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Urbanisation is known to change biodiversity patterns and plant–animal interactions such as pollination – a key ecological process. Floral traits like colour, size or UV-patterns are essential attractors for many pollinators. It is largely unknown, though, how the distribution of such floral traits within plant communities changes along an urbanisation gradient.

This study aims to understand to which extent floral traits known to attract pollinators are filtered by urban environments. We used dry grassland, spanning a broad urbanisation gradient in the Berlin metropolitan area, Germany, as a model ecosystem and identified the distribution of plant traits related to bee-perceived flower colours, UV reflection and flower size in 47 grassland patches. We analysed how these traits were related to abiotic and biotic factors at different spatial scales.

The most influent predictor was an abiotic factor measured at the landscape scale: the proportion of impervious surface, found to be positively related to UV-reflectance strength and floral UV patterns, but negatively to floral size diversity. At the local scale, abiotic factors showed an intermediary number of relationships. Temperature was negatively associated with the bee-colour 'green + UV-green' and with flower size. The light environment was negatively related to the same bee-colour and to floral size diversity. Biotic factors related to local pollinator communities were less important: species richness was negatively related to flower size, while proportion of bees to floral sizes diversity.

This study shows that floral traits known to attract pollinators are mostly filtered by abiotic factors related to urbanisation (share of impervious surface) or the urban heat island (local temperature). Biotic factors related to local pollinator communities were less important. These results increase our functional understanding of plant–animal interactions in cities by illustrating how urban environments modulate the attractiveness of plant communities to pollinators by filtering for floral plant traits.

Keywords: flower traits, plant assemblage, pollinator attraction, pollinator-mediated selection, urban ecology, urbanisation gradient

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Introduction

Urbanisation is an accelerating global trend with multifactorious effects on biodiversity patterns in cities (Aronson et al. 2014, Beninde et al. 2015) and on the functional composition of urban floras (Knapp et al. 2009, Williams et al. 2015). Changes in assemblages of plant traits can in turn impact major ecological processes like pollination (Fornoff et al. 2017). Among others, urbanisation can limit or foster the occurrence of plant species along urbanisation gradients, depending on the ability of plants to cope with the altered abiotic and biotic conditions. As a result, some species may become locally extinct while others will persist (Williams et al. 2009). The underlying processes can be linked to the ecological filtering theory (Keddy 1992), which predicts that only species with certain trait combinations are adjusted to urban stressors (Knapp et al. 2009).

Different urban drivers contribute to plant traits selection (Williams et al. 2009, 2015) and challenge plant recruitment (Piana et al. 2019). For example, habitat transformation and fragmentation as well as novel urban ecosystems modulate the establishment and long-term survival of plant species (Kowarik and von der Lippe 2018, Planchuelo et al. 2020). Furthermore, fragmentation of urban environments can lead to a loss of species that require large habitats (Beninde et al. 2015). In addition, harsh environmental conditions in cities can be related to the distribution and frequency of plant traits that often matter for pollination. For example, heat and drought stress (Pauleit et al. 2002, Dahlhausen et al. 2018) can favour species producing anthocyanins, the pigments responsible for the blue to pink coloration of the vast majority of angiosperms flowers (Schemske and Bierzychudek 2001, Warren and Mackenzie 2001, Wessinger and Rausher 2012). Also, flower colour or flower size are related to resource availability (Carroll et al. 2001, Strauss and Whittall 2006) and, finally, radiation can drive the diversification of floral UV-patterns among species (Koski and Ashman 2016).

Along with abiotic features of the urban environment, biotic features such as the presence of interacting animals relate to the occurrence of plant traits (Desaegher et al. 2019). Among these traits, the floral traits in particular are well investigated, as they are largely considered to have primarily evolved under the constraint of pollinators' selection (Faegri and van der Pijl 1978, Fenster et al. 2004, Harder and Johnson 2009). Known as pollination syndrome, this approach suggests that plant traits might be filtered by the presence or absence of specific pollinator organisms. Although a recent study indicates more pronounced effects of flowering plants on pollinators than vice versa in urban areas (Theodorou et al. 2020), the direction of causality in plant–pollinator functional relationships remains unclear, since other studies found pollinators to constrain the intraspecific expression of floral traits (Bode and Tong 2018, Irwin et al. 2018). These studies suggest that urban landscapes result in differentiated phenotypic selection for floral traits and conclude that pollination is the main species interaction being associated with patterns of floral traits selection. In detail, these studies documented a stronger selection for larger floral display size, measured as the number of open flowers per plant (Irwin et al. 2018), and flower size (Bode and Tong 2018) in urban sites than in rural areas. In addition, Desaegher et al. (2019) recently found entomophilous plants to be less frequent in urban areas, compared to rural areas, likely due to reduced pollinator availability.

An urban pollinator-mediated selection for floral traits can be due to pollinator declines in cities or to shifts in the composition of pollinator assemblages (Wenzel et al. 2020), as shown for bees and hoverflies (Bates et al. 2011, Verboven et al. 2014, Fischer et al. 2016, Persson et al. 2020). Pollinator-mediated selection of plants is therefore likely to happen in cities. Both field and laboratory experiments showed that convergence of floral assemblies on a restrained set of floral colours may reflect the visual abilities and preferences of the dominating pollinator guild, such as bees or flies (Chittka and Menzel 1992, Chittka and Raine 2006, Arnold et al. 2009, Shrestha et al. 2013b). The composition of pollinator communities can therefore be considered as a strong biotic filter shaping the conspicuousness of floral assemblies. Consistently, more recent studies in natural landscapes confirmed a pollinator-mediated selective pressure on floral attraction traits such as floral hues (Gray et al. 2018, Ishii et al. 2019) and floral UV Patterns (Koski and Ashman 2015) in plant assemblages.

