



# Intraspecific floral trait variation shifts with plant community structure along a land-use gradient

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## Abstract

Plant traits show multiple degrees of variation, owing to different environmental conditions or genetic predisposition. Land-use intensification, caused by fertilization, grazing, and mowing changes the biotic and abiotic conditions of a plant's environment. Land-use can have direct effects on plant traits, such as decreased flower height and size caused by grazing or mowing and enhanced vegetative growth upon fertilisation. Additionally, land-use can shape the plant community that indirectly affects inter or intraspecific competition for nutrition, space, and pollination for a plant individual. In this study, we aimed to elucidate the effects of land-use and associated changes in plant communities on the variation in floral morphology and rewards within and between populations. Floral traits for two common, self-incompatible meadow species – *Ranunculus acris* and *Trifolium pratense*, were recorded from semi-natural managed grasslands in Germany. Our study revealed that land-use intensity directly affected flower display size, which correlated with changes in pollen quantity and nectar sugar content. Variation in floral traits, however, varied primarily with changes in the surrounding plant community. Floral morphological traits showed lower intraspecific variation than floral reward traits. In plant-rich communities, both species increased floral display size, but this correlated with reduced pollen and nectar sugar production in *R. acris* and increased pollen and nectar sugar production in *T. pratense*, suggesting a species-specific modulation of floral traits that may have implications for plant–pollinator interactions and community-level pollination dynamics.

**Keywords** Floral rewards · Flower morphology · Intraspecific trait variation · Land-use intensity · Plant community · Pollination

## Introduction

Floral traits that attract pollinators are a key factor for determining the frequency and success of plant–pollinator interactions (van der Kooi et al. 2021). Besides differences

between species, floral traits can vary among individuals of the same species (Venjakob et al. 2020). Such intraspecific variation within a population hints at differences in the genetic composition and/or environmental conditions (non-genetic phenotypic plasticity) between plant populations (Venjakob et al. 2020; Weber et al. 2020; Wenzell et al. 2022) and may play a role in a plant's interaction with the biotic and abiotic environment (Westerband et al. 2021). For example, changes in floral size and reward production can affect their attractiveness to pollinators, consequently affecting the pollination success and fitness of the plant individual (Cresswell and Galen 1991).

Plant traits are affected by numerous abiotic factors, such as water stress, temperature change, and the interaction of these stressors (Strauss and Whittall 2006; Weber et al. 2020). For instance, flower size and plant height decreased with increasing drought (Glenny et al. 2018; Wu et al. 2022), whereas water and temperature stress independently resulted in a reduction of flower production and corolla

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surface (Descamps et al. 2018). Similarly, flower display size and colour intensity decreased in carotenoid-pigmented yellow flowers under sulphur limitation (Ausma et al. 2021). Floral reward production, a crucial trait for pollinator attraction, is also affected by abiotic factors. Floral reward quantity, such as nectar volume, decreased under drought stress (Wu et al. 2022), water stress (Carroll et al. 2001; Glenney et al. 2018) and higher temperatures (Descamps et al. 2018), while pollen grain size decreased with sulphur deficiency (Ausma et al. 2021). Moreover, pollen production is directly associated with flower size, with larger flowers typically producing more pollen (Hicks et al. 2016; van der Kooi et al. 2023), and can thus be indirectly affected by various abiotic conditions. Such variability driven by abiotic factors can be observed over a narrow time scale, sometimes within one generation (Walker et al. 2022).

Land-use management practices, such as fertilization, grazing and mowing, can affect both abiotic, environmental conditions and biotic conditions, such as plant and pollinator communities as well as their interactions (Peters et al. 2022; Weiner et al. 2011), with likely subsequent but hardly investigated effects on plant traits. For example, increased fertilization was found to positively correlate with flower production, flower longevity, corolla width and nectar production (Atasay et al. 2013; Wu et al. 2022). Although grazing and mowing typically remove existing flower heads, plants may allocate resources towards smaller but numerous flowers under light to moderate grazing (Mu et al. 2016). Fertilization typically decreases floral richness and diversity (Potts et al. 2009), often resulting in the rapid growth of grasses that outcompete flowering herbaceous species, thereby decreasing the floral resources for pollinators (Weber et al. 2020; Wu et al. 2022). Changes in flower community structure and diversity caused by land-use subsequently affect local pollinator communities (Weiner et al. 2011 b). For example, grazing and mowing remove grass tussocks, which decreases the shelter needed by invertebrates and can create an even less desirable environment for pollinators, potentially resulting in reduced pollinator abundance (Kindvall et al. 2022; Potts et al. 2003, 2009; Staab et al. 2025).

As a consequence, pollinator-dependent plant species may adjust their floral traits to local pollinator communities, as pollinators are known to play an important role in determining local floral trait phenotypes (Brown et al. 2011; Gervasi and Schiestl 2017; Weber et al. 2020). For example, flower colour can change from orange to red in *Disa ferruginea* depending on pollinator preferences (Newman et al. 2012). Similarly, directional selection and stabilization of plant height by pollinators have been observed in *Primula tibetica* (Wu et al. 2022), where shorter plants were less attractive to pollinators than longer plants. In *Ranunculus*

*acris* and *Raphanus raphanistrum*, syrphid pollinators preferred flowers with a comparatively larger floral display in a population, which is likely used as cue for reward quantity (Conner and Rush 1996; Totland 2004). Over time, this might result in plant communities with floral trait phenotypes that are most attractive to local pollinator communities, e.g., larger flowers in habitats where the majority of pollination is carried out by syrphids.

