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Flowers of ruderal species are numerous but small, short and low-rewarding

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Abstract

Weed species are ecological models that recently received considerable attention due to their particular strategies linked to their ruderal-competitive traits. They are known to have the potential to provide additional floral resources for insects in flower-poor agroecosystems. However, their floral traits are much more scarcely studied than those of plants found in other habitats, such as grasslands. The aim of this study was to describe the floral phenotype of weeds and to determine to what extent their floral traits match their ecological strategies as described based on leaf traits. We cultivated 19 forb weeds from perennial agroecosystems, previously identified in Mediterranean fields, in a greenhouse for seven months and collected data on 12 floral and 5 leaf traits. We tested whether these traits covaried and exhibited an ecological strategy at the phenotype scale. We found that in matters of flower production, weed species face a trade-off: either numerous small, low-stature flowers with small quantities of pollen and nectar, or few, large, higher-held flowers with more pollen and nectar. The floral traits were found to reflect Grime's CSR strategies: the weed species producing fewer but costlier flowers belonged to C-strategy species, whereas those producing more but less costly flowers belonged to species dominated by an R strategy These findings indicate that the potential of weeds as floral resources for insects is related to their ecological strategies, which are known to be affected by agricultural practices that filter species composition. This implies that, as for the provision of other ecosystem services, weed communities can be managed to select species with floral traits matching the requirements of flower-visiting insects like pollinators or parasitoid wasps.

1. Introduction

Floral traits are morphological, phenological, or physiological characteristics underlying the diversity of floral phenotypes and pollination types (Violle et al., 2007; E-Vojtkó et al., 2022). They reflect the carbon costs of producing and maintaining flowers and floral resources (i.e. nectar and pollen) over time (Lanuza et al., 2023). Floral traits also define more or less attractive displays for flower-visiting insects, which are key for plant-insect interactions and pollination success. Unlike leaf traits that determine plant growth and survival through resource acquisition and conservation, floral traits affect the likelihood of reproduction, another component of plant fitness, through pollinator attraction and seed production for animal-pollinated plants (Roddy et al., 2021). Pollinator attraction is known to strongly relate to visual cues and resource availability, determined by multiple traits such as flower height, surface area, colour, number, or flowering phenology (Fornoff et al., 2017; Hegland & Totland, 2005; Junker & Parachnowitsch, 2015; Rowe et al., 2020, Caruso et al., 2019) and is essential to achieve reproduction in insect-pollinated plants. Yet, integrative approaches to floral phenotypes are needed to understand how these visual cues and resource availability traits relate to their physiological construction costs (Lanuza et al., 2023). Studies on floral traits usually focus on insect-plant interactions and the identification of key floral traits for insect attraction (Hegland & Totland, 2005), and less frequently consider covariation among floral traits to describe plant strategies. In addition, and despite the importance of floral traits for plant reproduction, studies focusing on floral traits, unlike those on leaf traits, tend to cover a limited number of plant taxa (Roddy et al., 2021), and disproportionately from grassland ecosystems.

Furthermore, contrary to leaf traits, there is no accepted general frame representing plant floral strategies. As a consequence, floral traits have hardly been studied in relation to plant strategies (E- Vojtkó et al., 2020). The global spectrum of plant forms and functions describes the main plant strategies based on two major axes of trait covariation, one related to a trade-off between resource acquisition and conservation and the other one to plant size, neither taking into consideration flower costs and flower size (Díaz et al., 2016). The axes of covariation and fundamental trade-offs between floral traits remain unexplored, except for certain evolutionary compromises such as the negative relationship between flower size and number (Sargent et al., 2007; Worley & Barrett, 2000). This trade-off derives from the fact that plants cannot freely allocate their limited resources to both flower size and flower number. Ortiz et al. (2021) recently showed that certain visual cues floral traits, e.g. floral area, are associated with the quantity of pollen and nectar produced by the plant on 98 species of Mediterranean shrubland and woodland. Lanuza et al. (2023) recently explored the spectrum of reproductive traits in 1500 flowering plants worldwide, within a global set of plant-pollinator networks and identified two major covariations axes on floral traits. The first axis distinguished species that produced many and small flowers to those producing few, big and rewarding (nectar, pollen) flowers and the second one distinguished species from low to high autonomous selfing. In their study, floral resources were assessed by using the number of pollen grains and the quantity of nectar. However, the volume of pollen, pollen protein content, nectar accessibility or nectar sugar content have not been studied despite their major role in plant costs and pollinator attractivity (Fornoff et al., 2017; Gallagher & Campbell, 2017; Hatt et al., 2019; Parachnowitsch et al., 2019).

To reach a deeper understanding of the relationships and trade-offs between multiple floral traits, Roddy et al. (2021) recently proposed the development of a Flower Economics Spectrum (FES). The FES incorporates the multiple pathways by which floral traits can be shaped by multiple filters acting on flower functions. Its authors were inspired by the economics spectra previously proposed for the leaf (Díaz et al., 2016; Wright et al., 2004) and the roots (Roumet et al., 2016, Weemstra et al., 2016). In its current definition, the FES includes three major floral traits: (1) flower size, defined as the two-dimensional projected surface of the petals; (2) floral mass area (FMA), defined as the dry mass of the petals divided by their surface; and (3) flower longevity, defined as the number of days a flower remains functionally active. Floral mass area and flower longevity, known to relate to the carbon and water costs of floral structure production and maintenance (Roddy et al., 2016; Zhang et al., 2017), covary positively in an orchid genus (Zhang et al., 2017), but this relationship was not investigated in many taxa and still needs to be tested. In addition, the FES traits have not yet been linked to other floral construction traits such as pollen nutrient or nectar sugar content, nor to visual cues or resource availability traits known to attract pollinators such as flower height, flower area and the total number of flowers on a plant.

Addressing the question of covariations among these floral construction traits, which we call Floral Mass Area (FMA), flower size, flower longevity, pollen volume, pollen nutrient content, and nectar sugar content, could help to identify fundamental trade-offs in the flower economics spectrum. To identify the payback between a plant's investment in the construction of a flower and its attractiveness to pollinators, we explored covariations between two categories of traits: construction traits on the one hand and visual cues and resource availability floral traits, i.e. floral area and height, number of flowers, flowering onset and flowering duration, on the other hand. 'Construction costs floral traits' refer to the FES traits described above plus floral resource traits, i.e. nectar sugar content and pollen volume. These traits are linked to the costs, for the plant, of constructing floral organs. The 'floral visual cues and resource availability traits' refer to how insects perceive the flowers and to their availability for insects. These visual cues and resource availability traits have been repeatedly found to have a positive impact on attractiveness to insects: total number of floral units, reproductive height, floral area, flowering onset and flowering duration (Caruso et al., 2019; Fornoff et al., 2017; Hegland & Totland, 2005; Hernández-Villa et al., 2020; Junker & Parachnowitsch, 2015; Lundin et al., 2019; Rowe et al., 2020; Tuell et al., 2008).