Plant selection, mediated by pollinators' visual capabilities, is well established as a major driver of floral attraction traits composition in plant communities (Chittka and Menzel 1992, Shrestha et al. 2013a, 2014). However, previous studies largely did not specify the composition of pollinator assemblages (but see Koski and Ashman 2015). Although floral traits are sensitive to abiotic selection (Carroll et al. 2001, Strauss and Whittall 2006, Koski and Ashman 2016), the way abiotic factors shape floral trait composition is understudied compared to biotic interactions (Caruso et al. 2019, Dalrymple et al. 2020). Thus, previous studies have mainly focused on either biotic or abiotic filters (but see Dalrymple et al. 2020), and their respective selection strength on floral traits remain unclear. In order to improve the understanding of floral functional ecology, it is therefore essential to consider the entire range of selection agents (Dalrymple et al. 2020). Urban ecosystems remain very scarcely investigated (but see Bode and Tong 2018, Irwin et al. 2018, Desaegher et al. 2019) but offer opportunities to investigate the abiotic versus biotic selection pressure on floral traits – an understudied field in urban plant–animal interactions.

Our study aims to examine how floral traits in dry grassland plant communities relate to abiotic and biotic filters along an urbanisation gradient in Berlin. We focused on floral traits related to pollinator attraction (floral attraction traits) because the occurrence of these traits can be influenced by both environmental abiotic factors and pollinators (Caruso et al. 2019). Specifically, we investigated the expression of bee-perceived flower colours, the presence of patterns and strength of floral UV reflexions and the sizes of the flower units. To

disentangle the relative importance of abiotic versus biotic factors for the distribution of floral attraction traits in dry grasslands, we tested for the predictive power of: first, abiotic factors at the landscape scale (proportion of impervious surface, two landscape connectivity indices); second, abiotic factors at the local scale (temperature, light environment); and third, biotic factors (total pollinator richness, share of bee-pollinators within the pollinator assemblages).

We hypothesised that 1) abiotic urban filters influence plant species composition, thereby inducing a shift in floral attraction traits along an urbanisation gradient; that 2) the assemblage of pollinators along the urbanisation gradient is related to the occurrence of floral attraction traits, acting as a biotic filter; 3) that floral attraction traits are differently filtered by abiotic and biotic factors.

Material and methods

Study area and study system

Berlin is the largest city in Germany, with a surface area of 891 km^2 and a population of 3.8 million inhabitants in 2020 (Senate Dept for Urban Development and Housing 2021). The city has a large variety of land use types consisting of roughly 54% built-up areas, 21% woodlands, 12% parks, 6% water, 5% grasslands and 2% arable fields (Senate Dept for Urban Development and Housing 2021).

The study was conducted on a total of 47 sites (Fig. 1) belonging to the CityScapeLab Berlin, a research platform to untangle urbanisation effects on biodiversity and biotic interactions (von der Lippe et al. 2020). Forty-two of them were located in Berlin and five in the surrounding federal state of Brandenburg.

To study how abiotic and biotic factors filter floral traits along an urbanisation gradient, all sites were located in the same model ecosystem, i.e. in patches assigned to dry grassland according to the digital biotope maps of Berlin and Brandenburg (Senate Dept for Urban Development and Housing 2014). This type of ecosystem is an ideal study system because 1) it spans a broad urbanisation gradient in Berlin and surroundings and 2) it is generally of conservation concern in Berlin because they belong to the legally protected biotopes and due to the occurrence of species-rich plant communities and several endangered plant and animal species.

All dry grassland patches were stratified into six groups. First, two land-use historical continuity levels were determined by means of historical land-use maps leading to