Although certain floral traits, such as bigger floral displays (Conner and Rush 1996; Totland 2004) and high nectar sugar concentration (Gervasi and Schiestl 2017), increase the chances of pollination for a plant individual and may be selected, the level of variation in floral traits among plant individuals is likely driven by abiotic conditions. For example, plants showed low intraspecific variation under harsh conditions, where only a few traits are beneficial for survival (Ahmad et al. 2025), leading to canalization of traits (Møller et al. 2024). Contrastingly, in environments with reduced stressors and high pollinator abundance, intraspecific variation may increase, as plants may benefit from facilitation, i.e., pollinator attraction by neighbouring plants (Seifan et al. 2014), reducing their own energetic costs of pollinator attraction (Gervasi and Schiestl 2017; Maldonado et al. 2023). For example, higher conspecific abundance resulted in higher seed set in *Delphinium barbeyi* (Arrow-smith et al. 2023). Alternatively, according to increased variation hypothesis, intraspecific trait variation increases with species richness in order to reduce inter and intraspecific competition by occupying a larger niche (Kuppler et al. 2020), which is especially relevant for generalist plant species (Kuppler et al. 2020; Leménager et al. 2024). Long-term land-use clearly affects both direct abiotic filters, such as changes in soil nutrients, and indirect pressures, such as shifts in pollinator abundance, diversity and behaviour, with potentially contrasting or synergistic effects on floral trait phenotypes and their variation.

Few studies have assessed differences in the level of variation in floral traits within plant populations considering both direct (abiotic) and indirect (plant community-mediated) effects of land-use management practices. In our study, we address this knowledge gap and investigate the effects of land-use intensity and plant community on floral traits as well as their variation within and between populations. We analysed the effects of different land-use management components – namely fertilization, grazing and mowing – on floral size and reward production as well as intraspecific variation in these traits for two common meadow species, *Ranunculus acris* (Ranunculaceae) and *Trifolium pratense* (Fabaceae), on managed grasslands in Germany. These two plant species are self-incompatible flowering species that rely exclusively on cross pollination by insects for reproduction (Totland 1994; Lehman et al. 2022). We were

specifically interested in the interactive effects between plant communities and land-use components on floral traits and intraspecific variation. Therefore, our expectations were as follows:

- We expected that, out of all land-use components, higher fertilization would result in more optimal plant growth conditions resulting in niche alignment and thus significantly affect most floral traits, as nitrogen availability in the soil is known to determine plant biomass, including flower size (Atasay et al. 2013; Wu et al. 2022) and nectar volume (Gao et al. 2023).
- We hypothesized that fertilization, grazing and mowing had a direct impact on floral morphological traits, such as floral height, size, and number of open flowers. By contrast, floral rewards, such as nectar and pollen quantity as well as nectar sugar content, should be mostly affected by the surrounding floral community (potentially mediating competition or facilitation).
- Previous studies conducted at the same study sites revealed that intensive land-use management led to low plant diversity (Blüthgen et al. 2012), floral abundance (Weiner et al. 2011) and, by extension, lower pollinator abundance (Peters et al. 2022; Weiner et al. 2011). Hence, we predicted that on intensively managed plots with low flower density and likely decreased pollinator visitation per plant, plants show overall reduced variation in floral traits, as plant individuals experience no community mediated facilitation. Similarly, grassland plots with low land-use intensity and a higher abundance and diversity of pollinators, are expected to show comparatively higher variation in floral traits.

**Table 1** Geological and climatic overview for all three Biodiversity Exploratories. All climatic values were derived from the Biodiversity Exploratories Instrumentation Project (BExIS dataset ID 19007) from 2023–2024 data

|                           | Schorfheide-Chorin      | Hainich-Dün           | Swabian Alb                   |
|---------------------------|-------------------------|-----------------------|-------------------------------|
| Location                  | NE Germany              | Central Germany       | SW Germany                    |
| Size                      | ~1300 km <sup>2</sup>   | ~1300 km <sup>2</sup> | ~420 km <sup>2</sup>          |
| Geology                   | Young glacial landscape | Calcareous bedrock    | Calcareous bedrock with karst |
| Altitude a.s.l.           | 3–140 m                 | 285–550 m             | 460–860 m                     |
| Annual mean temperature   | 10.78 °C                | 9.16 °C               | 8.92 °C                       |
| Annual mean precipitation | 454.32 mm               | 645.06 mm             | 1077.32 mm                    |
| Relative humidity         | 83.33%                  | 84.29%                | 87.58%                        |
| Temperature extremes      | -14.58 to 32.65 °C      | -11.77 to 34.21 °C    | -14.28 to 32.31 °C            |

## Materials and methods

### Study species

Two common meadow species - *Trifolium pratense* and *Ranunculus acris* - were chosen for this study, as these plant species are found in considerable abundance in temperate grasslands. *Ranunculus acris* is a perennial herb that is widely distributed in German grasslands. It has yellow bowl shaped, terminal, self-incompatible, protogynous flowers (Totland 1994, 2004). Its main floral reward is pollen which is produced in 50–80 anthers per flower (Totland 2004), while nectar is secreted in comparatively small quantities from a gland at the base of each petal. *Trifolium pratense* is an important legume grown in fields and is used as fodder. It has a dense, globose inflorescence comprising of multiple pink/purple florets, which are self-incompatible and rely exclusively on bumblebee pollination (Lehmair et al. 2022). *Trifolium pratense* has a low pollen load but significant quantities of nectar (Hicks et al. 2016).

