustifolia	LF11	Purple	CD	AB	DE
L. angustifolia	LF12	Purple	A	BCD	FG
L. angustifolia	LF13	Purple	CD	A	FG
L. angustifolia	LF14	Purple	BC	AB	EF
L. angustifolia	LF15	Purple	CD	ABC	D
P. atriplicifolia	Little Lace	Purple	FG	ABCD	E
P. atriplicifolia	Little Spire	Purple	BCDE	ABCD	AB
P. atriplicifolia	PV Jelena	Purple	GH	ABCD	AB
P. atriplicifolia	PV Zasha	Purple	FG	BCDE	A
P. atriplicifolia	PV05	Purple	B	DE	BC
P. atriplicifolia	PV06	Purple	A	ABCD	BCD
P. atriplicifolia	PV07	Purple	AB	AB	ABC
P. atriplicifolia	PV08	Purple	G	BCDE	CDE
P. atriplicifolia	PV09	Purple	H	ABCD	BCDE
P. atriplicifolia	PV10	Purple	BCDEF	BCDE	CDE
P. atriplicifolia	PV11	Purple	BCDE	E	DE
P. atriplicifolia	PV12	Purple	BC	ABC	AB
P. atriplicifolia	PV13	Purple	CDEFG	A	BCDE
P. atriplicifolia	PV14	Purple	BCDE	BCDE	A
			0 – 21	0 – 906	0 – 30,000

significant (Tab. 3). Bumblebees did, however, visit *G. aristata* cultivars with multicoloured flowers significantly more often (t = 2.792, $P < 0.05$; Tab. 3). *D. cooperi* cultivars with purple (mean = 1.33, SD = 0.90; $P < 0.5$) flowers attracted significantly more bumblebees than those with orange flowers (mean = 0.40, SD = 0.23; Tab. 4), while cultivars with a UV-pattern (t = -2.268, $P < 0.05$; Tab. 3) were visited significantly less. Other flower colours were not significantly related to bumblebee visitation rate in *D. cooperi*. For *A. hybrida*, bumblebee visitation rate was significantly higher for pink (mean = 3.80, S.D. = 0.87; $P < 0.001$), purple (mean = 5.20, S.D. = 3.89; $P < 0.05$) and orange (mean = 2.53, S.D. = 1.15; $P < 0.05$) flowers compared to yellow (mean = 1.07, S.D. = 0.23) flowers. However, purple ($P < 0.05$) and orange ($P < 0.01$) flowers were visited significantly less than pink flowers (Tab. 4).

No floral traits were related to either honeybee or bumblebee visitation rate among *L. angustifolia* cultivars (Tab. 3). Visitation of *Lasioglossum* spp. to *G. aristata* cultivars had a significant negative relationship to cultivars with a higher number of flowers (t = -2.743, $P < 0.05$; Tab. 3) and cultivars with orange flowers (mean = 1.20, S.D. = 1.40; $P < 0.05$) were visited significantly more than red flowers (mean = 0.35, S.D. = 0.30). Yellow flowers (mean = 0.53, S.D. = 0.42; $P < 0.1$) were also visited less than orange flowers, though this was not significant (Tab. 4).

Discussion

In this study, we investigated how different cultivars from eight different ornamental plant genera differed in attractiveness to bees and how this was related to floral traits. For most plant genera, cultivars varied significantly in bee visitation rate, with floral traits showing significant variation among cultivars of all plant genera. Cultivars were mostly visited by honeybees and bumblebees and the degree of cultivar attractiveness varied between these bee groups. Of the 119 cultivars the majority was considered unattractive or poorly attractive to honeybees (82%) and bumblebees (56%). Only a small number of cultivars were highly attractive to honeybees (6%) and bumblebees (10%), with no overlap in highly attractive cultivars between each bee group. Only *G. aristata* was visited by other wild bee species, namely *Lasioglossum spp*.