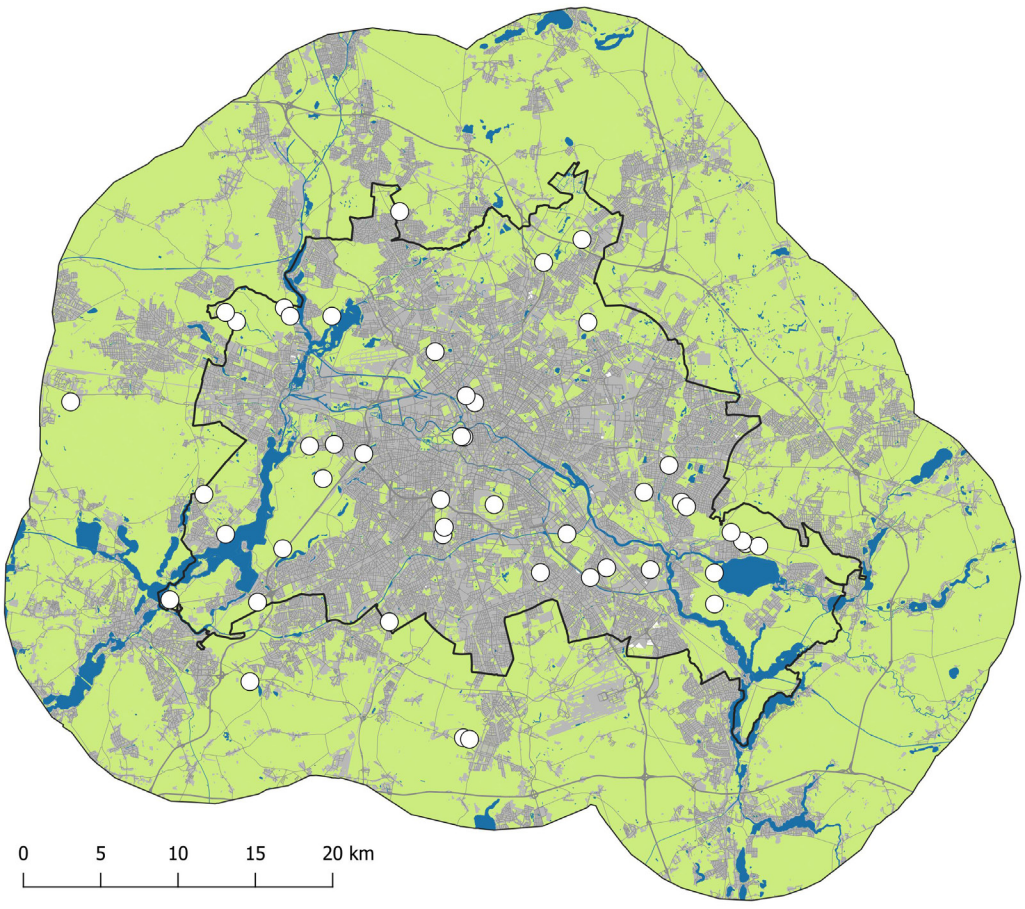

Figure 1. Location of the 47 study sites (white points) within the city borders of Berlin and a buffer of 10 km around Berlin (adapted from von der Lippe et al. 2020). Grey patches represent the sealed areas; green ones correspond to all types of green areas (including forests and parks); blue depicts waterbodies.

Table 1. Selected floral attraction traits and corresponding details on trait values calculation. The column trait information informs about the percentage of species for which we collected traits information.

Trait/data type	Trait values	Code	Trait calculation	Data base	Trait information
Bee-perceived colours					
Binary	'UV-blue + blue' (yes/no)	1/0	Proportions	FReD	78%
Binary	'blue-green' (yes/no)	1/0	Proportions	FReD	78%
Binary	'green + UV-green' (yes/no)	1/0	Proportions	FReD	78%
UV reflection					
Categorical	UV reflection strength: 0–7%/8–15%/16–27%/28–39%/40–66%/67–85%/85–100%	1–8	CWM	BiolFlor	78%
Binary	UV patterns (yes/no)	1/0	Proportions	BiolFlor	76%
Functional size of flower units					
Categorical	< 5 mm/5–10 mm/10–20 mm/20–30 mm/30–40 mm/> 40 mm	1–6	CWM/RaoQ	Flore Alpes	100%

a differentiation between 'old grassland' (already existed between 1910 and 1930) and 'new grassland' (established after this period). Second, we divided these two groups of land-use continuity into three levels of connectivity, defined by the share of dry grassland habitat in a buffer of 500 m around the respective patch. Finally, we selected dry grassland patches by creating random points in a similar number of biotopes in each group (for details on site selection see von der Lippe et al. 2020).

Vegetation survey

Vegetation relevés were conducted in 2017 on 4 × 4 m plots randomly located at the 47 grassland patches. To achieve a complete inventory of plant species, each plot was surveyed between March and April and a second time between July and August 2017. On each plot, all vascular plants were recorded, the species' cover was visually estimated in 10% increments (van der Maarel and Franklin 2012). The data were stored and tabulated with the software TURBOVEG for Windows (Hennekens and Schaminee 2001). The identification of the species followed Jäger (2011), the taxonomy Buttler and Thieme (2017).

As this study focuses on floral traits of entomophilous plant species, two groups of taxa were excluded from the analyses: wind-pollinated graminoids (Poaceae, Juncaceae, Cyperaceae) and juvenile woody species that do not flower at the sites due to grassland management.

Traits selection

In order to assess the visual attractiveness of plant species for pollinators, we selected three floral traits: the bee-perceived flower colour, the floral UV reflection and the size of the flower units. To analyse these traits, we classified and quantified separately the different values for each trait (see Table 1 for details).

Bee-perceived colour

Flower colouration is a key functional trait for plant–pollinator interactions (Oberrath and Bohning-Gaese 1999, Ômura and Honda 2005). We focused on bee-perceived colours because the human perception of flower colours is an inaccurate measure for pollination ecology and is not optimal for coding colours, even though some correlations exist due to partial overlap in the spectral perception (Chittka 1997). Bees' visual perception of flowers has been well researched over the last decades (Dyer et al. 2008, 2015). The bee colour hexagon model (Chittka 1992) is the most commonly used model in pollination ecology and considers the characteristic sensitivities of hymenopterans' photoreceptors (green, blue and UV). We followed the approach of Chittka et al. (1994), who divided the bee colour hexagon among six colour categories: UV-blue, blue, blue-green, green, UV-green and UV. We extracted information relative to the bee colour hexagon model from the Floral Reflectance Database FReD (Arnold et al. 2010). To visualise the distribution of species in the hexagon, we plotted them with coordinates obtained from the reflectance measurements (Fig. 2). To avoid too sparsely distributed categories (especially in the UV ranges), we merged the categories UV-blue and blue, and the categories green and UV-green, resulting in two aggregate categories: 'UV-blue + blue' and 'green + UV-green'. We kept the bee-colour 'blue-green', since the majority of species were assigned to this colour, but omitted the UV category, which was represented by only one species (*Papaver argemone*) occurring in two study sites. Since closely related plant species tend to have similar trait values (Swenson 2014), we substituted missing data by bee-colour information available for phylogenetic and phenotypically closely related species. More precisely, we selected species from the same genus and displaying the same human-perceived colour, except for *Armeria maritima* subsp. *elongata* and *Convolvulus arvensis*, for which similar-flowering substitution species belonging to the same families were found (Supporting information). This way, we collected trait information for 121 species, representing 78% of the considered plant species. Flower colour information remained however missing for 35 species, for which no species from the same genus displaying similar human-perceived colour was found in the data base.

UV reflection

Pollinators are able to perceive UV reflected rays and in some plant species, these rays are reflected by flowers in the form of patterns (Knuth 1891), which provide information about the location of flower rewards to pollinators (Petropoulou et al.

2001, Koski and Ashman 2014). We extracted information about the presence or absence of UV-patterns in flowers and about the strength of the UV reflection in the peripheral part of flowers from the database BiolFlor (Kühn et al. 2004).