### Experimental sites

The Biodiversity Exploratories is a large research framework in Germany, comprising 50 grassland and forest plots each in three different regions of Germany – Swabian Alb, Hainich Dün, and Schorfheide Chorin (Fischer et al. 2010). A detailed description of the geology and climatic conditions of the sites is provided in Table 1. Within the framework, the degree of fertilization, grazing and mowing is measured for each plot and combined within the land-use intensity (LUI) index (Blüthgen et al. 2012; Vogt et al. 2019). Fertilization is measured as kilograms of nitrogen added to the soil per hectare of land per year. Grazing is measured as the number of animals grazing per hectare, grazing system, and the duration of grazing per year. Mowing refers to the frequency with which the vegetation is cut in a given year. Grazing, mowing, fertilization, and land-use intensity (LUI) values were obtained from the LUI calculator on the BExIS website (Ostrowski et al. 2020). The land-use component measurements were standardised across all Exploratories and averaged over the past three years. We visited all grassland plots containing *Ranunculus acris* and *Trifolium pratense* according to the database created by the CoreBot project (Hinderling and Keller 2024 -dataset 31973, BExIS) in the peak flowering season (April/May for *R. acris* and July/August for *T. pratense*). *Ranunculus acris* was sampled from 34 Alb and 8 Hainich plots in 2023, and 35 Alb and 10 Hainich plots in 2024. *Trifolium pratense* samples were taken from 28 Alb, 30 Hainich, and 12 Schorfheide plots in 2023, and 27 Alb, 29 Hainich, and 16 plots from Schorfheide in 2024, respectively. *Ranunculus acris*

was not sampled from Schorfheide, because hardly any plots contained this species in sufficient abundance. Overall, 99 different grassland plots were visited over the course of three years across different regions. Out of these, 19 plots were not grazed, while 34 plots had high grazing intensity of more than 95.88 stocking units per hectare per year; 20 grasslands remained unmown, while 28 were mown more than once a year; 45 plots obtained no additional nitrogen fertilization, while 34 plots had more than 36.08 kg of nitrogen added per year (Table S.1).

## Floral trait measurements

### Flower size, height and flower numbers

Five plants were selected at random on each plot and the number of flowers on each plant was counted for *Ranunculus acris*. For *Trifolium pratense*, which spreads underground and likely has stalks from several individuals emerging in close proximity, the number of inflorescences on a stalk emerging from the ground were counted. The flower diameter for both species and the capitulum height of *T. pratense* inflorescences were measured using a digital calliper (Burg-Wächter Precise Digital Vernier calliper - PS 7215, Wetter, Germany). The distance of the base of the flower from the ground was measured using a foldable meter scale for both species.

### Nectar quantity and sucrose content

From five *Ranunculus acris* plants selected at random, flowers were picked below the second node and kept in tap water overnight. The flowers were kept close to a window so that they received sufficient sunlight in the evening. The next morning, nectar was extracted between 7–8 AM. *Ranunculus acris* petals have a small nectary at the base of the petal, hence the petals were removed and rinsed in ethanol for 5 min to dissolve all nectar in the ethanol, which was then frozen. The ethanol was allowed to evaporate under a fume-hood, then 10 µL of distilled water was added to each sample, before vortexing and recollecting the remaining liquid (i.e. nectar) in a microcapillary. The nectar was placed on a refractometer (Eclipse Professional, 0–50 Brix and 45–80 Brix, Bellingham+Stanley, Tunbridge Wells, UK) and the relative amount of sucrose solution (Brix) was measured from each individual.

For *Trifolium pratense*, the inflorescences were kept in water overnight, as described above. In the morning between 7–8 AM, the inflorescences were taped from the base and fixed upside down in an Eppendorf tube. The tubes were centrifuged at 6000 rpm for 10 s (MiniStar, VWR Avantor, Darmstadt, Germany) and the nectar was collected in glass

microcapillaries. The nectar volume was calculated using the following formula:

$$\frac{\text{Length of nectar column (mm)} * \text{Volume of microcapillary tube (}\mu\text{L)}}{\text{Length of microcapillary (mm)}}$$

The length of microcapillary and the nectar column was measured using a digital calliper, while the sucrose content (Brix) in the nectar was determined using a refractometer as described above.

### Pollen extraction

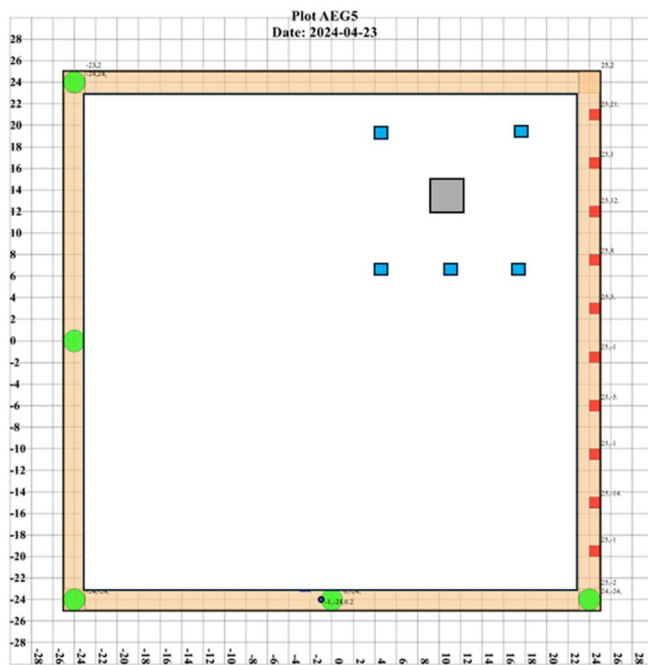
For pollen extraction, flowers were picked from within the 50 × 50 m boundary of the plots and spread on newspapers to dry at room temperature for at least 10 days. Overall, 250–500 *Ranunculus acris* and 75–250 *Trifolium pratense* were taken from each plot and pooled for pollen extraction. Dried flowers were weighed to calculate the average dry weight per flower. The flowers were then shaken in stacked sieves (Retsch woven wire mesh sieve, Germany), to separate pollen from other plant material first using a 180 µm and then a 150 µm sieve. The pollen was collected using a brush and the sieve was sanitized with ethanol before every sample. Leftover contamination (e.g., fine hairs) was removed using a plastic card that energized contaminants with the opposite charge as that of pollen. The extracted pollen was weighed and pollen weight per inflorescence / flower was calculated per plot.