In cultivated landscapes, weeds, i.e. plants occurring spontaneously in agroecosystems, represent a significant part of the flowering species and may be a precious source of food resources for insects (Balfour & Ratnieks, 2022; Bretagnolle & Gaba, 2015; Kratschmer et al., 2021). However, their potential for attracting flower visitors and providing resources compared with species from other, better studied, ecosystems such as grasslands, has not been fully assessed. From a functional point of view, weeds represent a distinctive pool of species. Recent studies suggest the existence of a "weed trait syndrome" combining leaf traits and phenological traits that are typical of ruderal strategies (*sensu* Grime CSR classification, 1974), selected mainly by the high level of disturbance caused by agricultural practices (Mahaut et al., 2020). For instance, weeds tend to have faster life cycles (e.g. earlier flowering date, low longevity) and more acquisitive strategies (e.g. higher specific leaf area) than non-weed species (Bourgeois et al., 2019), allowing them to cope with disturbance. Some weeds also adopt competitive strategies, investing in the interception of resources (water, light), especially in not-so-disturbed agroecosystems such as perennial crops (e.g. olive groves, vineyards), where the main management practice consists to mowing instead of tilling (Fried et al., 2022). However, it is not known whether this weed syndrome is also reflected in floral traits other than phenology, as floral traits of weeds have scarcely been studied (Hernández-Villa et al., 2020) compared with those of grassland species (Goulnik et al., 2020; Hegland & Totland, 2005). Despite their importance, weed floral traits have not yet been studied in the framework of the global spectrum of plant forms and functions as defined by Díaz et al. (2016), specifically whether they covary with leaf traits and contribute to plant strategies. It is generally hypothesised that leaf and floral traits are decoupled in insect-pollinated species but it is not always proved by experimental studies (Armbruster et al., 1999). E-Vojtkó et al. (2022) actually recently showed that, in two important European plant datasets, leaf traits and floral traits are mostly distributed along two independent axes of the plant spectrum, except for floral size that positively scaled with leaf area and plant size. Other studies suggest that leaf traits and floral traits could be related, in particular the size of leaves and floral organs (B. Lanuza et al., 2023; Feng et al., 2021; Lambrecht & Dawson, 2007). This could suggest that floral size also contributes to the first axis of variation of plant form and function, along with leaf area and seed mass. However, these relationships remain little studied, and across a small number of taxa only, calling for a more comprehensive investigation encompassing more species and ecosystems.

The aims of this study were (1) to describe the floral phenotype of weeds and to compare it with that of species dominating grasslands; (2) to test whether the flower economics spectrum (FES) applies to weeds and whether this FES is related to pollinator attraction through floral visual cues and resource availability traits, in other words, whether costly flowers are also attractive to pollinators, and (3) to find out whether weed floral and CSR strategies covary by testing the relationships between floral and leaf traits and checking whether they exhibit an ecological strategy at the phenotype scale. To address these objectives, we designed a greenhouse experiment to measure and compare under controlled conditions 17 floral and leaf traits of 19 species of entomophilous early-flowering weeds abundant in French Mediterranean olive groves and vineyards. In the present study, we focused exclusively on entomophilous weeds whose floral traits have been selected by pollinators, and therefore our conclusions cannot be extrapolated to other weeds such as *Poaceae*. Our hypotheses were that (1) weed floral phenotype is defined by smaller and less costly flowers than the floral phenotype of grassland species because the disturbance faced by weeds prevents them from investing in costly flowers; (2) construction traits on the one hand, and visual cues and resource availability traits, on the other hand, covary, with a trade-off between the number of flowers and the construction costs (i.e. Floral Mass Area, flower longevity, flower size, pollen volume, pollen nutrient content, nectar sugar content, floral area, reproductive height) of each flower, and finally (3) leaf and floral strategies covary, and CSR strategies can be integrated across the different organs, in other words, ruderal species display both more acquisitive and less costly leaf traits (e.g. high SLA, low LDMC) and floral traits (e.g. low FMA, small reproductive height and flower size, numerous flowers).

2. Materials and methods

2.1. Plant material

Nineteen weed species (Table 1) were cultivated in a greenhouse from February to August 2022. The species were chosen according to recent surveys carried out in 32 vineyards and olive groves in the countryside surrounding Montpellier, in southern France (Anonymised, 2023). The most abundant forb species found at the flowering stage during spring 2021 in the tilled or mown inter-rows were selected for the greenhouse experiment. The best-represented families were *Asteraceae* and *Fabaceae*, with 3 species each, and *Apiaceae*, *Caryophyllaceae*, *Geraniaceae* and *Plantaginaceae*, with 2 species each (Table 1). Four species were perennials: *Malva sylvestris*, *Plantago lanceolata*, *Ranunculus bulbosus* and *Sanguisorba minor*. The fifteen others were annual species. The seeds used came from French seed companies specialising in wild plants (Semence nature and Phytosem).

Table 1. List of the 19 weed species of the experiment (botanical family, floral unit type, following Baldock et al., 2015, and number of replicates (n)).

Family	Species	Floral Unit Type	n
Apiaceae	*Torilis arvensis*	Secondary umbel	13
Apiaceae	*Torilis nodosa*	Secondary umbel	11
Asteraceae	*Carduus pycnocephalus*	Single capitulum	16
Asteraceae	*Picris hieracioides*	Single capitulum	10
Asteraceae	*Senecio vulgaris*	Single capitulum	16
Brassicaceae	*Diplotaxis erucoides*	Single flower	16
Caryophyllaceae	*Arenaria serpyllifolia*	Single flower	16
Caryophyllaceae	*Cerastium glomeratum*	Single flower	16
Fabaceae	*Medicago arabica*	Single raceme	16
Fabaceae	*Medicago minima*	Single raceme	16
Fabaceae	*Trifolium campestre*	Single raceme	10
Geraniaceae	*Geranium dissectum*	Single flower	16
Geraniaceae	*Geranium rotundifolium*	Single flower	16
Malvaceae	*Malva sylvestris*	Single flower	16
Plantaginaceae	*Plantago lanceolata*	Spike	16
Plantaginaceae	*Veronica persica*	Single flower	16
Ranunculaceae	*Ranunculus bulbosus*	Single flower	9
Rosaceae	*Sanguisorba minor*	Spike	13
Rubiaceae	*Sherardia arvensis*	Single flower	12

2.2. Experimental design

The experiment was designed with 16 individual plants (replicates) per species randomly distributed in four adjacent blocks (76 plants/ block), for a total of 304 expected plants (Figure 1). However, certain individuals failed to germinate or flower during the experiment and consequently the final number of replicates varied somewhat across the species (Table 1). The blocks were moved around weekly inside the greenhouse for randomisation and rotated every four weeks to minimise light exposure biases. Each plant was grown in its own 3 L pot(depth : 21 cm, width :13 cm, length : 13 cm),, in sterilised soil composed of 75% of clay-loamy soil (2.11 g kg-1 N, 0.07 g kg-1 P, 1.36 g kg-1 K) and 25% of Sphagnum peat moss. The plants were watered manually during the first month to induce germination and emergence, and by sub-irrigation during the remainder of the experiment to ensure homogenised watering. The greenhouse was not heated to maintain temperatures close to outside temperatures (mean daily temperature 18°C). No flower-visiting insect could enter the greenhouse.