Size of flower units

Flower size is an important attractor for bee visits (Spaethe et al. 2001). Large flowers show increased pollinator visitation rates (Campbell et al. 1991, Sletvold et al. 2010). We extracted the sizes of flower units from the website Flore Alpes (<www.florealpes.com>) and classified them into six size levels (Table 1). We used categories to avoid mistakes in the attribution of values, possibly occurring when using non-self-measured values extracted from databases. We defined the six categories following Ricou et al. (2014) and used the average between the available minimum and maximum size values to determine the corresponding category. We then ensured species were sufficiently distributed among them. For flower unit, we addressed single flowers, or the whole inflorescence in the case of species displaying umbels, heads or capitula (e.g. *Apiaceae*, *Asteraceae* and some *Fabaceae*).

Abiotic predictors

We included abiotic predictors at the landscape and local scales into our analyses, since both matter for urban plants or pollinators (Williams et al. 2009, Ayers and Rehan 2021). These predictors have been established in the CityScapeLab Berlin (see von der Lippe et al. 2020 for details). At the landscape scale, we first chose the proportion of impervious surface in a buffer of 100 m from the edge of the grassland patches, as a well-established proxy for the level of urbanisation (Moll et al. 2019). The impervious surface has been quantified in ArcGIS ver. 10.3 (ESRI), based on the Berlin Impervious Soil Coverage map from the Berlin Environmental Atlas (Senate Dept for Urban Development and Housing 2016). Second, we included two measures of the spatial connectivity with regard to the surrounding biotopes patches: 1) dry grassland patches exclusively, 2) all vegetated open areas from which species can potentially migrate into dry grassland patches such as meadows, lawns, grasslands, gardens, parks, but excluding forests and woodlots, which are less attractive for many pollinators. We determined connectivity values based on the pairwise distances (d) between the centre of plots (i) and surrounding biotope patches (j), as well as the area (A) of these patches (j) according to (Hanski 1994) as follows:

$$C_i = \sum_{j \neq i} \exp\left(-\alpha d_{ij}\right) A_j$$

We used a = 1, which corresponds to a strong weighting of the patch areas. Patch areas and distances between vegetation plots and the surrounding biotope patches (separately for dry grassland patches and all open vegetated areas) were calculated by using ArcGIS ver. 10.3 (ESRI), based on the Biotope Types map from the Berlin Environmental Atlas (Senate Dept for Urban Development and Housing 2014). We considered connectivity measures as reverse variables of the landscape fragmentation, described by Williams et al. (2009).

At the local scale, we measured air temperature and sky view factor (SVF) as important environment features for both plants and pollinators (see von der Lippe et al. 2020 for details). The temperature was measured every ten minutes from March to December 2017 with USB data loggers (Lascar EL-USB-2+) fixed to a two-meter-high pole located at the northwest corner of each study plot. For this study, we calculated the mean values per plot for daytime. SVF was used as measure of light environment on the plots. Fisheye photos of the sky were taken from the plot midpoints at 1.5 m height in October 2017. SVF was calculated from the photos according to Holmer et al. (2001), using the software SOLWEIG1D ver. 2015a. The SVF measures the share of open sky, ranging from zero (completely obscured sky) to one (completely open sky).

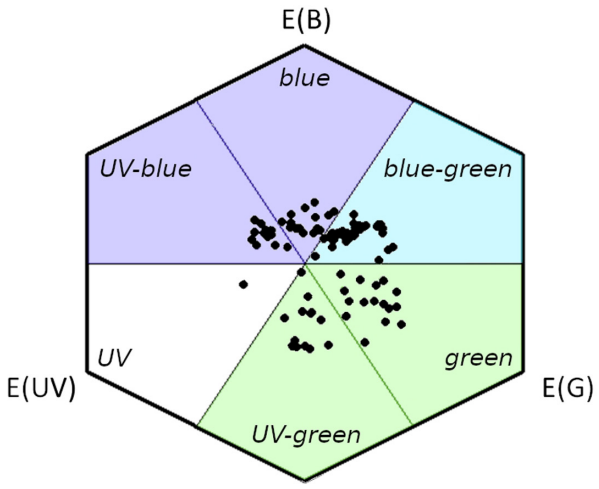

Figure 2. Bee colour hexagon and the floral colour loci of recorded species. Species coordinates are extracted from the FReD database (Arnold et al. 2010). Each point corresponds to a recorded species, or a species used as proxi in case of missing data. The hexagon is divided into six sectors corresponding to the bee-perceived colour categories as determined by Chittka et al. (1994). Background colours indicate the categories considered in this study: 'UV-blue + blue' (33 species), 'blue-green' (49 species) and 'green + UV-green' (36 species).

Biotic predictors

We analysed the composition of pollinator assemblages as a biotic predictor of the distribution of floral attraction traits in plant species. We sampled bees and hoverflies three times between May and September 2017 during periods of good weather (minimum 15°C, low wind, no rain and dry vegetation) (Bates et al. 2011). Using pan traps placed at each study site allowed us to simultaneously sample all sites using the same sampling effort with a reduced collector and temporal bias while obtaining a standard estimate of bee species

richness and abundance (Westphal et al. 2008, Devigne and De Biseau 2014). Pan traps consisted of 15-cm-diameter plastic bowls, spray-painted in UV-bright yellow, white and blue (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich, Germany) and filled with 300 ml of 4% formaldehyde solution and a drop of detergent to reduce surface tension. Pan traps had different colours (blue, white and yellow) to attract the widest possible range of pollinators (Bates et al. 2011, Gollan et al. 2011). Three pan traps (one of each colour) were randomly positioned at each site in a cluster, next to each vegetation plot, and attached to wood sticks 30 cm above the ground to minimise strata collection bias. We placed one set of traps in sites for three days. Once insects were sorted, we identified bees and hoverflies at the species level (Gathof et al. 2019). Other pollinator groups (e.g. butterflies, moths) were underrepresented in pan traps and therefore not identified. In order to avoid bias in the dataset, related to fluctuating abundances of honeybees due to beekeeping activities in the surrounding of the study sites, we excluded *Apis mellifera*. As predictor variables, we used 1) the combined species number of wild bee species and hoverfly species as total pollinator species richness and 2) the share of wild bees in the abundance of all pollinators (i.e. wild bees and hoverflies).

