



# Abiotic conditions affect nectar properties and flower visitation in four herbaceous plant species

Carolin Plos<sup>a,b,\*</sup>, Niklas Stelbrink<sup>b</sup>, Christine Römermann<sup>a,c</sup>, Tiffany M. Knight<sup>a,d,e</sup>,  
Isabell Hensen<sup>a,b</sup>

<sup>a</sup> German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103 Leipzig, Germany

<sup>b</sup> Institute of Biology, Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Große Steinstraße 79/80, 06108 Halle (Saale), Germany

<sup>c</sup> Institute of Ecology and Evolution with Herbarium Haussknecht and Botanical Garden, Friedrich Schiller University Jena, Philosophenweg 16, 07743 Jena, Germany

<sup>d</sup> Department of Community Ecology, Helmholtz-Centre for Environmental Research (UFZ), Theodor-Lieser-Straße 4, 06120 Halle (Saale), Germany

<sup>e</sup> Institute of Biology, Martin Luther University Halle-Wittenberg, Hoher Weg 8, 06120 Halle (Saale), Germany

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## ABSTRACT

Both plant nectar production and insect activity are highly dependent on abiotic environmental conditions. Furthermore, the foraging behaviour of insect pollinators can be affected by nectar properties. In the context of climate change, it is important to understand how plant-pollinator interactions respond to temperature and other abiotic factors. We investigated the effect of natural variation in temperature and solar radiation on nectar quantity (nectar volume) and quality (sucrose concentration and sucrose mass) and on flower visitation rates in four herbaceous plant species (*Dictamnus albus*, *Lamium album*, *Salvia officinalis*, *Vincetoxicum hirsutum*) in the Botanical Garden Halle (Germany). Temperature affected nectar properties in all four species. Solar radiation affected nectar quantity and quality in two species, most likely by affecting flower temperature. The number of flower visits was unimodally related to temperature for two species and positively related to solar radiation in another. The variable responses across plant species in the effects of abiotic factors on nectar properties and flower visitation patterns may be due to differences in flower shape and colour, to differences in the composition of flower visitors, or due to other unmeasured extrinsic factors that vary across patches where these species occur. Our study highlights the importance of considering direct and indirect effects of climate factors on pollinator visitation in multiple plant species.

## 1. Introduction

Pollination is amongst the most important ecosystem services for both natural and agricultural systems (Klein et al., 2007), as the majority of plant species require animal visitation in order to successfully reproduce (Ollerton et al., 2011; Rodger et al., 2021). Climate change has the potential to significantly threaten this critical interaction (González-Varo et al., 2013). Climate can directly affect insect flower visitors because insects have species-specific temperature optima for foraging (Corbet et al., 1993; Stone and Willmer, 1989; Zoller et al., 2020), and indirectly influence flower visitors by altering the rewards (e.g., nectar volume and sucrose amount) that plants offer (Descamps et al., 2018). To develop a general understanding of how climate change may alter pollination, it is important to understand how each of these

components will change in response to abiotic factors such as temperature and solar radiation (Maron et al., 2014), as these factors are likely to be affected by climate change (Rapp, 2014).

For a given community of potential flower visitors, the visitation rate and composition of visitor communities to flowering plants depends on the characteristics of the plant species. Plant species differ in their floral traits, such as the size, shape and colour of the corolla, scent and nectar composition, which are associated with their pollination syndrome (Faegri and Pijl, 1979; Rosas - Guerrero et al., 2014). These traits might differ significantly across even closely related plants (e.g. Basnett et al., 2021; Comba, 1999; Maćukanović-Jocić et al., 2011). For example, *Salvia officinalis* L. and *Lamium album* L. are both plant species in the Lamiaceae family that attract bees with their bilabiate corollas and nectar rewards. However, only bees with a long proboscis are able to

\* Corresponding author at: Martin Luther University Halle-Wittenberg, Institute of Biology, Geobotany and Botanical Garden, Gr. Steinstraße 79/80, 06108 Halle (Saale).

E-mail address: [carolin.plos@botanik.uni-halle.de](mailto:carolin.plos@botanik.uni-halle.de) (C. Plos).

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reach the nectar of *Lamium album* (Lye et al., 2009), whereas the nectar of *Salvia officinalis* is accessible to both long-tongued and short-tongued bees (Comba, 1999; Inouye, 1980; Mačukanović-Jocić et al., 2011).

Flower visitation rates are often mediated by rewards offered by the plant, which might also be affected by abiotic factors. Floral resources that plants produce, such as nectar, are directly affected by abiotic factors, such as temperature and solar radiation (Petanidou and Smets, 1996; Silva et al., 2004; Takkis et al., 2018). Nectar production measured at a certain site has been shown to be low at both low and high temperatures and to peak at intermediate temperatures forming a unimodal relationship with temperature (Petanidou, 2007; Takkis et al., 2018), and sugar concentration of nectar increases with temperature due to higher evapotranspiration (Corbet, 1990). Rapid evaporation due to high temperatures though might lead to nectar concentrations that are higher than those preferred by pollinators (Corbet, 1990), increasing the risk of plant-pollinator mismatches at high temperatures (Gérard et al., 2020). Solar radiation mediates photosynthetic activity of plants, which is associated with increasing nectar volume and sugar concentrations (Boose, 1997; Cawoy et al., 2008; Southwick, 1984). Furthermore, solar radiation can affect flower temperature more than ambient temperature itself and thus might also play an important role in influencing nectar properties in that way (Petanidou and Smets, 1996). Animal pollinators are known to adapt their foraging behaviour in response to the quantity and quality of floral rewards (Abrol, 2006; Fowler et al., 2016; Thomson, 1988; Waddington et al., 1981) and thus we would expect associations between nectar quantity and quality and flower visitation. In this way abiotic factors can have indirect effects on flower visitation rates.

Abiotic factors can also have a direct influence on pollinator activity and thus on potential flower visitation (direct effects). Temperature influences the activity patterns of insect pollinators due to species-specific thermal tolerances (Corbet, 1990; Corbet et al., 1993; Kühnel and Blüthgen, 2015; Stone and Willmer, 1989) and desiccation tolerances (Burdine and McCluney, 2019). Most insect pollinators are not active below a certain temperature and reduce their activity again when temperatures are too high, forming a unimodal relationship (Corbet et al., 1993; Kühnel and Blüthgen, 2015). Fewer studies investigated the effect of solar radiation on pollinator behaviour (e.g. Arnold and Chittka, 2012, focusing on artificial light; Kilkenny and Galloway, 2008, using a field study), but those that have typically observed reduced visitation of plants shaded compared to those that are sun-exposed.