### Floral community data

Five quadrats of 1 × 1 m area were placed roughly 5 m away in each direction from the weather station located within each plot (Fig. 1). Four quadrat measurements were taken approximately 5 m away from each corner of the weather station and one quadrat measurement was taken 5 m away from the centre of the weather station towards the middle of the plot. Within every quadrat, the number of flowers or inflorescences of the focal species (*Ranunculus acris* and *Trifolium pratense*; hereafter referred to as *R. acris* and *T. pratense* density, respectively), the total number of flowering species (species richness), and the overall number of flowers (flower density) were recorded. Relative abundances of focal species were calculated by dividing the number of focal species flowers by the total number of all flowers (across all plant species) in a quadrat.

### Statistical analysis

The entire data analysis was carried out in R version 4.2.2 (R core team, 2024). For simplicity, grazing, mowing, and



**Fig. 1** Diagram of the map of the sampling plots (using Plot AEG05 as an example) and a picture of a plot showing the weather station located within an agricultural field. Orange lines indicate the boundary of the plots. The grey square represents the weather station, while the blue squares represent the placement of the quadrats for measuring

**Table 2** Land-use components were categorised into high, intermediate, and low categories using a quantile binning method. The table shows the range of the categories and the number of plots under each category used

| Land-use component | Categories   | Range       | Plots sampled |
|--------------------|--------------|-------------|---------------|
| Grazing            | High         | >95.88      | 34            |
|                    | Intermediate | 22.56–95.88 | 32            |
|                    | Low          | ≤22.55      | 33            |
| Mowing             | High         | >1.33       | 28            |
|                    | Intermediate | 0.67–1.33   | 35            |
|                    | Low          | ≤0.66       | 36            |
| Fertilization      | High         | >36.08      | 34            |
|                    | Intermediate | 0.1–36.08   | 20            |
|                    | Low          | 0           | 45            |

fertilization will henceforth be referred to as land-use components. As the empirical data of land-use components was highly skewed, quantile binning for each land-use component was conducted at 33rd and 66th percentile to define the thresholds needed to classify land-use components into “high”, “intermediate”, and “low” categories for graphical representation (see Table 2). Plots were classified according to grazing intensity, fertilization, and mowing frequency. Grazing intensity was considered low when stocking rates were below 22.55 grazing units per hectare per year, and high when they exceeded 95.88 grazing units per hectare per year. Fertilization was categorized as low when no nitrogen was applied and high when nitrogen inputs were greater



flower community variables. These variables included the total number of flowers (flower density), number of flowering species (species richness), and total number of flowers of our focal species (focal species density)

than 36.08 kg N per hectare per year. Mowing intensity was classified as low when the average mowing frequency was less than 0.66 cuts over a three-year period, and high when plots were mown more than 1.33 times per year.

Assessment of the correlation between all floral traits, land-use components, and flower community variables was performed by computing each pairwise correlation with Pearson method using the “car” and “corrplot” package in R. Highly correlating variables (Fig. S.1) were removed from the subsequent analyses to avoid collinearity issues. Direct and indirect effects of land-use components and plant community variables on absolute values of floral traits were analysed by Structural Equation Modelling (SEM) using the “lavaan” package. The paths of the model were defined using knowledge from literature and previously defined hypotheses. Plant community and land-use variables highly correlated among themselves (Fig. S.1). Therefore, only two community variables, i.e., flower density and relative abundance of the focal species, and two land-use components, i.e., fertilization and grazing, were used in structural equation modelling for both focal species.

Variation in floral traits was assessed by calculating the coefficient of variation (CV) by dividing the standard deviation by the mean of every floral trait of five plant individuals for each plot. Generalized Linear Mixed Models (GLMMs) were used to analyse the effects of standardised

components of land-use on the CV of all floral traits using the “glmer” package. As pollen extraction required pooling all flowers from each plot to obtain sufficient quantities of pollen, individual plant-level measurements were not available, preventing the calculation of coefficients of variation. Therefore, variation in pollen weight and flower weight was not included in the GLMM CV analysis. The land-use component values were averaged over three years (2022 to 2024) and standardised for better fit. In addition to land-use components, floral community characteristics were included as fixed explanatory variables. These included the overall flower density and the relative abundance of the focal species. Interactions between land-use components and floral community variables were also considered. To account for spatial and temporal variation, plots nested within the Biodiversity Exploratories, and the year of sampling were included as random effects in all models. As we included several explanatory variables, i.e., land-use and floral community variables (separately as well as with interactions) as fixed effects, the dredge function from the “MuMIn” package was used to identify the best model for each trait based on the AIC and  $R^2$  values (Table S.2). Variance inflation factor (VIF) values for the models were obtained using the “car” package to identify any collinearity issues between the explanatory variables. All explanatory variables had a VIF value of less than 3 for all models, indicating low multicollinearity. The distribution of the residuals and the homoscedasticity of the models was checked using the “DHARMA” package. The distribution family of the GLMMs and the

interactions between the explanatory variables were simplified to optimise the models based on the results of the homoscedasticity tests. In case of model singularity, the year of observation was removed as a random variable from the model. Model dredging of the GLMMs is summarised in supplementary Table S.2.