Data analysis

In order to detect potential changes in floral traits among study sites, we quantified the floral trait values with three approaches, according to data type and always considering the cover of the recorded plant species as a proxy of flower production. First, for binary traits, we calculated the traits' proportions with the vegetative cover values directly (Table 1). Second, we calculated community weighted means (CWM) to quantify the categorical trait values (Table 1), considering the coded categorical values as continuous. This index provides a mean of the species trait values within the communities, weighted by their cover value. Third, we calculated the diversity of values displayed within one single trait by applying Rao's quadratic entropy (RaoQ) to the categorical levels of flower sizes. This measure considers the relative abundance of species as well as the pairwise measure of functional differences between species in the case of a multi-traits approach (Botta-Dukat 2005); however, the approach is also reliable for single-traits methods (Leps et al. 2006).

We analysed the effects of five selected abiotic and two biotic predictors on each functional trait using GLMs. Each trait value listed in Supporting information was analysed independently as a single response variable and tested against seven explanatory variables. The abiotic predictors cover the landscape scale (proportion of impervious surface, dry-grassland connectivity, vegetated open area connectivity) and the locale scale (mean daily temperatures, sky view factor); the biotic predictors were the pollinator species richness and the share of wild bees in the abundance of recorded pollinators.

Prior to the statistical analysis, we tested response variables for spatial autocorrelation using Moran's I autocorrelation coefficient (Supporting information). We checked non-collinearity between the explanatory variables as well, computing Pearson or Spearman correlation coefficients (respectively for normally or non-normally distributed data; Supporting information). Since overdispersion was detected for five from seven traits values, we used quasi-Binomial GLMs for the binary traits (bee perceived colours and UV patterns), and a quasi-Poisson to analyse the size diversity of flower units (Supporting information). Two variables (UV reflectance strength and the floral size diversity) displayed normal distributions and were therefore analysed with linear models. To select the best fitting model, we defined the minimum adequate model by analysis of deviance (Zuur et al. 2009) and used the residual deviance as a measure for goodness of fit, calculating the adjusted R^2, using the package rsq (Zhang 2017). The summaries of selected models are given in the Supporting information. All statistical analyses were carried out with R ver. 4.0.3 (<www.r-project.org>), using the R-package FD (Laliberté and Legendre 2010) to compute CWMs and RaoQ.

Results

Floral traits and pollinator data

In total, 156 herbaceous plant species were recorded (Supporting information), ranging from seven to 39 (mean = 21.78, SD = 6.57) species per grassland plot. We were able to compile information about bee colour for 121 or 78% of all considered plant species, representing 87% of the total herbaceous plant cover. Thirty-three plant species belonged to the colour category 'UV-blue + blue', 49 to the category 'blue-green' and 38 to the category 'UV-green + green'. One species belonged to the 'UV' category. We compiled information about UV reflection for 120 of the 156 species, representing 60% of the total herbaceous plants cover. Nearly a third of these (47) displayed UV patterns while 73 species did not. Finally, information about floral size was available for all species. Regarding pollinators, we collected 1964 individuals, including 105 wild bee species and 30 hoverfly species (Supporting information). The richness of bee species varied between three and 21 per plot (mean = 9.59, SD = 4.04) and that of hoverflies between one and nine (mean = 4.84, SD = 1.74).

Role of abiotic and biotic predictors for the distribution of attraction traits in grasslands

A range of abiotic and biotic predictors were significantly related to the distribution of floral attraction traits in the grassland plots. Among these traits, only the flower size diversity was spatially autocorrelated. Floral attraction traits were mostly associated with abiotic predictors. The proportion of impervious surface in a 100 m buffer was positively related to the UV-reflectance strength (GLM; $p = 0.004$; $R^2 = 0.181$; Fig. 3a) and the proportion of plant species displaying floral UV patterns (GLM; $p = 0.011$; $R^2 = 0.216$; Fig. 3b). In

contrast, impervious surface was negatively associated with the floral size diversity (GLM; $p = 0.024$; $R^2 = 0.267$; Fig. 3c). The two landscape connectivity indexes showed no significant relationships with the investigated trait distribution in the grassland plots. Both abiotic predictors measured at the local scale were associated with floral traits distribution. The temperature was negatively associated with the bee-colour 'green + UV-green' (GLM; $p = 0.046$; $R^2 = 0.239$; Fig. 3d) and with the size of flower units (GLM; $p = 0.029$; $R^2 = 0.191$; Fig. 3e). The light environment (SFV) was negatively linked to the bee-colour 'green + UV-green' (GLM; $p = 0.0392$; $R^2 = 0.239$; Fig. 3f) and to the diversity of flower sizes (GLM; $p = 0.017$; $R^2 = 0.267$; Fig. 3g). The proportion of bees was negatively associated with the diversity of floral sizes (GLM; $p = 0.041$; $R^2 = 0.267$; Fig. 3h). Pollinator richness also displayed a negative association with the size of flower units (GLM; $p = 0.047$; $R^2 = 0.191$; Fig. 3i).