The current state of our knowledge on the direct and indirect effects of abiotic factors on the visitation rate of pollinators is typically limited to studies focused on single plant species or crop plants (e.g., Abrol, 2010; Boose, 1997; Carroll et al., 2001; del Rio and Burquez, 1986; Silva et al., 2004), a single pollinator group or species (e.g., Corbet et al., 1993; Descamps et al., 2021; Kovac and Stabentheiner, 2011; Vicens and Bosch, 2000), and/or a single abiotic factor (e.g., Boose, 1997; Huber, 1956; Petanidou and Smets, 1996) or considering only plant or insect responses (e.g., Boose, 1997; Carroll et al., 2001; Vicens and Bosch, 2000). This is likely because collecting data on pollinator observations and nectar properties across abiotic environments is time consuming. However, examining responses across many plant species, pollinator groups and abiotic factors is critical to disentangle these complex interactions and relationships and for developing a general understanding of the patterns and their context dependence. Thus, this study goes one step further compared to existing studies by collecting a comprehensive dataset on (a) temperature and solar radiation, (b) flower visitations, (c) nectar quantity and quality, all measured simultaneously on four selected plant species growing under comparable soil, light, and climatic conditions in a botanical garden. While plants occur in different patches in the garden that might differ in external conditions, the otherwise similar conditions of the larger garden setting allow us to cautiously discuss differences across the investigated plant species in their responses of nectar properties or flower visitation associated to variation in abiotic conditions.

Based on the literature discussed above, we set up the following hypotheses: 1) The nectar quantity (i.e. nectar volume) of our study plants responds to temperature in a unimodal way and is positively related to solar radiation. The nectar quality (i.e. sucrose concentration and sucrose mass) is positively related to temperature and solar radiation. 2) Flower visitation rates are related to temperature in a unimodal way and are positively related to solar radiation. 3) Flower visitation rates are influenced by nectar quantity and quality. With this approach we aim to better understand the direct and indirect (i.e., through changing nectar properties) effects of abiotic drivers on pollinator visitation. This study is a basis for a better understanding on how plant-pollinator interactions might be affected by changes in climate and which role flower traits and pollinator composition might play in shaping these biotic interactions.

## 2. Materials and methods

### 2.1. Study site

The study was conducted in the Botanical Garden Halle (Saale) in Germany. In the study year (2020), the mean annual temperature of Halle (Saale) was 12 °C with a total annual precipitation of 401 mm (Deutscher Wetterdienst (DWD) Climate Data Center (CDC), 2021). All observations and measurements were conducted between mid-May and end of June, covering the main flowering period of the study species. Precipitation in the study months was 40 mm in May and 26 mm in June (Deutscher Wetterdienst (DWD) Climate Data Center (CDC), 2021). Thus, plants required additional irrigation that was applied consistently to all four species when required. Plants were growing in distinct monospecific patches of approximately 1 m<sup>2</sup>. All four observed plant species grew closely together in the systematic part of the botanical garden (see also Fig. S1), where plants grow in an open and plane area and in the same soil substrate (chernozem) with even soil depth (>100 cm). The distance between two patches ranged from ~10 to ~25 m. Thus, plants occurred in a similar background of abiotic conditions regarding climate, soil, exposure to wind and of other flowering plant species and had access to the same community of animal pollinators.

### 2.2. Study species

Four plant species were investigated: *Dictamnus albus* L., *Lamium album* L., *Salvia officinalis* L., *Vincetoxicum hirundinaria* MEDIK. (for more species information, see Table 1). The species were chosen as they all provide measurable amounts of nectar, had enough flowers to conduct a study with repeated nectar measurements and had overlapping flowering periods.

### 2.3. Abiotic factors

Our study considers the effects of natural variation in abiotic factors on our response variables rather than experimental manipulation of these factors. Considering natural variation has the advantage that animal pollinator responses, which will occur at larger spatial grains than most experiments can consider, will be influenced by this same natural variation in temperature and solar radiation. However, this method has the disadvantage that unmeasured factors might covary with our focal abiotic factors, and thus our inference is more limited. Temperature was measured with HOBO Loggers (Onset, HOBO Pro-v2 (U23-001)) at 30 cm height every 10 min. Loggers were equipped with sun shields and were placed directly next to the plants during flower visitor observations to measure the local microclimate experienced by the plant. Photosynthetic active radiation (PAR) was used as a measure of solar radiation intensity and was measured after every flower visitor observation interval approximately 1.5 m above the ground with a photometer in  $\mu\text{mol}/\text{m}^2\text{s}$  (HD2102.2, DeltaOhm). For an overview of the microsite

**Table 1**

Overview of the studied plant species and their characteristics as derived from [1] the BiolFlor Database (Klotz et al., 2002), [2] FloraWeb (BfN, 2011), [3] PhenObs Data (Sporbert et al., 2022) and [4] own measurements (see Methods section).

	<i>Lamium album</i> L.	<i>Dictamnus albus</i> L.	<i>Salvia officinalis</i> L.	<i>Vincetoxicum hirundinaria</i> Medik.
Family	Lamiaceae	Rutaceae	Lamiaceae	Apocynaceae
Flower shape [1]	true lip flowers, hymenoptere flower	hymenoptere flowers, lip flowers (Verbascum type)	true lip flowers, hymenoptere flowers	clamp trap flowers
Flower colour	white	pink	purple	yellowish white
Flowering time [1]	April - October	May - June	May - July	May - August
Flowering time 2020 [3]	07.04.–29.09.20 (peak flowering until 12.05.20)	25.05.–10.06.20	12.05.–28.07.20 (peak flowering until 24.06.20)	20.05.–16.09.20 (first peak until 24.06.20)
Main pollinators [1]	hymenoptera	hymenoptera	hymenoptera	diptera, hymenoptera
Habitat [2]	nutrient rich, ruderal	dry and warm	dry and warm, calcareous soils	dry and warm
Native Range [1]	Europe to Asia	Europe to Asia	Europe	Europe to western Asia
Temperature during observations [4]				
min T	13.16 °C	12.94 °C	12.44 °C	12.79 °C
max T	31.50 °C	31.07 °C	29.46 °C	28.67 °C
mean T	20.82 °C	20.70 °C	21.16 °C	21.20 °C

conditions (Temperature and PAR) measured at the four observed plant species see Fig. S2 in the supplements.