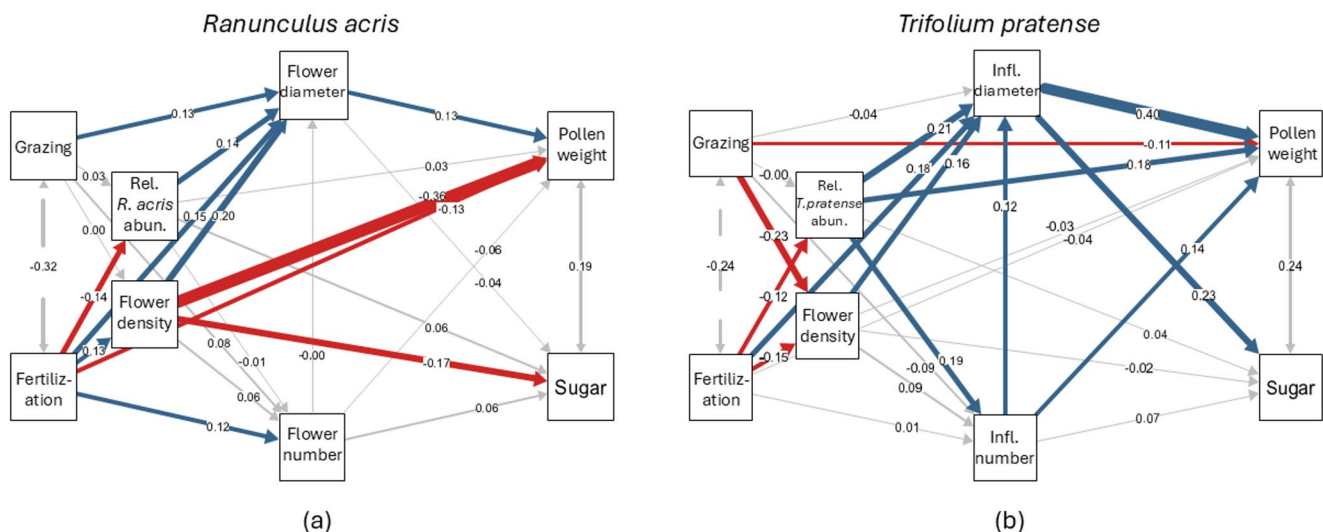
## Results

### Direct and indirect effects of land-use components and plant community on the absolute values of floral size and reward quantity

Path diagrams of structural equation model were used to study the direct and indirect effects of land-use components and plant community variables on the absolute values of *Ranunculus acris* and *Trifolium pratense* floral traits. Mowing was removed from the analysis as it correlated strongly with fertilization and grazing values (Fig. S.1), resulting in poorly fitting models (*R. acris*:  $\chi^2=10.554$ ,  $N=395$ ,  $p=0.103$ ; and *T. pratense*:  $\chi^2=16.892$ ,  $N=395$ ,  $p=0.010$ ). The path diagrams of models with the lowest test statistic values and non-significant p-values indicating a good fit and hence consistency with the model are displayed in Fig. 2 (*R. acris*:  $\chi^2=2.265$ ,  $N=395$ ,  $p=0.687$ ; Fig. 2a; and *T. pratense*:  $\chi^2=2.978$ ,  $N=395$ ,  $p=0.395$ ; Fig. 2b).

*Ranunculus acris* dataset with floral traits and plant community was recorded in April-May of 2023-24. The overall

Floral traits and rewards shaped by land-use and floral community



**Fig. 2** Path diagrams of structural equation models (SEM) showing the effects of land-use components, i.e., standardised fertilization, and grazing, as well as flower community variables, i.e., flower density and relative focal species abundance (Rel. *R. acris* / *T. pratense* abund.) on morphological traits and floral rewards of *Ranunculus acris* (a)

and *Trifolium pratense* (b). Blue arrows indicate significant positive effects, red arrows negative effects, solid grey arrows non-significant paths, double headed solid grey arrow show correlation and dotted grey arrows indicate covariation. Edge values represent standardised estimates of the model

flower density increased and relative *R. acris* abundance decreased with fertilization (Fig. 2a). Flower diameter and number increased with increasing fertilization. Flower diameter also positively correlated with grazing intensity and flower density and in turn resulted in an increased pollen weight per flower (Fig. 2a). Nectar sugar content did not correlate with land-use management nor with any floral trait, but plots with high flower density had *R. acris* flowers with a comparatively lower nectar sugar content and pollen quantity per flower (Fig. 2a).

*Trifolium pratense* floral traits and flower community was recorded in July–August for 2023–24. Fertilization negatively correlated with flower density and relative *T. pratense* abundance, while grazing was only negatively correlated with flower density (Fig. 2b). High fertilization correlated with increased inflorescence diameter (Fig. 2b). High relative abundance of *T. pratense* also correlated with a larger inflorescence diameter, in addition to higher number of flowers and increased pollen quantity (Fig. 2b). Pollen quantity and nectar sugar content also increased with inflorescence diameter (Fig. 2b).