Most plant genera and cultivars were visited by honeybee and bumblebee species all of which are generalist foragers (Hall et al. 2021; Lanterman Novotny et al. 2023). A generalized bee community is common for ornamental plants (Rollings & Goulson 2019; Erickson et al. 2022). The primary presence of either honeybees or bumblebees among the observed plant genera could be an indication that honeybees and bumblebees differ in foraging preferences (Garbuzov & Ratnieks 2014a). Not all plant genera and cultivars were visited by all observed bumblebee species. We observed bumblebee species with distinct patterns of visitation of plant genera, where certain plant genera were either (almost) exclusively visited *(D. cooperi/B. lapidarius*; *S. nemorosa/B. hypnorum*; *G. aristata/B. pratorum*) or refrained from (*A. hybrida/B. lapidarius).* As most plant genera overlapped in peak flowering time, this could indicate a preference for certain plant genera among bumblebee species when foraging for nectar, despite being generalist foragers which is consistent with previously published studies of bumblebee preference when foraging for nectar (e.g. Goulson & Darvill 2004) or pollen (Roulston & Cane 2000; Vaudo et al. 2016).

Most plant genera were visited by honeybees and bumblebees. The lack of visitation of other wild bee species can likely be attributed to the location of the experimental site and might reflect the available community. Bees from other taxa have been observed, but at a distance of 1.0-1.5 km from the study site which is likely to be too far for many of these species as the maximum foraging range for these taxa is 500-1250 m (Zurbuchen et al. 2010). It is unlikely that these plants are unattractive to these bees, as studies such as Garbuzov & Ratnieks (2014b, 2015), Rollings & Goulson (2019) and Erickson et al. (2021, 2022) do show that ornamental plants, including several plant genera in this study, are capable of attracting bees from numerous taxa. To get more insight in the attractiveness of the plant genera studied to other bee species than honeybees and bumblebees, it would be valuable to replicate this study at a location(s) with a more (known) diverse bee community. Another interesting next step would be to see whether highly attractive cultivars are just as attractive to bees in more garden-like settings, where there are generally fewer flowers and other, more diverse, plant- and pollinator

Table 3. Output of separate MLR analysis with backward selection for *A. mellifera*, *Bombus* spp. and *Lasioglossum* spp. Non-significant variables have been noted with 'ns' and not applicable variables have been noted with 'NA'. The explained variance for each plant genera related to *A. mellifera* visitation rate: *G. aristata* R^2adj = 0.67, *S. nemorosa* R^2adj = 0.63, *D. cooperi* R^2adj = 0.69, *A. hybrida* R^2adj = 0.59, *L. stoechas* R^2adj = 0.15, *L. angustifolia* R^2adj = -0.15, and *P. atriplicifolia* R^2adj = 0.21; to *Bombus* spp. visitation rate: *G. aristata* R^2adj = 0.47, *S. nemorosa* R^2adj = 0.14, *D. cooperi* R^2adj = 0.48, *A. hybrida* R^2adj = 0.83, *L. stoechas* R^2adj = 0.58, , *L. angustifolia* R^2adj = 0.02, and *P. atriplicifolia* R^2adj = 0.48; and to *Lasioglossum* spp.: *G. aristata* R^2adj = 0.50.