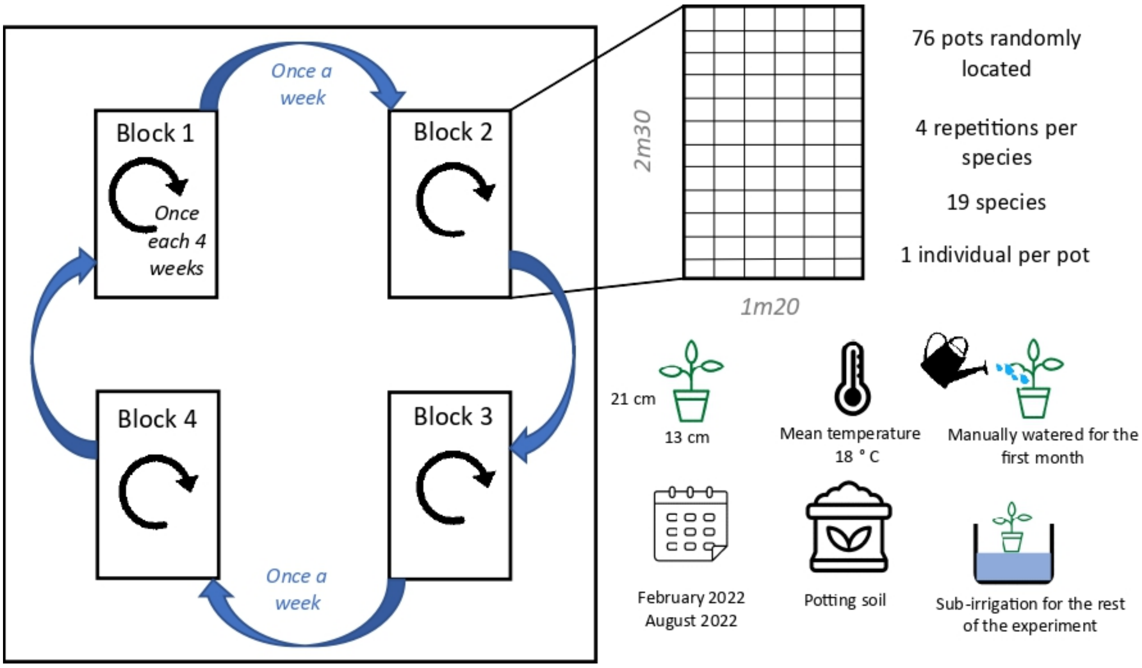

Figure 1. Experimental design and abiotic conditions of the experiment.

2.3. Construction-related traits

We selected seven construction-related floral traits, including the three traits of the Flower Economics Spectrum (FES) according to the standardised protocols (Roddy et al., 2021): flower size, FMA, flower longevity, pollen volume, pollen nitrogen content, pollen C/N ratio, and nectar sugar content. These traits are considered to be related to the construction and maintenance costs of a flower. Flower size (FS cm^2) was measured as the area of scanned fresh dissected and flattened petals of the flower. This trait relates to the petal tissues produced by the plant, it relates to the carbon investment to be produced. Floral mass area (FMA g m^{-2}) was determined as the oven-dried weight of the dissected petals divided by flower size. Flower longevity was the number of days a floral unit remained open and functionally active. Both FMA and flower longevity are linked to costs in water to maintain the flower turgescent and in carbon to the construction of the flower tissues (Zhang et al., 2017).

Pollen volume (mm^3) was calculated as the mean volume of one pollen grain in mm^3 multiplied by the number of pollen grains in a floral unit. The number and mean size (mm^3) of pollen grains ($n = 10$) in a floral unit were measured according to the protocols of Baude and Michelot-Antalik (*pers. com.)* with a Fuchs-Rosenthal C-Chip haemocytometer and with the ImageJ software (version 1.53m). We extracted the pollen immediately after the initial anthesis by collecting the stamens and storing them in 99% alcohol at 2°C in a refrigerator before analysis. Pollen nitrogen content and C/N ratio were measured on the same pollen samples as above using elemental combustion analysis (NF ISO 10694; Carlo Erba Instruments model E1 1108).

Samples from nine species were below the detection threshold to measure C and N content (0.5 mg) and were therefore pooled, either at the block scale by pooling the four repetitions of one block (*Geranium dissectum*, *Geranium rotundifolium*, *Medicago arabica*, *R. bulbosus* and *S. minor*) or at the species scale by pooling all the repetitions of the species, to obtain a reliable measurement (*Sherardia arvensis*, *Torilis arvensis*, *Trifolium campestre* and *Veronica persica*). The pollen traits relate directly to investment in male fitness but are also considered as a food reward for insects that feed on this resource. We measured the nectar sugar content (µg μl^{-1}) with High-Performance Liquid Chromatography (HPLC Dionex, amperometric detection, NaOH150mM eluent, isocratic mode, 1mL/min flow). The nectar was sampled with microcapillary tubes to obtain a sample of 10 µl of nectar per plant, which was the minimum volume needed for the analysis. This volume was obtained after sampling 2 to 26 floral units depending on the species. The nectar was directly extracted from the floral unit when possible (which was the case in *D. erucoides* and *M. sylvestris* only) and was diluted with distilled water for 2 minutes when the volume available was very low. Nectar samples were frozen in liquid nitrogen at -20°C before analysis. The nectar sugar content is a direct investment in the attraction of insects and is a costly reward to produce that mediates the interactions between plants and insects and can be positively linked to plant reproductive success (Parachnowitsch et al., 2019). The presence of glucose, fructose and saccharose and their concentration were measured. The three types of sugars were pooled to obtain the total nectar sugar content.

Each trait was measured on each individual plant of all 19 species except FMA, pollen nitrogen content and C/N ratio (16 species). FMA was not measured on *S. minor* because this species lacks petals. FMA is also missing for *Torilis nodosa* and *Arenaria serpyllifolia* because petal weight was below the detection threshold of the scales (10^{-5} g). Similarly, pollen nitrogen content and C/N ratio were not measured on *A. serpyllifolia*, *Cerastium glomeratum* and *T. nodosa* because pollen weight was beneath the detection threshold of the scales (10^{-5} g). Pollen volume was measured on 17 species: it was not measured on *T. nodosa* and *T. arvensis* because fragments of stamens were mixed with the pollen grains, making them impossible to count precisely (Table 2).

Table 2. List of the category, unit, mean, standard deviation (sd), range and number of species (n) for each trait considered

Category	Trait	Unit	Mean (sd)	Range	n
Construction-related floral traits	Flower size	cm^2	3.15 (± 3.85)	0.05 – 11	18
	Flower longevity	days	6.5 (±4.04)	1.56 – 14.8	19
	Floral Mass Area	$g\ m^{-2}$	28 (±38.6)	5.55 - 161	16
	Pollen volume	cm^3	5.25 (±12.6)	0.03 – 52.6	17
	Pollen nitrogen content	$g\ kg^{-1}$	7.04 (±2.11)	3.27 – 11	16
	Pollen carbon content	$g\ kg^{-1}$	44.3 (±2.4)	40 – 48.8	17
	Nectar sugar content	$\mu g\ \mu l^{-1}$	127(±403)	0.09 - 1646	18
Visual cues and resource availability - floral traits	Total number of floral units	-	307 (±399)	3.7 – 1462	19
	Reproductive height	cm	44.9 (±40.7)	9.79 - 166	19
	Flower area	cm^2	2.03 (±3.11)	0.03 – 12.1	19
	Flowering duration	Sum of temperatures	897 (±300)	469 – 1672	19
	Flowering onset	Sum of temperatures between germination and flowering	1460 (±385)	774 – 2086	19
Leaf traits	Leaf area	cm^2	17.7 (±21.6)	0.27 – 91.5	19
	Leaf Life Span	days	55.9 (±12.8)	25.9 – 72.4	19
	Leaf Mass Area	$g\ m^{-2}$	28.3 (±5.3)	21.4 – 40	19
	Leaf Nitrogen Content	$g\ kg^{-1}$	4.75 *(±1)*	2.06– 6.2	19
	Leaf C/N ratio	-	10.2 (±3.54)	6.05 – 20.2	19