### Effects of land-use components on intraspecific variation in floral traits within and between plots

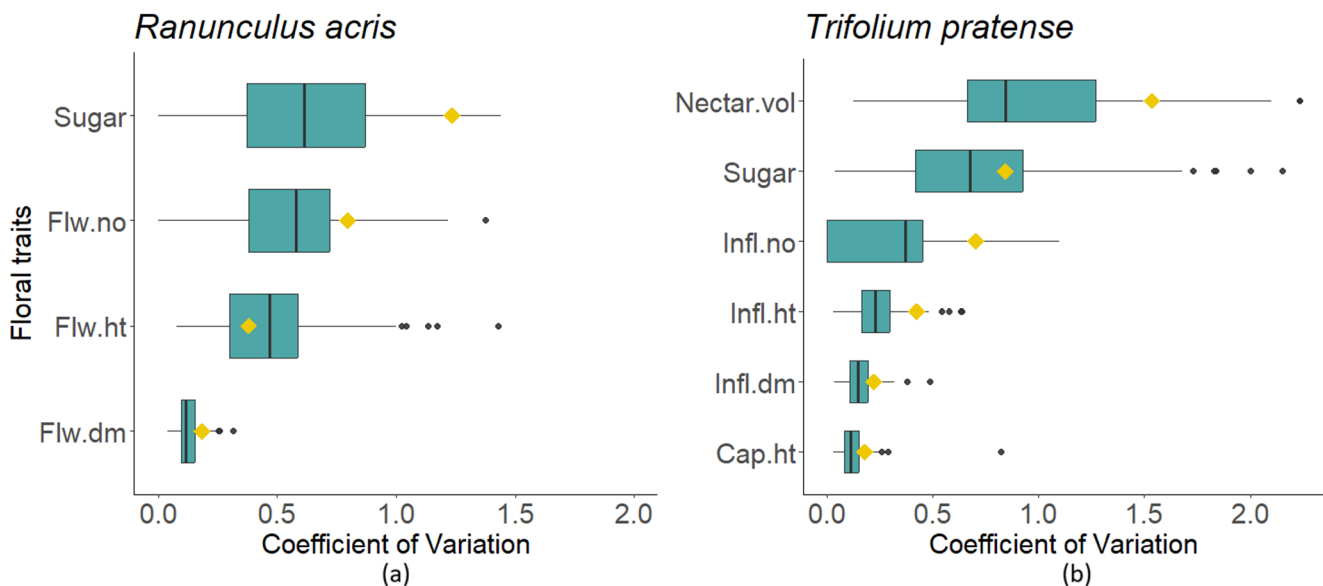
For both focal species, across all floral traits, coefficients of variation (CV) among plots were higher than those observed within a single plant population from an individual plot, with the exception of *Trifolium pratense* nectar sugar content and *Ranunculus acris* flower height from the ground (Fig. 3).

The CV of the flower diameter of *Ranunculus acris* was the least ( $<0.5$ ), while nectar sugar content varied the most with values reaching more than 1 (Fig. 3a). For *T. pratense*, inflorescence diameter, height from the ground, and capitulum height showed low intraspecific variation ( $<0.5$ ; Fig. 3b). On the other hand, nectar volume and sugar content were highly variable ( $>1$ ; Fig. 3b).

### Effects of land-use components, plant community and their interactions on floral trait variation within plots

For *Ranunculus acris*, neither the land-use components and floral community variables nor their interactions had any significant effect on CV of flower diameter and flower number per plant individual (Table S.2), except for variation in flower height from the ground significantly which decreased with mowing intensity ( $\chi^2=6.095$ ,  $p=0.01$ ; Fig. 4a, Table S.2), and variation in nectar sugar content, which increased with overall flower density independent of land-use components ( $\chi^2=12.659$ ,  $p<0.001$ ; Fig. 4b, Table S.2).

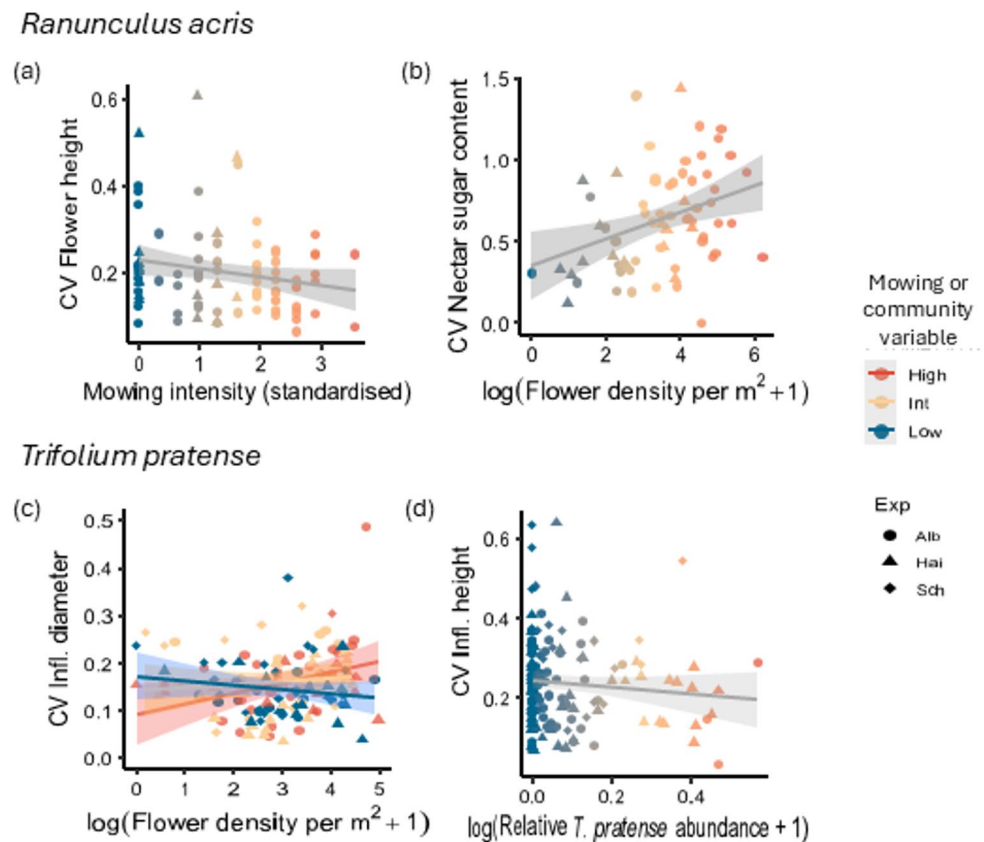
Intraspecific variation was significantly affected by floral community variables for two out of six *Trifolium pratense* traits (Fig. 4c, d; Table S.2). Variation in inflorescence diameter significantly increased with flower density in plots with high but decreased with low mowing intensity ( $\chi^2=7.964$ ,  $p=0.011$ ; Fig. 4c). Variation in inflorescence height decreased with relative *T. pratense* abundance regardless of land-use intensity ( $\chi^2=9.125$ ,  $p=0.02$ ; Fig. 4d).