Apis mellifera

	Gaillardia aristata			*Salvia nemorosa*			*Delosperma cooperi*			*Sedum telephium*			*Agastache hybrida*			*Lavandula stoechas*			*Lavandula angustifolia*			*Perovskia atriplicifolia*		
Independent variables	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p
(intercept)	3.802	5.746	1.860E-04 ***	130.588	3.757	0.004 **	3.800	6.485	2.05E-05 ***	0.893	3.065	9.030E-03 **	-0.884	-4.079	0.002 **	23.420	2.051	0.061 ·	-2.270E+00	-0.383	0.709	3.147	2.057	0.064 ·
NSC per plot	-1.753E-06	-2.095	0.063 ·	-15.104	-2.687	0.023 *	4.625E-05	5.715	7.11E-05 ***	-4.430E-03	-2.498	0.026 *	4.24E-08	2.341	0.037 *			ns	-8.252E-08	-0.507	0.623	5.647E-08	1.958	0.076 ·
Corolla tube depth			ns	-41.513	-3.375	0.007 **			NA			NA	5.31E-02	3.974	0.002 **	-26.930	-1.880	0.083 ·	5.795E-01	0.800	0.442	-3.666	-1.839	0.093 ·
Nr. flowers per plot			ns			ns			ns			NA			ns			ns	5.542E-05	1.250	0.240			ns
Hue angle			ns			ns			ns			NA			ns			ns	1.239E+00	0.566	0.584			ns
Multicoloured flowers			ns			NA			ns			NA			NA			NA			NA			NA
Flower colour			Tab. 4			Tab. 4			ns			ns			ns			ns			NA			NA
UV - present	-0.924	-2.472	0.033 *			NA			ns			NA			NA			NA			NA			NA

Bombus spp.

	Gaillardia aristata			*Salvia nemorosa*			*Delosperma cooperi*			*Sedum telephium*			*Agastache hybrida*			*Lavandula stoechas*			*Lavandula angustifolia*			*Perovskia atriplicifolia*		
Independent variables	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p	Estimate	t	p
(intercept)	-6.698E+01	-2.474	0.031 *	-2.681	-1.553	0.144	0.800	2.424	0.038 *	3.443	2.838	0.014 *	2.728	2.891	1.530E-04 ***	5.217E+00	4.141	1.160E-03 **	1.001E+00	1.301	0.222	2.964	5.135	2.470E-04 ***
NSC per plot	1.379E+01	2.694	0.021 *	0.525	1.821	0.092 ·			ns	-0.018	-2.708	0.018 *			ns	1.414E-06	4.549	5.47E-04 ***	2.853E-08	1.350	0.207			ns
Corolla tube depth			ns			ns			NA			NA	-1.996	-5.180	4.130E-04 ***			ns	5.051E-02	0.536	0.604			ns
Nr. flowers per plot	-6.647E-04	-1.879	0.084 ·			ns			ns			NA			ns			ns	-3.711E-08	-0.006	0.995	2.220E-04	3.607	0.004 **
Hue angle			ns			ns			ns			NA			ns			ns	-4.494E-01	-1.581	0.145			ns
Multicoloured flowers	3.017	2.792	0.018 *			NA			ns			NA			NA			NA			NA			NA
Flower colour			ns			ns			Tab. 4			ns			Tab. 4			ns			NA			NA
UV - present			ns			NA	-0.800	-2.268	0.049 *			NA			NA			NA			NA			NA

Lasioglossum spp.

	Gaillardia aristata		
Independent variables	Estimate	t	p
(intercept)	2.782	4.296	0.001 ***
NSC per plot			ns
Corolla tube depth			ns
Nr. flowers per plot	-1.707E-04	-2.743	0.019 *
Hue angle			ns
Multicoloured flowers			ns
Flower colour			Tab. 4
UV - present			ns

Table 4. The results of post-hoc pairwise comparisons using Tukey's HSD reveal how individual flower colours compare to each other for each MLR with flower colour included as an independent variable.

Apis mellifera

Gaillardia aristata				*Salvia nemorosa*			
Contrast	estimate	t	p	Contrast	estimate	t	p
orange - red	1.882	4.856	0.001 ***	pink - purple	7.820	3.259	0.009 **
orange - yellow	1.278	2.680	0.023 *	pink - white	-6.750	-1.546	0.153
red - yellow	-0.604	-1.587	0.144	purple - white	-14.560	-2.733	0.021 *

Bombus spp.