All relationships considered, abiotic factors were more associated with the distribution of floral trait values than the biotic ones (Fig. 4). The proportion of impervious surface around the studied grassland patches was significantly related to three trait values, while both abiotic factors measured locally (temperature and SVF) were respectively associated with two traits. Biotic filters played a limited role, since the proportion of wild bees and the pollinator richness were respectively associated with one single trait.

Discussion

How the response of functional plant traits to urban environmental conditions influences biodiversity patterns and ecological processes is an important question for understanding urban biodiversity (Knapp et al. 2021). Floral traits are key in plant–pollinator interactions and outside cities their distribution in plant communities is known to be mediated by environmental factors (Caruso et al. 2019). This is the first study that investigates the relative importance of abiotic and biotic factors in shaping the floral trait distribution in the same type of a plant community along an urbanisation gradient. Our findings demonstrate that both abiotic and biotic factors were related to floral trait distribution in dry grassland, but in different ways. Abiotic factors related to urbanisation were the most influential predictors while biotic factors related to local pollinator communities were less important. The proportion of impervious surface around the studied grassland patches was significantly related to three of the seven investigated trait values, while abiotic factors measured locally were associated with less floral traits. Biotic filters played a limited role.

Role of the abiotic factor

Our findings confirmed our first hypothesis that floral attraction traits in dry grassland plant species are mediated by abiotic factors. In particular, the proportion of impervious surface, a well-established indicator of urbanisation (Moll et al. 2019), was significantly related to three of the seven investigated trait values. High proportions of impervious surface can limit the availability of natural and semi-natural habitats and therefore filter species that are not adapted to anthropogenic habitat transformations, with consequences for the occurrence of specific traits (Palma et al. 2016). For example, flowers displaying UV-patterns were more frequent in grasslands located in densely built areas than in grasslands surrounded by higher shares of pervious surface. This adds evidence to the findings of Knapp et al. (2008), who generally found higher proportions of plants displaying UV-reflecting flowers in urban compared to rural areas. However, our analyses go further, as we show a direct link to the proportion of impervious surface along an urbanisation gradient. The higher proportion of species displaying UV patterns in densely built areas and the increased UV reflection strength of flowers relate to an increased attractiveness for pollinators (Rae and Vamosi 2013). These results suggest the presence of a facilitative strategy within plant communities in highly urbanised areas. Facilitative strategies at the plant community level such as floral signal convergence were already found to be a common phenomenon in varying ecosystems such as tropical forests (Feinsinger 1987, Dalrymple et al. 2020) or temperate grasslands (Hegland et al. 2009, Hegland and Totland 2012). Our results suggest that such strategies also exist in urbanised areas.

At the local scale, light environment was significantly related to the occurrence of bee-perceived flower colours in different ways. Specifically, the 'green + UV-green' flowering species occurred less in light exposed environments. The observed shifts in colour values could result from a linkage between habitat transformation at the landscape scale and the on-site light environment, possibly due to low SVF values – indicating more shady habitats – in densely built areas (Mirzaee et al. 2018). However, the proportion of impervious surface was not related to the SVF (Supporting information), indicating an independent effect of the light environment on the floral attraction trait of dry grassland species.

An initial way to interpret these relationships would be the sensory drive theory, which postulates that urban environmental conditions are likely to be important drivers of signalling colours, since they can bias the conspicuousness (Endler 1992). The ambient amount of light shaped by the surrounding physical structure and its impact on flower colours has been investigated for several ecosystems (Altshuler 2003, Binkenstein and Schaefer 2015, Dalrymple et al. 2020). Our findings show an association between the light environment and the occurrence of flower colours within urban environments, contrasting with studies on tropical forests (Altshuler 2003) and temperate forests and grasslands (Binkenstein and Schaefer 2015). In a recent study, Dalrymple et al. (2020) found the chromatic contrast of flower colours to be correlated with solar radiations across a broad range of ecosystems. Although the broad scale differs in size from our study, their findings are congruent with our results and support the idea that light environment drives the distribution of pollinator perceived floral colouration.