#### 2.4. Nectar measurements and flower availability

To measure nectar properties, we sampled nectar three times a day in the morning between 9 am and 10 am, at midday between 12 am and 1 pm and in the afternoon between 3 pm and 4 pm on 13–18 days per plant species. To avoid nectar consumption by flower visitors prior to sampling, at least five flowers per population were covered with fine mesh bags for at least one hour (Corbet, 2003). After conducting flower visitor observations on all four study plants, nectar samples were taken with 1 µl micro capillaries (minicaps®, Hirschmann®) from five of the bagged flowers. All nectar was taken from each sampled flower. Care was taken not to sample the same flower multiple times to avoid errors due to possibly damaged flowers. The nectar volume in the capillary was measured with a ruler in mm and then calculated to µl. Nectar samples were placed in 2 ml Eppendorf tubes and were stored at –20 °C until further analysis. In case of starting rain (which occurred on five sampling days), nectar measurements were stopped for that day as nectar can be diluted by rain (Corbet and Delfosse, 1984). The sucrose concentration (in% or g/100 g) of the nectar samples was measured using a handheld refractometer modified for small volumes (Eclipse, Bellingham & Stanley). Using the calibration table of Kearns and Inouye (1993) the sucrose mass concentration (mg/µl) of the nectar samples was calculated. From this the mean sucrose mass per flower (mg/flower) was calculated. The mean values over the five sampled flowers were calculated for nectar amount, sucrose concentration and sucrose mass.

As previous studies reported that flower visitations are strongly influenced by flower availability (Arroyo-Correa et al., 2021; Barbir et al., 2016; Grindeland et al., 2005; Ohashi and Yahara, 1998), we also assessed the flower availability of our focal species. The number of open flowers of an individual plant or a plant population will correlate to the total amount of available floral resources (e.g. total nectar volume and total sugar mass) (Mueller et al., 2020) and furthermore increases flower attractiveness (flower display/total flower display) for potential pollinators (Descamps et al., 2021; Potts et al., 2003). The number of all open flowers of the observed plant patch was counted on each sampling day. In case of very large numbers of flowers as observed for *S. officinalis* (max. 7900 flowers) the flowers of a quarter of the patch were counted and extrapolated.

#### 2.5. Flower visitor observations

All flower visitors of the four plant species were observed on 13–18 days each, covering the main flowering period of the investigated

species. In case of starting rain, observations were stopped for that day. Observations were conducted three times a day in the morning between 9 am and 10 am, at midday between 12 am and 1 pm and in the afternoon between 3 pm and 4 pm. Flower visits of every insect were counted for 10 min per plant species considering the whole plant patch (~1 m<sup>2</sup>). The number of flower visits in the 10-minute observation interval was considered as the visitation rate in this study.

Visiting insects were identified to morphotypes leading to different levels of determination: Honey bees (*Apis mellifera*) and bumble bees (*Bombus* sp.) were identified to species level. All Brachycera (suborder) specimens excluding syrphid flies (Syrphidae, family) were considered flies. Furthermore, we distinguished between hover flies (Syrphidae), wasps (Vespoidea, superfamily), beetles (Coleoptera, order) and wild bees (Apiformes without *Apis mellifera* and *Bombus* species). In total 168 observation intervals were conducted with on average 42 observation intervals per plant species.

#### 2.6. Statistical analysis

##### 2.6.1. Nectar properties

To better understand the mechanisms driving variation in nectar properties, nectar amount, sucrose concentration and sucrose mass were tested for correlation using Pearson's correlation (function *cor.test*) for each plant species. To test the hypothesis that nectar properties are unimodally associated to temperature and positively associated to solar radiation, per plant species we assessed the effect of these abiotic factors on a) nectar amount per flower, b) sucrose concentration and sucrose mass per flower using linear mixed effect models (package *lmerTest*, function *lmer*) (Kuznetsova et al., 2017). Due to the relatively low number of replicates we were not able to jointly model the predictor effects across all species by including species as covariate. Thus, we decided to run separate models per species and to compare the estimates. To test for a unimodal relationship between temperature and nectar properties, we included the quadratic term of temperature in the models. Observation day was included as a random factor to account for non-independence of the data (temporal autocorrelation). To identify the factors (temperature and/ or solar radiation) that were associated to changes in nectar properties of each plant species, the models were simplified step-wise until the most parsimonious model for each plant species was identified. The explanatory variables temperature and solar radiation were tested for correlation using Pearson's correlation (function *cor.test*) before analysis ( $r = 0.21$ ;  $p = 0.01$ ).

##### 2.6.2. Flower visitation

To visualise how flower visitor composition varied across the focal plant species and identify significant pollinator groups to each plant

species, we used non-metric multidimensional scaling (NMDS). Pairwise dissimilarity across observation intervals was calculated using the function *metaMDS* from the R package *vegan* (Oksanen et al., 2020) using Bray-Curtis distance and 999 iterations.

Because 31 of our 168 observation intervals had no flower visitors, we first tested whether the presence or absence of flower visitors during an observation interval was driven by abiotic factors using a generalised linear mixed effects model (family binomial) with all abiotic factors (temperature, the quadratic term of temperature and solar radiation) and plant species as explanatory variables and the number of flowers as a covariate (see more details in Table S1, Fig. S3, supplements). As there was no significant effect of any of the explanatory variables on the presence/absence of flower visitors, zero observations were excluded in further analyses (Table S1, Fig. S3).