Delosperma cooperi				*Agastache hybrida*			
Contrast	estimate	t	p	Contrast	estimate	t	p
orange - purple	-0.933	-2.592	0.029 *	orange - pink	-0.377	-3.289	0.008 **
orange - red	-0.867	-1.880	0.093 ·	orange - purple	0.014	0.127	0.902
orange - white	0.400	0.617	0.552	orange - yellow	0.282	2.556	0.029 *
orange - yellow	0.200	0.309	0.765	pink - purple	0.390	3.071	0.012 *
purple - red	0.067	0.154	0.881	pink - yellow	0.659	5.895	0.000 ***
purple - white	1.333	2.124	0.063 ·	purple - yellow	0.269	2.347	0.041 *
purple - yellow	1.133	1.805	0.105				
red- white	1.267	1.967	0.081 ·				
red - yellow	1.067	1.656	0.132				
white - yellow	-0.200	-0.254	0.806				

Lasioglossum spp.

Gaillardia aristata			
Contrast	estimate	t	p
orange - red	1.434	3.894	0.003 **
orange - yellow	0.805	1.921	0.081 ·
red - yellow	-0.629	-1.788	0.101

communities. This would also show whether cultivars are consistently perceived as highly attractive or unattractive by more diverse bee communities.

Our results show that differences in bee visitation rate among cultivars were related to variation in floral traits. Which floral traits determined variation in visitation rate differed between honeybees and bumblebees. Nectar sugar content and flower colour were important factors in attracting honeybees and bumblebees, while corolla tube depth was only important to honeybees. We generally found that honeybees visited cultivars with a shorter corolla tube significantly more, particularly when proboscis length (6.0 ± 0.1 mm) (El-Aw et al. 2012; Mirmoayedi 2013; Shawer et al. 2021) was shorter than the corolla tube depth of a cultivar (Klumpers et al. 2019) as this can greatly affect nectar accessibility, foraging efficiency and handling time (Plowright 1987; Stang et al. 2007; Klumpers et al. 2019). For bumblebees the corolla tube depth generally did not pose a restriction, except for *A. hybrida* cultivars where bumblebees mainly visited the cultivars with the shortest corolla tubes (7-11 mm). Despite bumblebees having longer proboscises (*B. terrestris*; 7.6 ± 0.5 mm (mean ± S.D.), *B. pascuorum;* 8.5 ± 0.6 mm (mean ± S.D.), *B. lapidarius*; 7.7 ± 0.4 mm (mean ± S.D.; Goulson et al. 2005) than honeybees, their proboscises were still too short to effectively and efficiently collect nectar from *A. hybrida* flowers with very long corolla tubes. For some *A. hybrida* cultivars with longer corolla tubes nectar robbing by *B. terrestris* individuals was observed. This foraging tactic allows bees to access otherwise inaccessible nectar (Goulson et al. 2007; Leadbeater & Chittka 2008; Lichtenberg et al. 2020; Wester et al. 2020). Interestingly, honeybee visitation increased alongside an increase in corolla tube depth among *A. hybrida* cultivars. This was highly unanticipated since all *A. hybrida* cultivars had corolla tubes considerably longer (7-20 mm) than a honeybee proboscis. The *A. hybrida* cultivar most visited by honeybees had the longest corolla tube and the highest nectar sugar content of all 119 cultivars, which resulted in nectar filling up a larger part of the corolla tube (Tavares et al. 2016). Since flowers with a deeper corolla tube can produce more nectar (Plowright 1987; Klumpers et al. 2019), this likely increased nectar accessibility enough for honeybees to access the nectar again.

Flower colour also had a considerable role in cultivar attractiveness, although the preferred plant genera differed between honeybees and bumblebees. It was observed that certain purple-coloured cultivars of *S. nemorosa* and *A. hybrida* were perceived as highly attractive to honeybees and bumblebees, respectively. However, pink-coloured flowers were visited significantly more for both plant genera and white *S. nemorosa* flowers were also preferred over purple. For both plant genera this can be attributed to the favourability of other floral traits. Bees are known to deviate from their innate colour preferences and adapt their foraging strategy in favour of more rewarding or easily accessible flowers (Jones et al. 2015; Bauer et al. 2017; Erickson et al. 2022). For instance, *S. nemorosa* cultivars with pink flowers often also had a short corolla tube and were visited significantly more by honeybees. Additionally, pink *A. hybrida* and white *S. nemorosa* cultivars produced considerably more nectar compared to cultivars with yellow or purple flowers, respectively. Interestingly, *G. aristata* and *D. cooperi* cultivars with a UV-pattern were visited less honeybees and bumblebees, while flowers with a UV-pattern are generally perceived as more attractive (Chen et al. 2020). Relatively few bumblebees were observed visiting *D. cooperi* and even less honeybees visited *G. aristata,* which is likely the reason for these deviating findings.