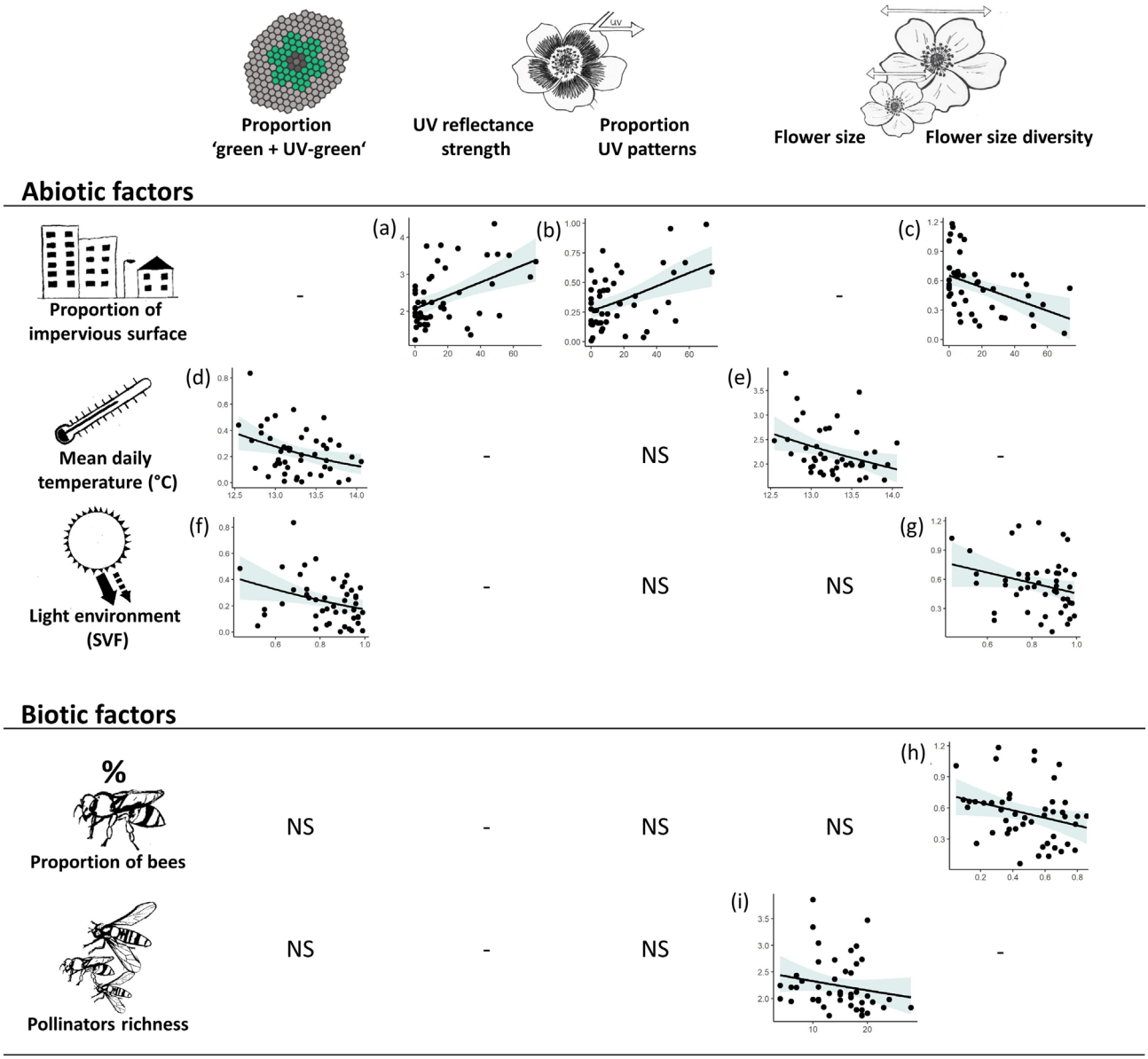

Figure 3. Effect sizes and CI (95%) of GLMs showing relationships between the tested abiotic and biotic predictor variables (x-axis) and the investigated attraction traits (y-axis). Only plots corresponding to significant relationships in GLMs are displayed (plots a–i; $p < 0.05$). The tested factors retained in the models but showing no significant effect are indicated with 'ns'.

In addition to light environment, we detected a similar relationship between 'green + UV-green' flowering species and the mean daily temperatures. We assume the observed effects induced by abiotic factors on flower colour to be linked to a protection mechanism established by plants in response to stressors, including heat and UV damage (Warren and Mackenzie 2001, Mori et al. 2005, Strauss and Whittall 2006). Our results suggest that such protection mechanisms also occur in urban environments and may result in a filtering of species producing at least limited amounts of anthocyanins. This pigment is responsible for many colourations such as human-perceived pink, purple or blue (Davies 2008). This could explain that species displaying flowers reflecting in the 'UV-blue + blue' and 'blue-green' range well persist, while the ones reflecting in the 'green + UV-green' range are disfavoured in harsh conditions.

Still, a review conducted by van der Kooi et al. (2019) led to the assumption that adapting flower colour may not be an efficient strategy to protect the floral organs from challenging ambient conditions, compared to other floral traits such as shape, orientation, pubescence or opening-closing movements. Our findings support this concept too, since we found higher temperatures to be related to small flower units. According to the resource-cost hypothesis, displaying reduced