Next, to test the hypothesis that the number of flower visits relates to temperature in a unimodal way and is positively associated to solar radiation, per plant species we performed generalised linear mixed effects models (family quasipoisson) using the package *lme4* and the function *glmer.nb* (Bates et al., 2015). As above, due to the relatively low number of replicates we were not able to jointly model the predictor effects across all species by including species as covariate and decided to run separate models per species and to compare the estimates. Temperature, the quadratic term of temperature and solar radiation (measured as PAR) served as explanatory variables and the number of flowers on the observation day was included as covariate. To identify the factors (temperature and/ or solar radiation) that were associated to changes in the flower visitation rate of each plant species, the models

were simplified step-wise until the most parsimonious model for each plant species was identified. As above, observation day was included as a random factor to account for non-independence of the data (temporal autocorrelation). The explanatory variables temperature and solar radiation were tested for correlation using Pearson's correlation (function *cor.test*) before analysis ( $r = 0.21$ ;  $p = 0.01$ ).

### 2.6.3. Correlation between nectar production and flower visits

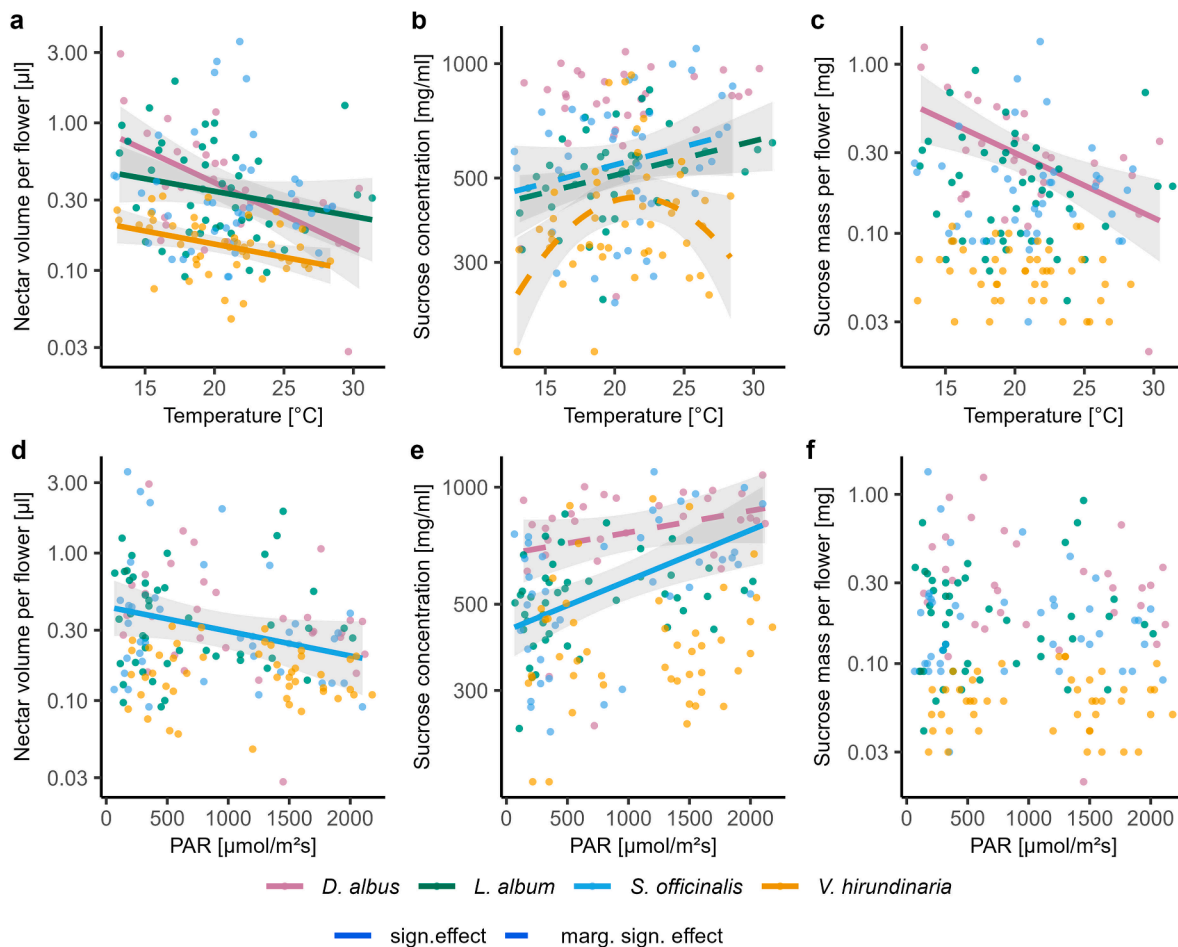
To investigate whether and to what extent flower visitation rates were correlated to nectar quantity and quality of the different focal plants, we tested for correlation of both variables using Pearson's correlation (function *cor.test*) for each plant species separately.

All statistical analyses were performed in R version 4.0.4 (R Core Team, 2021).

## 3. Results

### 3.1. Correlation between nectar properties

Nectar properties were partly correlated with one another (Table S2, Fig. S4, supplements). A strong positive correlation was found for nectar volume and sucrose mass per flower for all species. Nectar volume and sucrose concentration were significantly negatively correlated for all species. Sucrose mass and sucrose concentration were not correlated with each other for any of the plant species. An overview about general differences in the nectar properties between the investigated plant species is given in the supplements (Fig. S5).



**Fig. 1.** Effect of abiotic factors temperature and solar radiation (PAR) on the nectar volume per flower [ $\mu$ l] (a, d), the sucrose concentration of nectar [mg/ml] (b, e) and the sucrose mass per flower [mg] (c, f). Colours indicate different plant species. Solid lines indicate significant effects ( $p < 0.05$ ), dashed lines indicate marginal significant effects ( $p < 0.1$  and  $> 0.05$ ).

### 3.2. Effect of abiotic factors on nectar quantity and quality

Temperature was an important factor explaining variation in nectar quantity and quality. Nectar volume significantly decreased with temperature for three out of four studied species and significantly decreased with solar radiation for one species (Fig. 1). The most parsimonious models describing variation in nectar volume of *D. albus* and *V. hirundinaria* only contained temperature as explanatory variable (*D. albus*:  $estimate_{Temp} = -0.45$ ,  $p = 0.005$ ,  $n = 31$ ); *V. hirundinaria*:  $estimate_{Temp} = -0.03$ ,  $p = 0.002$ ,  $n = 46$ ) (Fig. 1a). For *L. album* the most parsimonious model contained temperature ( $estimate_{Temp} = -0.26$ ,  $p = 0.04$ ,  $n = 45$ ) (Fig. 1a) and the quadratic term of temperature with a marginally significant effect ( $estimate_{Temp^2} = 0.15$ ,  $p = 0.06$ ,  $n = 45$ ). The most parsimonious model describing variation in nectar volume of *S. officinalis* only contained PAR. Nectar volume of *S. officinalis* was negatively associated with PAR ( $estimate_{PAR} = -0.33$ ,  $p = 0.025$ ,  $n = 41$ ) (Fig. 1d).