**Fig. 3** Intraspecific variation (measured as coefficient of variation, CV) in floral traits across and within plots for *Ranunculus acris* (a) and *Trifolium pratense* (b). Yellow diamond shaped points represent the CVs across all plots/populations while the coloured box plots illustrate the distribution of CVs for the traits measured within one popula-

tion. Traits for *Ranunculus acris*: flower diameter (Flw\_dm), height (Flw\_ht), number (Flw\_no.), and nectar sugar content (Sugar); for *Trifolium pratense*: inflorescence diameter (Infl\_dm), capitulum height (Cap\_ht), height from the ground (Infl\_ht), number (Infl\_no.), nectar volume (Nectar.vol), and nectar sugar content (Sugar)

**Fig. 4** Effects of land-use and plant community on intraspecific variation (displayed as coefficients of variation, CV) in *Ranunculus acris* (a, b) *Trifolium pratense* (c, d) and colours indicate standardised mowing intensity for plots a, c, flower density for b, and relative *T. pratense* abundance for d. Red indicates high ( $>1.5$ ), yellow for intermediate (0.65–1.5), and blue denotes low ( $<0.65$ ) mowing intensity. Data point shapes indicate the Exploratory (Exp): circles for Swabian Alb, triangles for Hainich National Park, and diamonds for Schorfheide-Chorin biodiversity reserve. The trendlines represent the linear regression model fitted to the data. Coloured lines indicate interactive effects, while grey lines indicate the lack of interaction between floral community and land-use components



## Discussion

Agricultural practices are known to influence plant fitness as well as ecological communities (Schroeder et al. 2021). However, the effect of such practices on floral traits at the individual plant level remains understudied, even though plant-insect interactions typically occur at this scale, calling for a better understanding of both the direct and indirect effects of land-use on intraspecific floral trait variation.

As per our expectations, fertilization had a positive effect on the flower diameter of both focal species and on flower production of *Ranunculus acris*, likely because more nitrogen in soil leads to higher plant biomass (Atasay et al. 2013). Increased grazing intensity also correlated with bigger *R. acris* flowers (Fig. 2a). Heavy grazing is considered a comparatively harsh condition for plants which can prompt investment into bigger, more attractive flowers (Gélvez-Zúñiga et al. 2025). Similarly, the variation of flower height decreased under high mowing intensity (Fig. 4a), indicating that plants may prioritize flower production over shoot elongation in a stressful environment. Alternatively, larger flowers on plots with high grazing intensity might be a result of reduced competition for nutrition, as *R. acris* contains ranunculin, a compound that renders the plant unpalatable for many grazers (Lamoureaux and Bourdôt 2007). Therefore, intensive grazing may remove surrounding plants,

resulting in higher nutrient availability for *R. acris* which might thus produce larger flowers. In *Trifolium pratense*, intense grazing correlated with reduced pollen weight extracted per flower (Fig. 2b), which may suggest reallocation of resources towards structural parts under grazing stress, especially as *T. pratense* is palatable to grazers (Greveniotis et al. 2025). Moreover, pollen weight per flower as well as the nectar sugar content increased with inflorescence number and diameter for *T. pratense* (Fig. 2b). These results align in part with our second hypothesis suggesting that land-use intensity directly impacts floral morphology and subsequently floral rewards.

While land-use intensity showed some direct effects on floral trait absolute values, the variation in floral traits was more strongly affected by either floral community variables or their interaction with land-use components (Fig. 4, Table S.2). Competition between plant species can result in pollen limitation via reduced conspecific pollen deposition (Caruso, 2000). According to the sexual selection theory, pollen limitation selects for traits that attract pollinators for successful reproduction, such as flower size (Caruso, 2000). Both focal species in our study showed an increase in flower or inflorescence diameter on plots with high overall flower density (Fig. 2). Interestingly, three out of four *R. acris* floral traits varied with overall flower density, while the same number of *T. pratense* floral traits (i.e., inflorescence

diameter, number, and pollen weight) increased with its relative abundance (Fig. 2). Flower diameter of *R. acris* positively correlated with overall flower density, while pollen weight per flower and nectar sugar content showed a negative correlation (Fig. 2a). *Ranunculus acris* is mainly visited and pollinated by flies that use flower size as a cue for nectar quantity, hence bigger flowers are visited more frequently (Conner and Rush 1996; Totland 2004). Moreover, areas with high overall flower density generally attract higher abundance of pollinators (Alonso-López et al. 2022; Potts et al. 2009; Weiner et al. 2011), but might simultaneously increase interspecific competition for pollinators and nutrients (Kuppler et al. 2020; Seifan et al. 2014). The observed discrepancy between flower size and reward may suggest that *R. acris* plants, growing on flower dense plots, might instead benefit from heterospecific individuals and invest less in floral rewards. Moreover, optimal foraging theory states that pollinators tend to visit several neighboring flowers in a florally dense plot to reduce energy expenditure per foraging trip (Seifan et al. 2014), potentially facilitating pollination across plant species, which likely allows for more variation in areas with high flower density. Interestingly, intra-specific variation in nectar sugar concentration has been shown to affect pollinator visitation and increase overall exogamous visitation across plant individuals, provided that some plants produce nectar with above-average sugar concentration (Maldonado et al. 2023). This strategy can reduce the energy costs per pollinator visit for most plant individuals (Maldonado et al. 2023). Such a tradeoff might also explain the higher variation in nectar sugar content in *R. acris* observed on plots with greater overall flower density (Fig. 4b), which agrees with our hypothesis that plots with higher overall flower abundance show increased floral trait variation. These conclusions remain, however, speculative without data on seed set or pollen deposition on flowers.