Other floral traits that were not evaluated in our study could influence cultivar attractiveness. Pollen quantity and quality may have influenced *D. cooperi* or *G. aristata* attractiveness as these are known to be pollen plants. Cultivars of these plant genera had a low nectar sugar content (fitting for pollen plants) and bees have been observed actively collecting pollen for these plant genera. *G. aristata* cultivars were visited by *Lasioglossum spp*. which are oligolectic on Asteraceae pollen. However, Erickson et al. (2022) found that for several ornamental plants, pollen quality and quantity did not affect pollinator visitation frequency. For the other plant genera in our study, the role of pollen might be less important as these plants are nectar plants and many cultivars produce little to no pollen. Scent can play a role in the attraction of pollinators. Visitation by certain bee species appears to be related to specific volatile compounds, even in ornamental flowers (Erickson et al. 2022). However, it does not necessarily influence visitation frequency of bees at the community level (Erickson et al. 2022). Moreover, the response of bees to scent often comes from flower-naïve bees, as more experienced bees are less attracted by odour signals and more to other floral traits (Dobson 1987; Dötterl & Vereecken 2010).

Research is not yet conclusive about the extent and mechanisms of neighbour effects among plants, though the consensus is that neighbouring plants can affect a plant's attractiveness (Wolowski et al. 2017; Torices et al. 2021). A highly attractive cultivar can increase pollinator visitation of a neighbouring cultivar, whereas competition between neighbouring plants can decrease pollinator visitation (Wolowski et al. 2017; Torices et al. 2021). Due to the fixed positions of the cultivar plots, we were unable to account for the influence of neighbouring plants on cultivar attractiveness for which randomised neighbouring plots would have been ideal. However, compared to a 2022 study (de Haan, unpublished) at the same experimental site involving some of the same plant genera and cultivars, 88% of *D. cooperi, G. aristata*, *S. nemorosa* and *S. telephium* cultivars had different neighbouring cultivars compared to our 2023 study. The remaining 12% had either one or two of the same neighbouring cultivars as in 2022. In both cases, the same or different neighbouring cultivars, we found considerable overlap in highly attractive and unattractive cultivars compared to 2022. In addition, we found the same highly attractive cultivars for both 2022 and 2023, despite these cultivars having an unattractive neighbour in 2022 and another highly attractive neighbour in 2023. This suggests that neighbouring cultivars had little to no effect on cultivar attractiveness in this study.

Previous studies have explored the attractiveness of ornamental perennials to bees and other flower-visiting insects (Garbuzov & Ratnieks 2014, 2015; Garbuzov et al. 2015, 2017; Rollings & Goulson 2019; Erickson et al. 2020, 2021). However, very few have included the effect of both functional and visual floral traits on the attractiveness of plants to bees (but see Garbuzov & Ratnieks 2014a; Erickson et al. 2022). We observed similar patterns regarding corolla tube depth compared to both previous studies, where bees visited *S. nemorosa* cultivars with a short corolla tube more often (Erickson et al. 2022) and among *Lavandula* spp. corolla tube depth was a consistent but non-significant factor for bee visitation (Garbuzov & Ratnieks 2014a). In contrast, we observed honeybees visiting *A. hybrida* cultivars with a long corolla tube more often, whereas Erickson et al. (2022) only observed much larger bees (*X. virginica*) to visit such cultivars. Preference for flower colour also varied, though this can likely be attributed to our cultivars displaying more variation in colour along with a larger sample size per plant genus. A small sample size may also have prevented Erickson et al. (2022) from finding any relationship between nectar sugar content and bee visitation rate, as nectar production is highly variable, whereas we observed this to be significantly related across all studied plant genera. This shows how a larger sample size could be beneficial when looking at variations in floral traits, as it can represent a broader range of trait variations which is especially present in ornamental plants.