The abiotic factors that explained changes in sucrose concentration varied across plant species. The most parsimonious model explaining the variation in sucrose concentration contained only solar radiation for *D. albus* ( $estimate_{PAR} = 56.66$ ,  $p = 0.08$ ,  $n = 31$ ) (Fig. 1e), only temperature for *L. album* ( $estimate_{Temp} = 33.22$ ,  $p = 0.09$ ,  $n = 45$ ) (Fig. 1b), both temperature and solar radiation for *S. officinalis* ( $estimate_{Temp} = 73.00$ ,  $p = 0.06$ ,  $n = 41$ ;  $estimate_{PAR} = 78.52$ ,  $p = 0.03$ ,  $n = 41$ ) (Fig. 1b, e), and temperature and the quadratic term of temperature for *V. hirundinaria* ( $estimate_{Temp} = 50.56$ ,  $p = 0.07$ ,  $n = 46$ ;  $estimate_{Temp^2} = -44.81$ ,  $p = 0.06$ ,  $n = 0.06$ ,  $n = 46$ ) describing an overall unimodal relationship (Fig. 1b).

The sucrose mass per flower [mg] significantly decreased with temperature for *D. albus* ( $estimate_{Temp} = -0.31$ ,  $p = 0.03$ ,  $n = 31$ ) (Fig. 1c) while PAR did not affect sucrose mass (most parsimonious model). Sucrose mass of the other investigated species was not affected by temperature and PAR (Fig. 1c, f).

### 3.3. Composition of flower visitors

The four observed plant species showed different but partly overlapping pollinator communities (Fig. 2). *Dictamnus albus* was mostly visited by honey bees (*Apis mellifera*) (~93% of visits). *Salvia officinalis* was mostly visited by wild bees (47% of visits) and bumblebees (40% of visits) (Fig. 2). A single species of bumblebee, *Bombus pascorum*, accounted for about 22% of all visits to *S. officinalis*, followed by *B. sylvarum* (7%), *B. terrestris* (7%) and *B. hypnorum* (3%). *L. album* had the fewest visits, and these visits were by bumblebees (81%), wild bees (12%), and syrphid flies (Syrphidae) (5%). Most frequent bumblebee species visitors were *B. pascorum* (54% of all visits) and *B. hypnorum* (21% of all visits). *Vincetoxicum hirundinaria* was mainly visited by

honey bees (52%), flies (Diptera) (30%) and syrphid flies (Syrphidae) (9%). The proportion of visits made by each pollinator group to each plant species is given in Fig. 2.

### 3.4. Effects of abiotic factors on flower visitation rates

The different plant species showed different patterns in how the measured abiotic factors affected the number of flower visits. For each plant species the results only from the most parsimonious models are reported. Temperature affected the number of flower visits in the hypothesised unimodal manner for *D. albus* ( $estimate_{Temp} = 0.45$ ,  $p = 0.009$ ,  $estimate_{Temp^2} = -0.36$ ,  $p = 0.005$ ,  $n = 27$ ) and *L. album* ( $estimate_{Temp^2} = -0.41$ ,  $p = 0.02$ ,  $n = 25$ ) (Fig. 3a). However, no effect of temperature on the visitation of *S. officinalis* and *V. hirundinaria* was found (Fig. 3a). Solar radiation (measured as PAR) affected the number of flower visits only for *S. officinalis* ( $estimate_{PAR} = 0.24$ ,  $p = 0.006$ ,  $n = 43$ ) describing a positive relationship (Fig. 3b). The number of flowers of the observed population positively affected the number of visits for *D. albus* ( $estimate_{No\ of\ flowers} = 1.11$ ,  $p < 0.001$ ,  $n = 27$ ), *L. album* ( $estimate_{No\ of\ flowers} = 0.46$ ,  $p = 0.007$ ,  $n = 25$ ) and *S. officinalis* ( $estimate_{No\ of\ flowers} = 0.45$ ,  $p = 0.001$ ,  $n = 43$ ) (Fig. 3c). No effect of the number of flowers on the number of visits was found for *V. hirundinaria* (Fig. 3c).

### 3.5. Correlation between nectar properties and flower visits

There was no clear pattern of correlation between nectar properties and flower visits. Nectar amount was negatively correlated to flower visits for *V. hirundinaria* ( $r = -0.42$ ;  $p = 0.006$ ) (Fig. 4a, Table 2). Other tested plant species showed no correlation of nectar amount and flower visits. Sucrose concentration was significantly correlated to flower visitation for two out of four species. *Salvia officinalis* showed a positive relationship between sucrose concentration and flower visits ( $r = 0.48$ ,  $p = 0.001$ ; Fig. 4b), while visits of *L. album* were negatively related to sucrose concentration ( $r = -0.43$ ,  $p = 0.02$ , Fig. 4b). Sucrose mass per flower showed a significant correlation with flower visits only for *V. hirundinaria* with a negative correlation ( $r = -0.39$ ,  $p = 0.02$ , Fig. 4c).