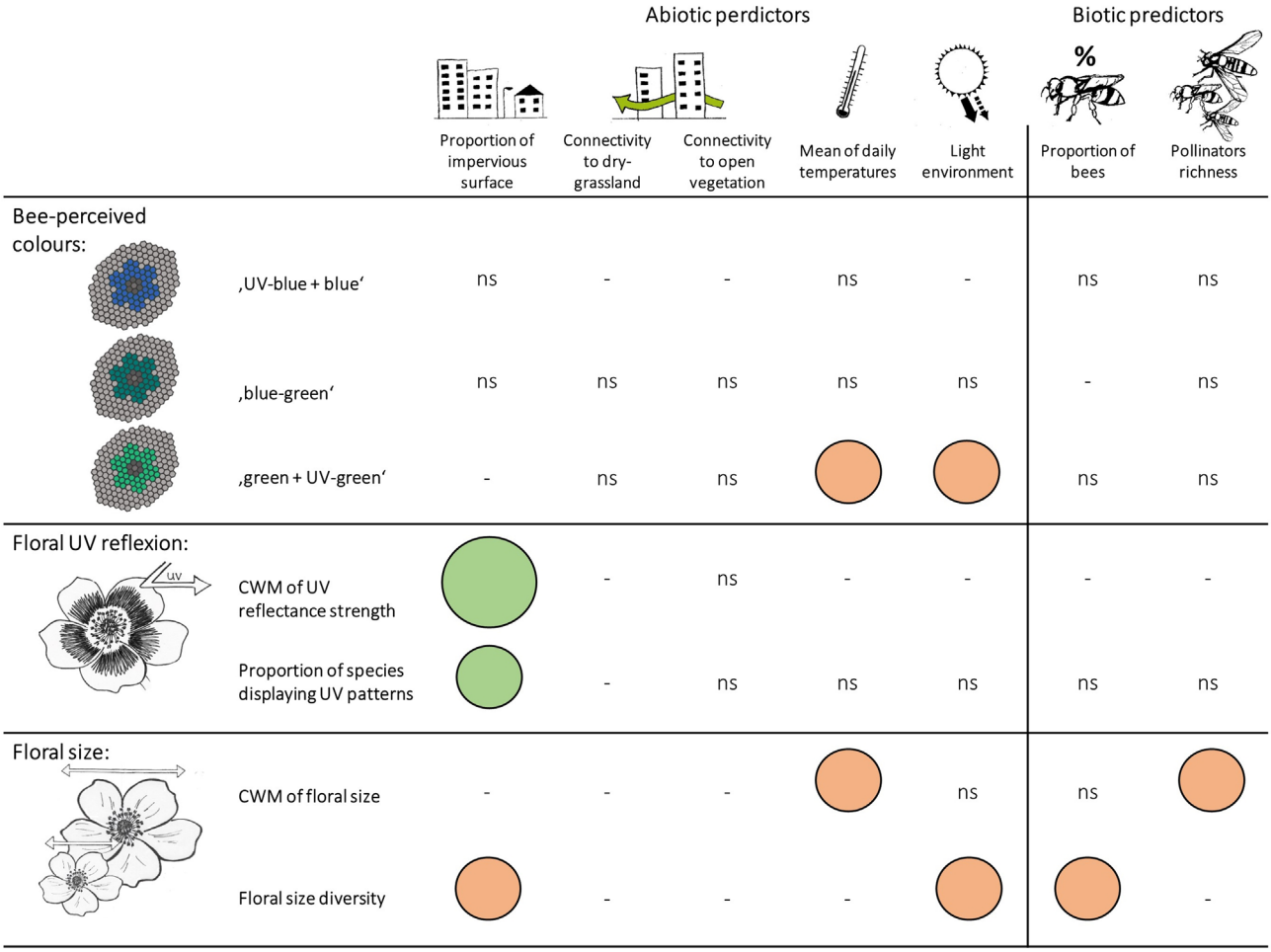

Figure 4. Overview of relationships between traits and predictors. Positive relationships are displayed by green dots, negative by orange. Relationships with $0.01 < p < 0.05$ are depicted in small dots and relationships with $p < 0.01$ in larger dots. The tested factors retained in the models but showing no significant effect are indicated with 'ns'.

corollas is favourable for plants growing under stressful environmental conditions (Herrera 2005). Although displaying larger flowers may be more efficient to attract pollinators, flower size may therefore result from a resource-cost compromise between low-energy morphology and pollinator attractiveness (Strauss and Whittall 2006). Our results are in line with these hypotheses and add evidences of species displaying smaller inflorescences to be less sensitive to warmer conditions and desiccation and therefore more likely to persist in warm urban areas. Our study thus suggests that the urban heat island modulates not only plant phenology (Jochner and Menzel 2015) but also the distribution of functional floral traits.

Role of the biotic factor

Several studies have observed relationships between floral traits and biotic factors within a range of ecosystems (Cariveau et al. 2004, Bode and Tong 2018, Irwin et al. 2018, Dalrymple et al. 2020). However, in our study, biotic factors were less important for floral traits distribution than abiotic ones. We found significant relationships suggesting that the size of flowers is under pollinators' constraint, as previously found in urban areas (Bode and Tong 2018, Irwin et al. 2018). Moreover, the proportion of bee-pollinators was negatively associated with the diversity of flower sizes, suggesting that bees apply a phenotypic selection on a narrow range of flower sizes. We failed to detect a relationship between pollinators' richness and the range of colours displayed by plant species in dry grasslands, as expected. However, we cannot entirely exclude that pollinator-mediated selection does constrain the expression of floral colours within urban plant communities, since our methodological approach covered wild bees and hoverflies – but not other flies, butterflies and beetles, which are relevant pollinators as well (Rader et al. 2016).

Relative importance of abiotic and biotic filters on trait selection

We observed the biotic factors to be less associated with the distribution of floral trait values than the abiotic ones. These contrasted associations confirm our third hypothesis – in

accordance with a recent meta-analysis (Caruso et al. 2019). Other floral traits such as 'efficiency traits' could be more constrained by pollination and therefore be more strongly associated with shifts in pollinator assemblages, as found by Caruso et al. (2019). Although pollinator-mediated selection on floral traits happen in natural environments (Koski and Ashman 2015, Gray et al. 2018, Ishii et al. 2019), its limited role in cities might be due to the fact that links between floral traits and pollinators evolve over a very long time (Ollerton et al. 2009). Urbanisation is often related to the development of novel ecosystems, harbouring species with different eco-evolutionary experiences, since urban environments often distinctly differ from the environments species experienced in their evolutionary past (Heger et al. 2019). The time-span might be thus too short for a pollinator-mediated trait selection in urban settings.

Conclusion

Our study supports the functional understanding of plant–animal interactions in cities by illustrating how urban environments modulate the attractiveness of plant communities to pollinators by filtering for floral plant traits. We identified the relative importance of abiotic versus biotic factors in driving the floral traits' composition within dry grassland along a broad urbanisation gradient, and found a prevailing role of abiotic factors related to urbanisation. The importance of abiotic factors has been underestimated in the past and our results support the need to reconsider their role as major filters of floral traits. If we brought evidence that urban environmental conditions can trigger facilitation strategies within grassland plant communities, similar mechanisms are likely to occur in other urban ecotypes such as forests or gardens, which could be the object of future investigations. Furthermore, the observed association of floral attraction traits with urbanisation are likely to have implications for the composition of urban pollinator assemblages. However, no formal relationships have been established to date; future studies should thus aim to assess the implication of floral traits for pollinator conservation in cities.

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Author contributions

Valentin Cabon: Conceptualization (equal); Formal analysis (lead); Writing – original draft (equal). **Alice Kracht**: Conceptualization (equal); Writing – original draft (equal). **Birgit Seitz**: Data curation (lead). **Ingo Kowarik**: Writing – original draft (supporting). **Moritz von der Lippe**: Writing – original draft (supporting). **Sascha Buchholz**: Supervision (lead); Writing – original draft (supporting).

Data availability statement

Data are available from the Github Digital Repository: <https://github.com/vcabon/FloralTraitsUrbanisation> (Cabon et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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