2.4. Visual cues and resource availability floral traits

We measured five traits pertaining to visual cues and resource availability, known to be linked to the capacity of a floral unit to be seen and to attract pollinators (Fornoff et al., 2017; Lázaro et al., 2013; Ricou et al., 2014; Rowe et al., 2020). We counted the total number of floral units by plant, i.e. all the floral units discernible at peak bloom, whether as bud, flower, fruit or wilted flower. The number of floral units is linked to the floral display, known to attract pollinators in the landscape (Hegland & Totland, 2005). We measured the plant reproductive height (cm) as the height of the highest open floral unit at peak bloom, which is also linked to the insect capacity to detect the flower and to its visitation rate (Lazaro et al., 2013 ; Rowe et al., 2020). We measured the floral area (cm²) as the overall area (approximated to a circle or rectangle shape depending on the floral unit) of the highest open floral unit at peak bloom (Fornoff et al., 2017). The floral area has been repeatedly found to be linked with insect visitation (Lundin et al., 2019 ; Rowe et al., 2020 ; Tuell et al., 2008). Finally, to assess the temporal availability of these flowers, we recorded the onset of flowering as the number of days and the accumulated degree days (°C) between germination and the anthesis of the first flower. Similarly, we determined the flowering duration as the number of days and the accumulated degree days (°C) between the opening of the first flower and the closing of the last flower on each plant. The degree days were calculated as the sum of the daily mean air temperatures above 0°C. For the phenological traits, each individual plant was checked daily. The phenology determines the period and the timing at which the flowers are available to be visited by insects and to deliver them food resources.

All the traits, except the total number of floral units and the phenological traits, were measured at the floral unit level, which was defined depending on the botanical family as a single flower, a spike, an umbel, a capitulum or a raceme (Baldock et al., 2015) (Table 1). All the traits, their categories, mean and range of attributes are listed in Table 2.

2.5. Leaf traits

Five leaf traits were measured on all individual plants to explore possible correlations with floral traits: leaf area, leaf mass per area (LMA), leaf nitrogen content (LNC), leaf C/N ratio and leaf life span (LLS). Leaf area, homologous to flower size, was the scanned surface in cm^2 of a fresh leaf after 24 hours of rehydration in distilled water (Pérez-Harguindeguy et al., 2013). Leaf area is linked to the plant size, including seed size and plant height (Diaz et al., 2016). LMA, homologous to floral mass area, was the oven-dried leaf mass divided by the leaf area in $g\ m^2$ (Poorter et al., 2009). It is linked to conservative plant strategies, with slower growth and a lower photosynthetic rate. LNC and the leaf C/N ratio, homologous to the pollen N content and the pollen C/N ratio, were measured by elemental combustion analysis (NF ISO 10694). LNC is linked to acquisitive strategies while the leaf C/N ratio is linked to conservative strategies. LLS, homologous to flower longevity,is the number of days the leaf was functionally active (Pérez-Harguindeguy et al., 2013). The most recently emerged leaf was marked and checked daily until the emergence day of the tracked leaf , for which emergence day was recorded, that was marked and checked daily until its senescence. Longer-lived leaves tend to have higher dry matter content, higher LMA and lower LNC and are linked to conservative plant strategies.

To describe the dominant strategy of the species according to Grime, we used Pierce et al.'s (2017) method for calculating CSR plant strategies for each individual plant. This method calculates Grime's dominant strategy of species using three leaf traits that were measured during the experiment: leaf dry matter content (%), which is the oven-dried mass of a leaf divided by its water-saturated fresh mass and is linked to conservative strategies (Diaz et al., 2016), specific leaf area ($mm^2\ mg^{-1}$), which is the one-sided area of a fresh water-saturated leaf divided by its oven-dried mass (Pérez-Harguindeguy et al., 2013) and the inverse of LMA, linked to fast life cycles and acquisitive strategies through efficient photosynthesis (Diaz et al., 2016), and leaf area (mm^2).

2.6. Floral traits of grassland species

In order to compare our weeds with grassland species, we used the data (floral area, pollen volume, reproductive height, and nectar sugar content) collected by Goulnik et al. (2020) on 51 grassland species in 16 semi-natural mesophilic mown grasslands of northern France according to protocols similar to those described in section 2.2 (Goulnik et al., 2020). Nectar sugar concentration was measured using a refractometer (0–50 Brix and 45–80 Brix, Eclipse, Bellingham and Stanley, Tunbridge Wells, UK), instead of HPLC, using the formula $S = 10dvC$ with d as the density of a sucrose solution at concentration C and v the volume of nectar produced by one flower (Baude et al., 2016). The formula for the density d was: d = 0.0037921C + 0.0000178C2 + 0.998860 (Corbet et al., 2001).

2.7. Statistical analyses

All the statistical analyses were performed using R version 4.2.1 (R Core Team, 2022). We manipulated the data with the *tidyverse* package and created the figures with the *ggplot2* package (Wickham et al., 2019).

We tested for phylogenetic signals in each trait variation using the Abouheif-Moran test from the *adephylo* package (Jombart et al., 2010, 2017), which is based on Moran's *I* statistics with a matrix of phylogenetic proximity (Abouheif, 1999; Pavoine et al., 2008). The phylogenetic trees were obtained with *V.PhyloMaker2* (Jin & Qian, 2019, 2022) with the mega trees from Zanne et al. (2014). We used Kruskal-Wallis test and post-hoc paired Wilcoxon tests to test the differences in trait values between species.

Trait values not normally distributed and with over-dispersed data were log-transformed for the analysis. The log-transformed traits were the following: flower size, flower longevity, FMA, pollen volume, nectar sugar content, total number of floral units, reproductive height, floral area, and leaf area.

We used t-tests to compare the mean trait values of weed and grassland species for the floral area, reproductive height, pollen volume and nectar sugar content.

We used Spearman's correlation tests to detect correlations among mean floral and leaf trait values. We used Spearman's tests because traits were not linearly related to each other, and we corrected p-values with the False Discovery Rate (FDR) corrections (Verhoeven et al., 2005) using the *psych* package (Revelle, 2017). FDR corrections aim at controlling the proportion of significant results that are in fact type I errors, but they are less conservative than Bonferroni corrections when multiple tests are carried out on the same variables (Verhoeven et al., 2005). We used a PCA that included all floral traits to represent the multiple floral traits covariations using the package *FactoMineR* (Lê et al., 2008). We used the package *missMDA* (Josse & Husson, 2016) for managing missing values.

To explore possible covariations between leaf and floral strategies in our weeds, we extracted the species coordinates from the first two dimensions of the floral traits PCA and tested their correlations with their % of C and R strategy according to Pierce et al.'s (2017) method for calculating Grime's strategies using their leaf area, leaf dry matter content and specific leaf area.

3. Results

3.1. Weed floral traits variation

For six traits (flower size, FMA, pollen volume, nectar sugar content, total number of floral units and floral area), values were highly dispersed between species, with a standard deviation greater than the mean (Table 2). Flower size varied from 0.05 cm^2 in *A. serpyllifolia* to 11 cm^2 in *Picris hieracioides*. FMA varied from 5.55 $g.m^{-2}$ in *G. dissectum* to 161 $g.m^{-2}$ in *Carduus pycnocephalus*. Flower longevity ranged from 1.57 days in *C. glomeratum* to 14.8 days in *P. lanceolata*. Floral area ranged between 0.03 cm^2 in *A. serpyllifolia* and 12.1 cm^2 in *M. sylvestris*. Pollen volume ranged from 0.02 mm^3 in *Medicago minima* to 52.5 mm^3 in *M. sylvestris*. Finally, the total number of floral units per plant ranged from 3.69 in *S. minor* to 1462 in *C. glomeratum*.