## 4. Discussion

The objective of this study was to investigate the direct and indirect effects (through nectar quantity and quality) of temperature and solar radiation on the visitation of pollinators of four focal plant species. We found that temperature was an important abiotic factor, affecting nectar volume and sucrose concentration of three plant species while solar radiation (PAR) influenced the nectar volume and sucrose concentration of only one species (Fig. 1). Temperature was unimodally related to the

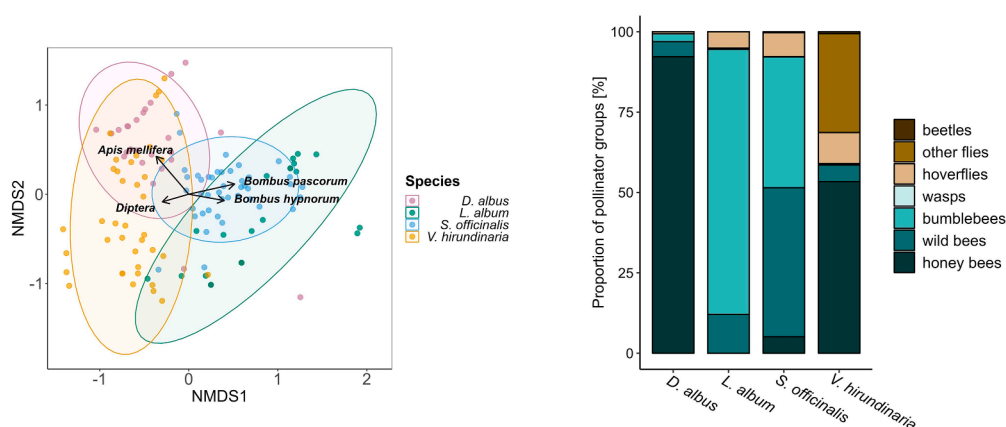
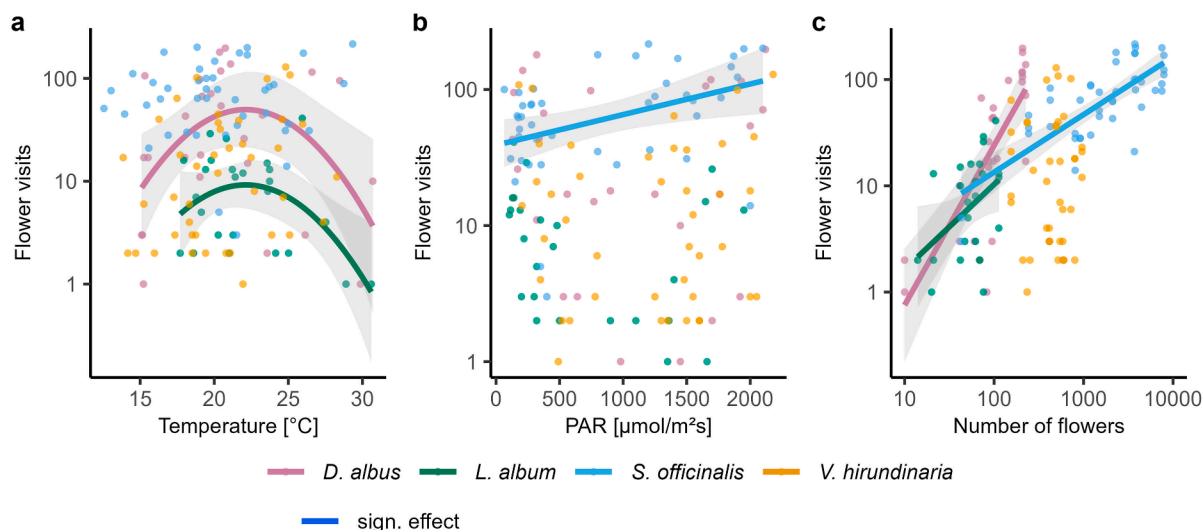
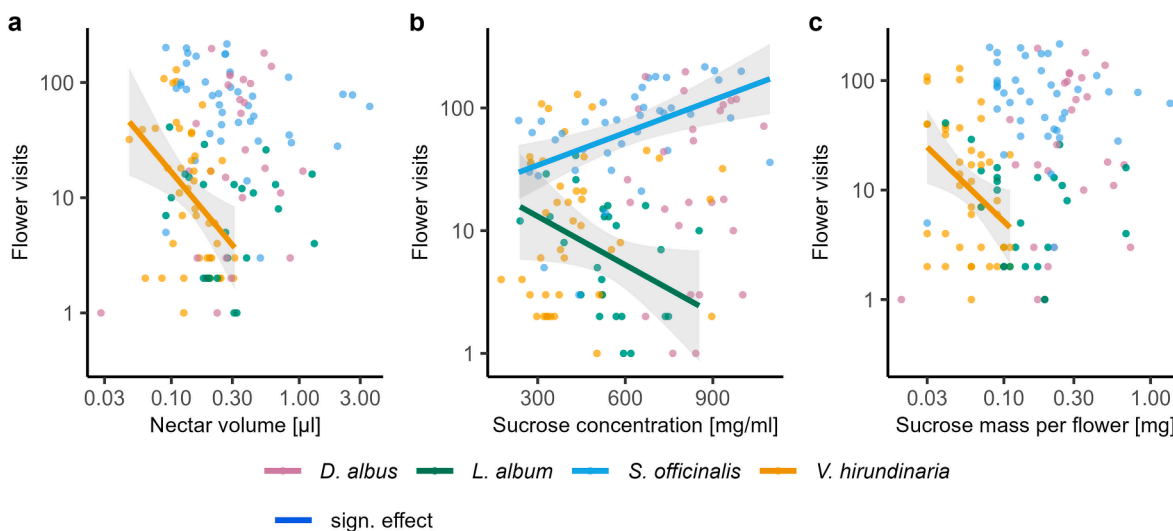


Fig. 2. Left: NMDS of the composition of flower visitors observed at the four focal plant species in the Botanical Garden Halle. Each point describes the visitor community of one 10 min observation interval per plant species. Colours indicate target plant species. Arrows indicate flower visitors that were significantly correlated with the axes. Right: Proportion of pollinator groups that were observed at the focal plant species.



**Fig. 3.** Relationship between a) temperature, b) solar radiation, c) the number of flowers with the number of flower visits observed at each plant species. Colours indicate different plant species. Solid lines indicate significant effects ( $p < 0.05$ ).