Overall, this study demonstrates that ornamental plants have the potential to be highly attractive to (generalist) bees (mostly honeybees and bumblebees), though the degree of attractiveness strongly depends on the cultivar and plant genus. Our results also highlight how minimal changes in floral traits can affect the overall attractiveness of a cultivar drastically and that bee species respond differently to these variations. It is important to emphasise that concessions on phenotypical characteristics are not necessary to create ornamental plants that are highly attractive to both humans and bees. This is useful information for plant breeders and should be used as an incentive to select for ornamental plants that can support bee populations while simultaneously enhancing urban green spaces.

Conclusion

With this study we demonstrate that differences in bee visitation rate among cultivars were directly related to variation in floral traits. For plant genera with a high degree of variation in floral traits, bee visitation rate differed significantly among cultivars of the same plant genus. We primarily observed honeybees and bumblebees, who despite being generalists, did not find the same cultivars and plant genera to be attractive. Moreover, among bumblebee species visitation patterns between plant genera varied, indicating that even generalist bee species have a preference for certain plant genera. Our results showed that cultivars with floral traits that promote nectar accessibility and foraging efficiency were visited more often, although the importance of these traits differed between honeybees and bumblebees. These associations between floral traits and pollinator preference are generally consistent with previously published studies of native plant–pollinator interactions, indicating that patterns of preference in generalist bees are largely conserved among ornamental plants. Only a few combinations of floral traits resulted in highly attractive cultivars, while the majority of cultivars were considered to be unattractive, receiving little to no visits. Thus, certain varieties of ornamental plants can be used for managed pollinator habitats, such as gardens, to support bees and floral phenotype may be used by plant breeders as a general guideline for informing cultivar selection for managed pollinator habitats such as gardens. Nevertheless, since pollinator species and taxonomic groups are known to exhibited distinct patterns of attraction to visual, chemical and nutritional traits of flowers, managing these habitats with a broad selection of plants and phenotypes will be necessary for supporting a species-rich and functionally diverse pollinator community (Normandin et al. 2017; Kremen et al. 2018). Planting native species, such as those typically considered 'weeds' (Balfour & Ratnieks 2022), remains important to support diverse bee communities as ornamental plants are not attractive or useful for all bee species, especially not for specialized bee species (Seitz et al. 2020). Overall, our study contains valuable information for plant breeders, showing which floral traits play a key role in the attractiveness of ornamental plants to generalist bee species and highlighting the potential to create ornamental plants that can support bee populations.

ACKNOWLEDGEMENTS

We thank Ellen van Sambeek and the rest of the Dümmen Orange Aalsmeer team for their guidance and hospitality, Dümmen Orange for access to the experimental site and plant material and Hanco Zwaan for providing access to the Jasco V-770 spectrophotometer.

AUTHOR CONTRIBUTION

Concept and design FV, JCB and SGTK, data collection FV, data analysis FV, writing manuscript FV, edits and approval for publication FV, JCB and SGTK.

DISCLOSURE STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data files used for statistical analysis are available here: https://github.com/femmsver/Ornamental_2024.git

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Overview of cultivar names and the number of plants per cultivar per plant genus

Table S2. Peak flowering time per plant genus

Table S3. Overview bee community surrounding the study site

Table S4. Overview plant community surrounding the study site

Table S5. Observed bee species for each cultivar per plant genus

Table S6. Analysis method visitation rate per plant genus

Table S7. Analysis method floral traits per plant genus

Figure S1. Visualization corolla tube depth per plant genus

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ISSN 1920-7603