Abouheif-Moran's tests showed that phylogeny affected none of the measured traits ($p > 0.05$ for all traits). We therefore exclude phylogeny as an explicative factor in the following analyses.

The species effect was significant in all the measured traits ($p < 0.001$ for all traits) meaning that all the traits differed between the 19 species. The species clumped into at least four significantly different groups in matters of leaf C/N ratio, and up to eleven groups for total floral units number and leaf area.

3.2. Covariations within and between construction traits and visual cues and resource availability traits

Among construction-related traits, we found positive correlations between floral mass area (FMA) and flower longevity ($r = 0.65$, $p = 0.026$; Figure 2), flower size and pollen volume ($r = 0.85$, $p < 0.001$) and more marginally between nectar sugar content and pollen volume ($r = 0.60$, $p = 0.051$). No other significant correlation was found among construction-related traits; in particular, the relationships between FMA and flower size, and flower size and flower longevity were not significant (Figure 2).

Among visual cues and resource availability traits, we found negative correlations between floral area and the total number of floral units ($r = -0.61$, $p = 0.02$, Figure S1), and between the total number of floral units and flowering onset ($r = -0.55$, $p = 0.035$), and a positive correlation between reproductive height and floral area ($r = 0.55$, $p = 0.035$, Figure S1).

Regarding the relationships between construction traits on the one hand and visual cues and resource availability traits on the other hand, our results revealed very strong positive correlations between reproductive height and pollen volume ($r = 0.81$, $p = 0.001$), reproductive height and flower size ($r = 0.74$, $p = 0.004$), floral area and flower size ($r = 0.82$, $p = 0.001$) and floral area and pollen volume ($r = 0.76$, $p = 0.004$) (Figure S2).

The floral traits PCA explains 56.7% of the total variance for the first two principal axes (Figure 3). The first component (PC1) explained 37.8% of the total variance and was determined by high pollen volume (correlation with the axis: $r = 0.91$), floral area ($r = 0.84$), flower size ($r = 0.79$), reproductive height ($r = 0.77$), nectar sugar content ($r = 0.57$), flower longevity ($r = 0.57$) and total number of floral units (negatively, $r = -0.61$). The second component (PC2) explained 18.9% of the total variance and was positively associated with pollen nitrogen concentration ($r = 0.76$) and negatively with pollen C/N ratio ($r = -0.77$) (Table 3). Among the five leaf traits added as illustrative variables, only leaf area was positively correlated to PC1 (0.71). The other leaf traits were poorly represented in the PC1-PC2 plan. The species with the highest score on PC1 was *M. sylvestris* and the species with the lowest score was *A. serpyllifolia*. The species with the highest score on PC2 was *Senecio vulgaris* and the species with the lowest score was *M. sylvestris*. *M. sylvestris* was the species that contributed most to PC1 and PC2 but when the analysis was run without this species the same variables contributed similarly to the first and second dimensions.

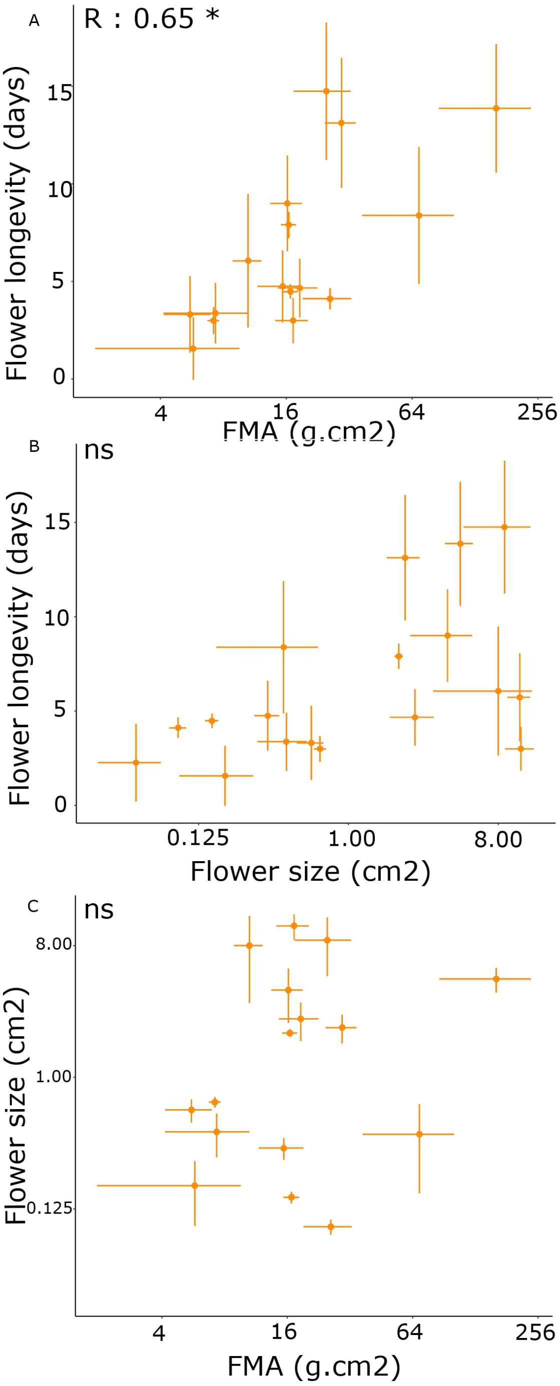

Figure 2. Plot of correlations between the three floral traits of the Flower Economics Spectrum proposed by Roddy et al. (2021). A. Flower longevity and Floral Mass Area (Spearman's r = 0.65, p = 0.026). B. Flower longevity and flower size (Spearman's r = 0.48, p = 0.145). C. Flower size and FMA (Spearman's r = 0.21, p = 0.622). Notes: ns not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 3. The first two principal axes (principal components) of the floral traits PCA, indicating their most contributive variables, their correlation with each axis, and their interpretation.

Principal axis	Variables	Correlation with the axis	Interpretation
First floral PCA axis 37.8% of variance	Pollen volume	0.91	This axis opposes species that produce few flowers but larger, taller, with a longer life span, greater pollen volume and nectar sugar content, to species that produce many flowers, which are smaller, lower-held, shorter-lived and with fewer resources for pollinators
	Flower area	0.84	
	Flower size	0.79	
	Reproductive height	0.77	
	Nectar sugar content	0.57	
	Flower longevity	0.57	
	Total number of floral units	-0.61	
Second floral PCA axis 18.9% of variance	Pollen nitrogen content	0.76	This axis opposes species with a higher pollen nitrogen content to species with a lower pollen nitrogen content and a higher C/N pollen ratio
	Pollen C/N ratio	-0.77	