**Fig. 4.** Correlation between nectar properties and insect visitation, solid lines indicate significant correlations.

**Table 2**

Pearson’s correlation coefficients  $r$  and significance levels for the correlation between nectar properties and flower visits of the respective plant species.

flower visits of:	Nectar amount [μl]		Sucrose concentration [mg/ml]		Sucrose mass [mg]	
	$r$	$p$ -value	$r$	$p$ -value	$r$	$p$ -value
<i>Dictamnus albus</i>	0.31	n.s.	0.07	n.s.	0.35	n.s.
<i>Lamium album</i>	-0.02	n.s.	-0.43	0.02	-0.2	n.s.
<i>Salvia officinalis</i>	-0.21	n.s.	0.48	0.001	-0.01	n.s.
<i>Vincetoxicum hirundinaria</i>	-0.42	0.006	0.13	n.s.	-0.39	0.02

visitation of pollinators for two plant species and PAR was positively related to pollinator visitation for one species (Fig. 2). Surprisingly, we found that flower visitation rate was not consistently affected by nectar quantity and quality (Fig. 4). Interestingly, the flower-visitor interactions of the four species responded differently to abiotic factors. We are limited in our ability to conclusively test mechanisms for species

differences, due to the limited number of species and the fact that the species were studied in four distinct locations within the garden (see Fig. S1 for an overview of the study site). However, we discuss the potential roles of differences across species in floral traits and the types of floral visitors. This research should hopefully motivate more case studies to build towards a larger comprehensive survey of floral traits, nectar properties, flower visitors and their response to abiotic conditions.

#### 4.1. Effect of abiotic factors on nectar quantity and quality

In contrast to our expectation that nectar quantity and quality respond unimodally to temperature, we found linear negative responses (Fig. 1a,c). One explanation for this result could be that we lacked days with very cold temperatures, which were rare during our study period. Similar results were found by Adjaloo et al. (2015), where temperatures were never very cold (minimum 28 °C) but included very hot sampling days (maximum 42 °C). Only in *V. hirundinaria*, we found a quadratic relationship between sucrose concentration and temperature (Fig. 1b). The increase in sucrose concentration could be explained by evaporation of nectar with increasing temperatures (Corbet, 1990), and beyond certain temperatures, physiological stress due to high temperatures

could in turn explain decreasing sucrose concentrations (Pacini and Nepi, 2007; Petanidou and Smets, 1996; Scaven and Rafferty, 2013). Sucrose mass of nectar was mostly unaffected by temperature or solar radiation (Fig. 1c,f). This could be due to the fact that sucrose mass per flower is relatively constant in many plant species (Nicolson and Thornburg, 2007; Schwerdtfeger, 1996) - it may even be genetically fixed (Klinkhamer and Wijk, 1999; Mitchell and Shaw, 1993). This coincides with the foraging preferences of the most frequent pollinators (pollinator classes) (Nicolson and Thornburg, 2007; Schwerdtfeger, 1996). For *D. albus* effects of temperature on sucrose mass reflected the same patterns as found for nectar volume (Fig. 1a,c), what may reflect a change in overall nectar production due to temperature (Pacini and Nepi, 2007; Petanidou and Smets, 1996; Scaven and Rafferty, 2013) as sucrose amount and nectar volume were strongly correlated (Fig. S4a).

Nectar volume decreased with increasing temperature or solar radiation while for most species, sucrose concentration increased in parallel (Fig. 1), indicating higher evapotranspiration of nectar (Corbet, 1990; Fowler et al., 2016; Nicolson and Thornburg, 2007). Furthermore, nectar volume and sucrose concentration were negatively correlated for all four species (Fig. S4b) which supports the assumption that higher evaporation at higher (flower) temperatures is the mechanism explaining our observed patterns (Fowler et al., 2016; Nicolson and Thornburg, 2007).

Temperature affected nectar properties more strongly than solar radiation in our investigated plant species (Fig. 1). Whether the change in nectar properties was stronger associated to temperature or solar radiation could be mainly related to the flower traits of our studied species. Solar radiation can increase flower temperature even more than ambient temperature (Hanan, 1970; Rougerie-Durocher et al., 2020) and could therefore override direct temperature effects. That might play a role especially for darker coloured flowers (*S. officinalis*, *D. albus*) as flower temperature of light-coloured flowers (*L. album*, *V. hirundinaria*) is less affected by radiation than by ambient temperature (McKee and Richards, 1998). Furthermore, nectar in open flowers (*D. albus*) is more susceptible to evapotranspiration than nectar in flowers with deep corollas (Corbet, 1978; Plowright, 1987). The effect of solar radiation on nectar properties might overrule the effect of ambient temperature depending on flower colour and shape. Thus, flower colour and shape might help explaining differing response patterns in nectar properties to abiotic conditions like temperature or solar radiation.

The plant species we selected yielded small but measurable amounts of nectar on average ranging from 0.2  $\mu\text{l}$  (*V. hirundinaria*) to about 0.5  $\mu\text{l}$  in the other three species (Fig. S5). We would expect that plants with very small nectar amounts that were not included in our study due to practicability reasons would be even stronger affected by high temperatures and solar radiation (Corbet, 2003). However, since nectar measurements are very difficult to make for these species (but see Aronne and Malara, 2019), not much is known about these relationships.

#### 4.2. The direct and indirect effect of abiotic factors on flower visitation rates

In our study, flower visitation was explained by a combination of direct and indirect (nectar quantity and quality) effects of temperature and solar radiation. Our results were species specific, which might be explained by 1) the different ways in which nectar resources were shaped by abiotic conditions and 2) different flower visitor compositions observed at the studied plant species that might have different needs and adaptations to abiotic conditions and nectar rewards. As in other studies, visitation was positively driven by the number of flowers (Barbir et al., 2016; Descamps et al., 2021; Fowler et al., 2016; Grindeland et al., 2005; Mueller et al., 2020). In our study, this phenomenon is also evident, wherein the impact of the number of flowers is notably strong (Fig. 3c), potentially obscuring the influence of abiotic factors to some degree.

In two species, we found the expected unimodal relationship between flower visitation and temperature (*D. albus*, *L. album*; Fig. 3a),

which might be explained by the thermal tolerances of honeybees and bumblebees (Corbet et al., 1993) that were their main visitors (Fig. 2). No relationship between flower visitation and temperature was found for *S. officinalis* and *V. hirundinaria* that both had a more diverse composition of flower visitors compared to the other two species (Fig. 2). Their very diverse composition of flower visitors (a variety of wild bees and bumblebees at *S. officinalis*; honeybees, flies incl. syrphid flies at *V. hirundinaria*) might explain the absence of a relationship between temperature and visitation as visitors might show high thermal niche complementarity (Kühnel and Blüthgen, 2015). A positive association between solar radiation and flower visitations was only found in one species (*S. officinalis*), where heat gain due to solar radiation might be more important for their flower visitors than ambient temperatures (Kovac and Stabentheiner, 2011).