In contrast to *R. acris*, most *T. pratense* floral traits did not correlate with overall flower density. Instead, inflorescence diameter, number of flowers and pollen weight per inflorescence increased with *T. pratense* relative abundance (Fig. 2b). As *T. pratense* is a legume and can therefore fix nitrogen, it may not face strong competition for nutrients irrespective of plot-level flower density (Zheng et al. 2023). Consequently, *T. pratense* plants might have sufficient nutrients for large inflorescences and floral rewards, which may support flower detection by pollinators (such as bumblebees) that use flower-size as a long distance cue (Ortiz et al. 2021; Rowe et al. 2020). Moreover, our results showed low variation in *T. pratense* inflorescence diameter under low, and high variation under high mowing intensity (Fig. 4c). The cutting stress as a consequence of mowing was shown to induce premature flowering (Bouchet et al. 2017), resulting in numerous small flowers (Dee and Baum

2019), potentially reducing the flowers' attractiveness to pollinators. Similarly, variation in inflorescence height from the ground decreased with relative *T. pratense* abundance (Fig. 4d). Flower height has been shown to positively correlate with bumblebee visitation (Rowe et al. 2020). Plant individuals growing in dense conspecific populations might thus achieve most visits if they maintained a certain height.

In accordance with our expectations, morphological traits, such as flower diameter, open flowers, flower height from the ground, and capitulum height (in case of *T. pratense*), showed comparatively low intraspecific variation, particularly within plots, whereas the floral rewards seemed to be highly variable both within and between plots (Fig. 3). Intraspecific floral trait variation was almost always lower within than between populations. This might be a result of site-specific abiotic environmental conditions, such as soil properties (Parachnowitsch et al. 2019; Wu et al. 2022), water availability (Glenny et al. 2018; Parachnowitsch et al. 2019; Wu et al. 2022), and surrounding landscape heterogeneity, which may affect floral traits directly or – in the case of landscape heterogeneity – indirectly through varying pollinator abundance and diversity (Weiner et al. 2011). Thus, the degree of intraspecific variation depends strongly on the local environmental conditions of a plant population.

Future studies should assess the consequences of the observed variation in floral traits on actual fitness, e.g., pollen deposition and ideally seed set, of plant individuals varying in traits in relation to different land-use intensities and hence plant communities. While our results indicate effects of the surrounding flower density on floral traits, we lack the pollinator data needed to test whether the observed effects were mediated by pollinator behavior, which represents an interesting topic for future studies on floral trait variation in different plant communities. Further in-depth knowledge of the mechanisms underlying effects of land-use management on floral traits could be gained by phytometer experiments, or controlled greenhouse or semi-field experiments disentangling all the factors that are naturally correlated in real-world settings, such as pollinator-driven trait divergence. Notably, we used five plant individuals per plot to calculate coefficients of variation (CV) for floral traits. While this approach should be reliable for a comparative approach as used in our study, CVs are sensitive to low sample sizes and future studies would benefit from a larger sample size, especially for highly variable traits such as nectar volume and sugar concentration. While our study looked at the overall mowing, grazing, and fertilization intensity, mowing time and height are additional factors which have a strong impact on flower community structure (Jantunen et al. 2007; Johansen et al. 2019; Piqueray et al. 2019) and should be addressed in future analyses. Similarly, different species of grazing animals may differently affect the regrowth of

plant species, as, for instance, cattle grazed pastures show higher flower diversity than sheep grazed pastures (Cutter et al. 2022). Finally, fertilizer type – organic or inorganic – is known to affect plant species richness (Shi et al. 2024).

Our study provides insight into the (potentially interacting) direct and indirect effects of land-use intensity on two generalist plant species. Specialized plant species might, however, show lower variation in floral traits independent of the environment, as they are thought to be under a higher selection pressure by specific pollinators compared to generalist species which are likely more sensitive towards abiotic, environmental conditions (Kuppler et al. 2020). Hence, studies investigating the differential effects of direct abiotic versus indirect community- and potentially interaction-mediated effects of phenotypic plasticity in floral traits should be expanded to more plant species with different degrees of specialization to fully understand how interactions between environmental stressors and (a)biotic conditions determine floral trait plasticity.

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**Author contributions** All authors conceptualized and designed the study. V.B. collected and curated the data. V.B., A.K., C.J.v.d.K., and S.D.L. analyzed the data. V.B. and S.D.L. led the manuscript writing, while all authors contributed towards reviewing and editing the manuscript.

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**Data availability** The raw data for floral traits for this project is publicly available in the Biodiversity Exploratories Information System (BExIS; (<https://www.bexis.uni-jena.de>)), with dataset id: 32258 (Bansal, 2026a) and 32297 (Bansal, 2026b). The plant community

dataset is available in BExIS repository, with accession number 32296 (Bansal, 2026c). The datasets and the R codes used for this study are available for download here: [<https://doi.org/10.5281/zenodo.18480920>] (Bansal et al., 2026). All datasets are permanently archived in BExIS data repository.

## Declarations

**Competing interests** The authors declare no competing interests.

**Conflict of interest** The authors declare no conflict of interest.

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