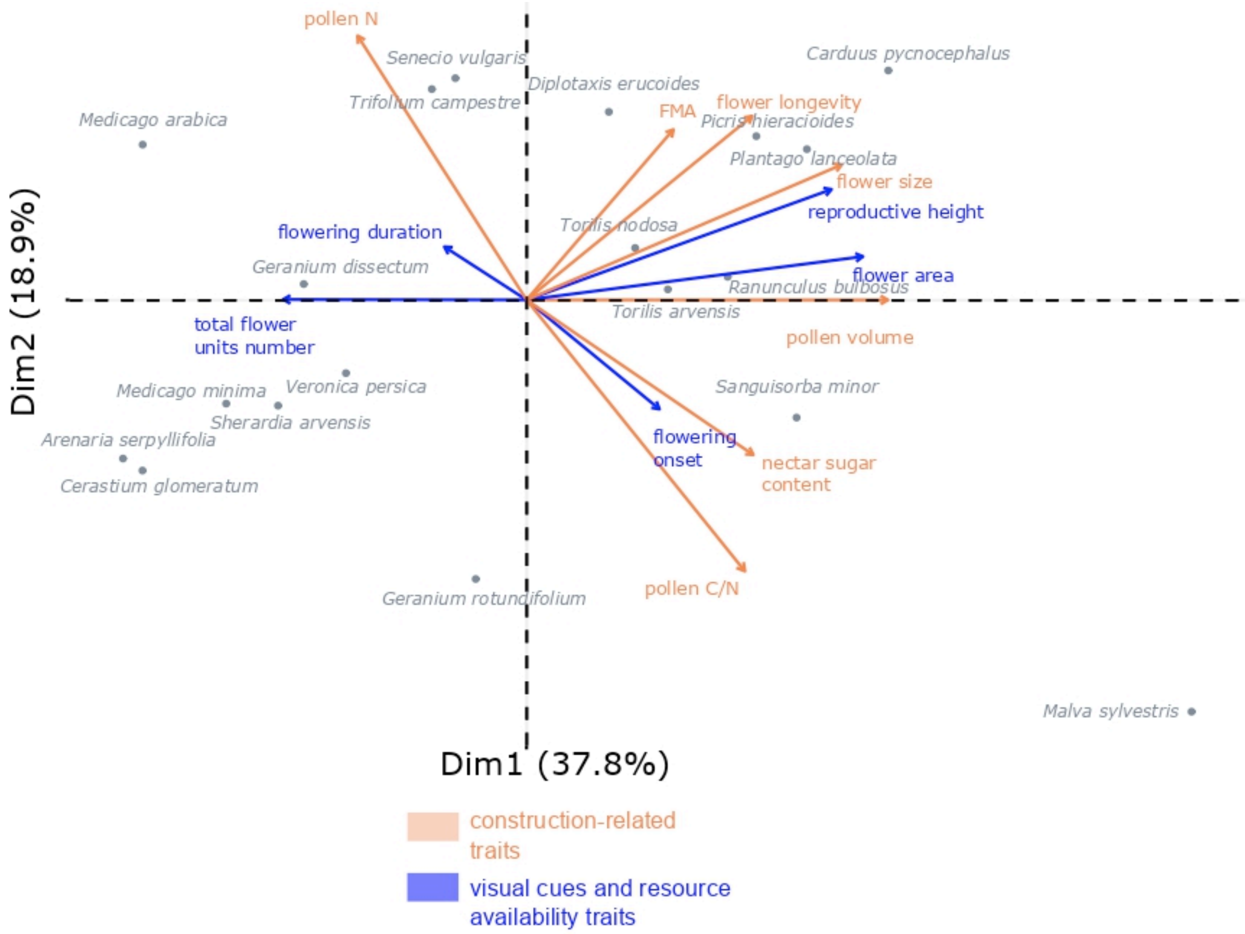

Figure 3. Principal component analysis run on all the floral traits. Construction-related traits are represented by orange arrows and visual cues and resource availability traits are represented by blue arrows. Individuals are the mean trait values for each species. The first dimension (37.8%) opposes species with high values for flower size, floral area, reproductive height and pollen volume to species bearing a high number of floral units. The second dimension (18.9%) opposes species with high pollen nitrogen content to species with high C/N ratio.

3.3. Covariations between floral traits and leaf traits

Leaf area was the most dispersed leaf trait, ranging from 0.23 to 91.5 cm^2 (Table 2). *S.arvensis* had the smallest leaf area and *C. pycnocephalus* was the largest. *S. arvensis* was also the species with the highest C/N ratio (20) and the lowest LNC (2.1 g kg^{-2}) (Table 2). *S. vulgaris* had the lowest LMA (21.4 g m^{-2}) and *T. nodosa* had the highest (40 g m^{-2}). Finally, *T. campestre* had the shortest leaf life span (25.9 days) while *C. glomeratum* had the longest (72.4 days) (Table 2).

We found a strong positive correlation between flower size and leaf area (r = 0.74, p = 0.0004) and more marginally between FMA and LMA (r = 0.47, p = 0.0636) (Figure S3). No correlation was found between pollen nitrogen content and LNC, between pollen C/N ratio and leaf C/N ratio, nor between flower longevity and LLS. Finally, leaf area was also positively related to pollen volume (r = 0.88, $p < 0.001$) and to reproductive height (r = 0.87, $p < 0.001$). No other leaf trait correlated with other floral traits.

Using Pierce et al.'s (2017) method, we found that 12 species were ruderal (R) -strategy dominant, one was competitive (C) strategy dominant and 7 were both R and C strategy dominant (Figure 4, Table S1). The floral PC1 axis, i.e. linked to great flower size, flower area, reproductive height, pollen volume and low total number of floral units, was negatively correlated with the % of R strategy ($r = -0.75$, $p < 0.001$) and positively to the % of C strategy ($r = 0.7$, $p = 0.001$). The floral PC2, i.e. associated with pollen nutrient content, correlated with none of Grime's strategies (Figure 5).

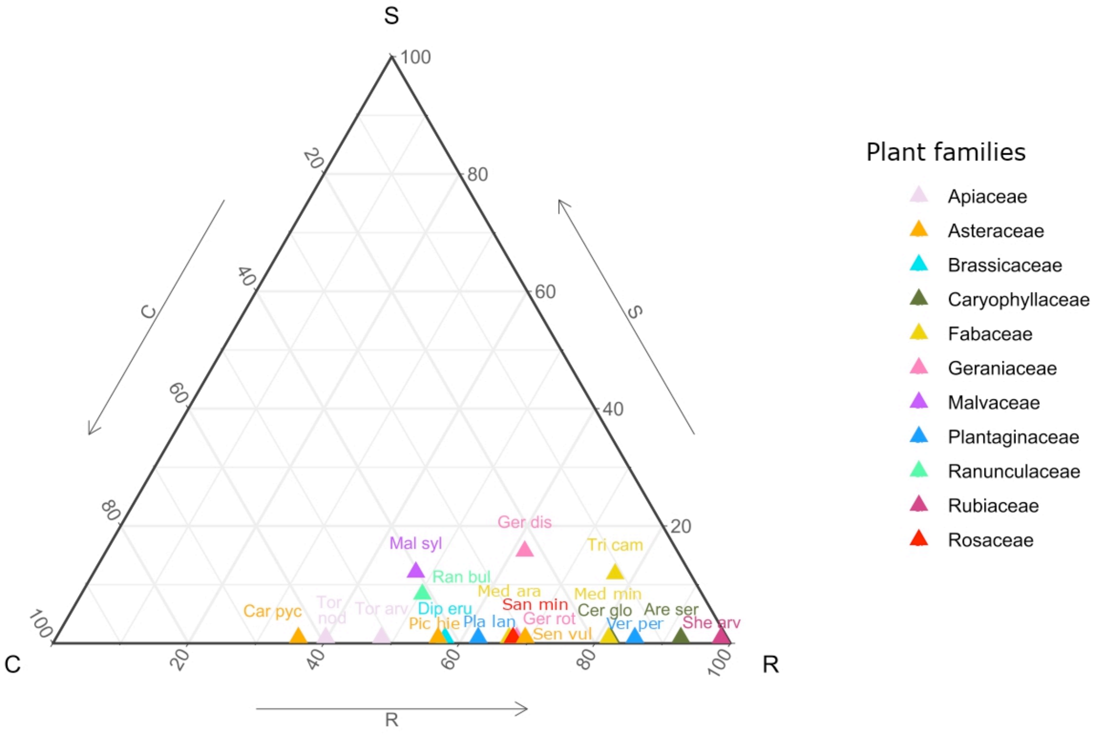

Figure 4. CSR values of the 19 weed species obtained on the basis of their LDMC, SLA and leaf area values according to the algorithm of Pierce et al. (2017). 12 species follow a mainly ruderal (R) strategy, one a mainly competitive (C) strategy, and 7 a mixed R and C strategy.