Flower visits were not consistently correlated to nectar properties as expected (Fig. 4). Depending on the flower visitor community observed at our target plant species (Fig. 2) we might differently interpret our findings. For example, honeybees (main visitors of *D. albus*) are known to respond rapidly to changes in nectar availability (Seeley et al., 1991). Thus, the decreases in flower visitation and nectar volumes at higher temperatures can be interpreted as an indirect effect of temperature on flower visitation. Other visitor groups, like for example flies (important visitors of *V. hirundinaria*), might be less able to respond to changes in nectar availability (Fowler et al., 2016; Hendriksma et al., 2019; Inouye et al., 2015). The negative correlation between nectar volume and sucrose mass, respectively, with flower visits found for *V. hirundinaria* (Fig. 4) seems counterintuitive but might reflect the consumption pattern of nectar foragers, meaning that we observe low standing-crops when many flower visitors are present as plants are able to modify nectar secretion as a function of the removals (Zimmerman and Pyke, 1986). Pollinator exclusion from flowers was conducted one hour prior sampling, what might have been not enough to secrete new nectar for *V. hirundinaria*. It might be that this species reproduces nectar on a slower rate than the other tested plant species and the result is due to our methodology. Our general intention regarding the nectar sampling was to measure the nectar quantity and quality as it is available to the pollinators (standing crop) (Corbet, 2003). To ensure that our sampled flowers were not emptied right before nectar sampling we chose the one-hour covering to balance sampling problems regarding reabsorption or evaporation of the nectar that could arise with longer covering (Corbet, 2003; Kearns and Inouye, 1993). Generally, the produced nectar volumes of *V. hirundinaria* were rather small (<0.2  $\mu\text{l}$ ) and therefore conclusions on the causality for those negative correlations are hard to draw and patterns could also be random. Flower visitation of *L. album* and *S. officinalis* was oppositely correlated to increases in sucrose concentration (Fig. 4b). On the one hand, rapid evaporation of nectar due to high temperatures might lead to nectar concentrations higher than those preferred by pollinators (Corbet, 1990) as well as increase nectar viscosity that might hinder nectar uptake by bumblebees (main visitors of *L. album*) (Harder, 1986). On the other hand, increasing sucrose concentrations might increase attractiveness for flower visitors (Kim et al., 2011; Krömer et al., 2008; Nicolson, 2007), as bees usually adapt their foraging behaviour to maximise nutritional uptake (Pyke, 1984), which can be achieved at higher nectar concentrations (Hendriksma et al., 2019). Thus, parts of our observed visitation patterns may reflect indirect effects of temperature or solar radiation mediated by altered nectar properties.

There may be further reasons why insect visitation might be indirectly affected by temperature and solar radiation that are not related to the nectar properties we measured: First, flower visitors might not primarily be attracted by nectar but by floral volatiles (Jürgens et al., 2008) or are foraging primarily for pollen. Volatile emission of flowers increases with temperature and radiation (Jakobsen and Olsen, 1994), increasing flower attractiveness for pollinators. Second, higher flower and nectar temperatures increase the attractiveness for foragers, even though sucrose concentration seems to stronger drive forager choice

(Whitney et al., 2008). Moreover, colour perception differs between different visitor groups and might be differently affected by changing ambient light conditions (Chittka et al., 2014; Lunau, 2014; van der Kooij et al., 2021). Future studies should incorporate these aspects to provide a more holistic view of flower traits and their influence on pollinator attractiveness in the context of changing climate conditions (Junker and Parachnowitsch, 2015).

Besides the indirect effects of temperature and solar radiation on flower visitation, abiotic conditions can also directly impact distinct visitor communities in unique ways, owing to variations in their thermal tolerances (Corbet et al., 1993) and the complementarity of their thermal niches (Kühnel and Blüthgen, 2015). The combination of direct and indirect effects on flower visitation might explain the absence of a consistent correlation pattern between visits and nectar quantity and quality in our investigated plant species.

### 4.3. Conclusion

This research contributes to a better understanding of direct and indirect effects of environmental conditions on flower visitation patterns, which can affect the reproductive success of plants. Temperature and solar radiation affected nectar quantity and quality differently, and our results suggest that this might be due to differences in flower traits of plant species. However, observations on a larger set of plant species covering a wider range of flower shapes and colours as well as a more controlled study design like a common garden would be necessary to confirm this hypothesis. Flower visitation patterns were shaped by a combination of direct effects of temperature on pollinator activity and indirect effects of temperature and solar radiation on nectar quantity and quality. Additionally, the composition of flower visitors that were observed at the focal plant species influenced these direct and indirect responses, as different insect groups have different requirements and adaptations to temperature and nectar quantity and quality. Botanical gardens offer good opportunities to study flower visitation on various plant species, as many plant as well as pollinator species co-occur in a small area and under comparable conditions (Nordt et al., 2021; Vilella-Arnizaut et al., 2022). In order to understand impacts of climate change on pollination we need to consider that flower traits and pollinator composition might be crucial aspects that will influence species-specific responses to changing abiotic conditions. Thus, this study contributes to a better understanding of the factors influencing biotic interactions (i.e. pollination), which is essential for understanding and predicting the impacts of climate change. More experimental studies (like e.g. Descamps et al. (2021)) on a variety of plant species, covering different functional groups and flower types investigating the effects of climate change on plant-pollinator interactions are needed to estimate the manifold impacts of changing abiotic conditions on plants, their flower visitors as well as plant-pollinator interactions.

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### CRedit authorship contribution statement

**Carolin Plos:** Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Niklas Stelbrink:** Investigation. **Christine Römermann:** Conceptualization, Methodology, Formal analysis, Writing – review & editing. **Tiffany M. Knight:** Methodology, Writing – review & editing. **Isabell Hensen:** Conceptualization, Supervision, Resources, Writing – review & editing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

The data that supports the findings of this study will be openly available via the iDiv data repository. <https://doi.org/10.25829/idiv.3520-a8m9v4>

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### Data availability statement

The data that support the findings of this study will be openly available via the iDiv data repository.

### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.flora.2023.152279](https://doi.org/10.1016/j.flora.2023.152279).

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