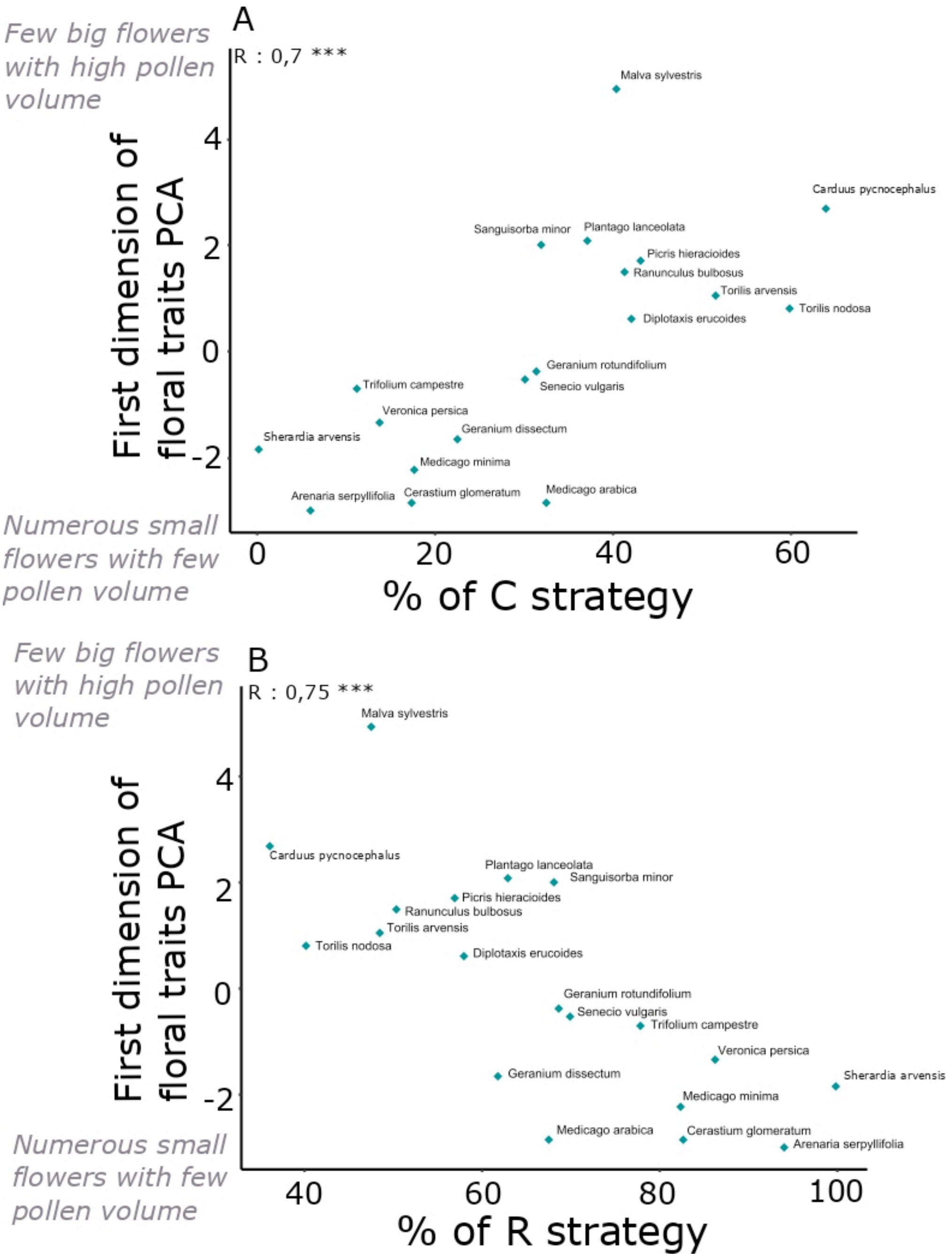

Figure 5. Plot of correlations between each species' coordinate along the first axis of the PCA and each of the C and R percentages of its strategy. A. % of C strategy and values of first floral PCA axis (Pearson's $r = 0.7$, $p = 0.001$). B. % of R strategy and values of first floral PCA axis (Pearson's $r = 0.75$, $p < 0.001$).

3.4. Comparisons between weed and grassland floral traits

Weed species had a smaller floral area (2.03 ± 3.11 cm^2 *vs* 6.25 ± 9.41 cm^2, p = 0.006) and a lower nectar sugar concentration (122 ± 403 µg $µl^{-1}$ *vs* 412 ± 339 µg $µl^{-1}$, p = 0.014) than grassland species (Figure 6). However, there was no difference in reproductive height (weeds: 44.9 ± 40.7 cm *vs* grasslands: 37.8 ± 14.89 cm, p = 0.468) and pollen volume (weeds: 5.25 ± 12.6 mm^3 *vs* grasslands: 3.13 ± 2.49 mm^3, p = 0.565) between weeds and grassland species.

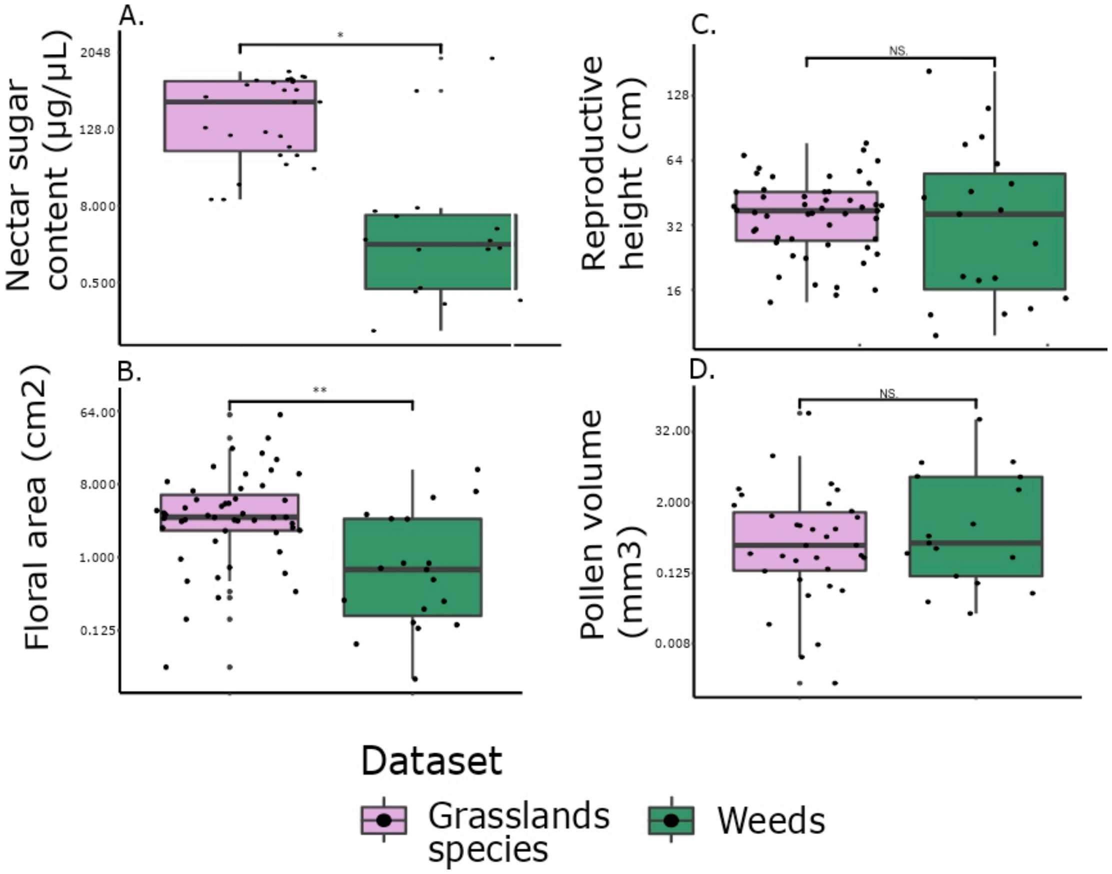

Figure 6. Comparisons between the floral traits of weeds (n = 19) and grassland species (n = 52). (A) Nectar sugar content (p = 0.014). (B) Floral area (p = 0.006). (C) Reproductive height (ns). (D) Pollen volume (ns). Notes: ns not significant; * p < 0.05, ** p < 0.01, *** p < 0.001.

The coefficient of variation of the floral area was comparable in weeds (1.66) and in grassland species (1.67) but was greater in weed species regarding both reproductive height (weeds: 0.94, grasslands: 0.4) and nectar sugar content (weeds: 3.53, grasslands: 0.86). On the other hand, the coefficient of variation of pollen volume was higher in grassland species (3.67) than in weed species (2.61).

4. Discussion

4.1. Trade-off between number and cost of produced flowers

Our main finding was that four traits were strongly positively correlated all together: two visual cues traits, i.e. reproductive height and floral area, and two construction traits, i.e. pollen volume and flower size (Figure S2). This finding suggests that, as hypothesised, expensive flowers tend to be also more visible and more attractive to pollinators. However, we did not find any relationship linking visual cues and resource availability traits with pollen nutrient content, nectar sugar content, FMA or flower longevity. This gives further support to the hypothesis that flower size and pollen volume are two construction traits on which pollinator selection has the greatest impacts (Lanuza et al., 2023), whereas other construction traits respond more to abiotic constraints (Teixido et al., 2016). Two phenological traits were also measured: flowering duration was found to be independent of the other floral traits whereas flowering onset was not. Weed species that flower early tend to produce more floral units, composed of flowers with smaller floral areas than the others. This confirms the findings of previous studies suggesting the existence of a trade-off between flower area and flower number (Sargent et al., 2007; Worley & Barrett, 2000). Flower size as described by Roddy et al. (2021) seems an interesting and easily-measurable proxy for both floral construction costs and attractiveness to pollinators, even when, as is the case here, it is not directly linked to nectar, which is an important food resource. This trait could be used at the community scale to gauge weed floral resources available to pollinators in agroecosystems. To do so, it seems important to harmonise with standardised protocols the way floral traits are measured (Michelot-Antalik et al., in prep).

To gain a deeper understanding of these bivariate relationships and find whether an integrated floral strategy exists in weed species, we explored all weed floral traits with multivariate analysis. PC1 described floral strategies by opposing, on the one hand, weed species with numerous floral units but with each flower small, held close to the ground and poor in rewards (such as *A. serpyllifolia* or *M. arabica*), and, on the other hand, weed species producing fewer but larger, higher and more rewarding flowers (such as *M. sylvestris* or *C. pycnocephalus*). This result using flower area in cm^2 is completely consistent with the study of Lanuza et al. (2023) with a larger number of species, although flower size was approximated with inflorescence or flower length in cm in their study. Both floral strategies, i.e. producing a lot of small flowers *vs* few large flowers, can be relevant for attracting pollinators because even though flowers with high values for floral traits are known to attract pollinators (Caruso et al., 2019), blossom surface area, strongly linked to the number of floral units, is also a major trait for pollinator attraction, including in weed species (Hernández-Villa et al., 2020; Kratschmer et al., 2019). We assume that species with different scores on PC1 attract different communities of pollinators as we know that high-held flowers can be more attractive to large pollinators than smaller ones (Rowe et al., 2020). Indeed, Lanuza et al. (2023) found that species with high scores on their PC1, also linked to size *vs* number of flowers, were mainly visited by bees and *Lepidoptera* whereas species with low scores were mostly visited by *Coleoptera*, *Diptera* and non-bee *Hymenoptera*. However, it is important to note that our study and the one by Lanuza et al., 2023 did not consider several important flower traits, such as flower scent, reflectance and even nectar volume, which could have led us to slightly different results given their major role in pollinator attraction (Junker & Parachnowitsch, 2015; Kantsa et al., 2017).

The second axis of the PCA only integrated pollen nutrient content and was completely independent from all other morphological, phenological and visual cues traits. The nutrient allocation to pollen could be more specifically linked to other fitness characteristics, such as the energy allocated to the future seeds (Campbell & Halama, 1993), which could explain why this dimension is independent from the other floral traits considered here. We nonetheless found this result surprising because pollen is a very important protein resource for pollinators (Pernal & Currie, 2001) and we had expected it to correlate with other floral traits.

Phenological traits (flowering duration, flowering onset) contributed to neither of the two axes. This indicates that, in our weed flowers, temporal availability, which is a key element of pollinator attraction (Larson & Funk, 2016), was related neither to floral construction nor to morphological visual cues. These phenological traits were the only floral traits Bourgeois et al. (2019) integrated into their weed syndrome, but they do not seem to be related to the main dimensions describing weed floral strategies. It is possible the relationship may have gone undetected in our experiment due to the long duration of flowering observed in the greenhouse, with mild temperatures and watering.

4.2. Weed floral phenotype

We hypothesised that weed flowers would be smaller, held at a lower height, and with a lower pollen volume and nectar sugar content than grassland flowers as they are adapted to highly disturbed environments that prevent them from investing in costly flowers. However, our results partly confirmed this hypothesis: weed flowers studied here were smaller (mean difference: 4 cm) and had lower nectar sugar content than grassland species. Weeds and grassland species held their flowers at the same height and produced the same quantity of pollen (Figure 6). Given that these four traits are known to be linked to pollinator attraction (Fornoff et al., 2017; Hegland & Totland, 2005; Lázaro et al., 2013; Lundin et al., 2019; Rowe et al., 2020; Tuell et al., 2008), this could indicate that the weed communities from the studied olive groves and vineyards are less attractive than these grassland communities to pollinators and other flower-visiting insects. Differences in flower size and height may also reflect that weed species experience less intense competition for pollinators than grassland species because agricultural landscapes are usually poorer in flowering species and floral resources (Baude et al. 2016). However, some weed species studied here, like *P. lanceolata* or *R. bulbosus,* are also present in grassland agroecosystems and this could explain why we don't find differences for all traits. We also found that weeds expressed a broad phenotypic variability in almost all floral traits, indicating that they form a heterogeneous community regarding available floral resources. For example, regarding reproductive height and nectar sugar content, the coefficient of variation found in weeds was respectively two- (0.94 vs 0.40) and four- (3.50 vs 0.86) fold that of grassland species. These discrepancies could be due to differences in the pollinator communities present in both types of ecosystems as grasslands are more homogenous and less disturbed within and across years compared with vineyards and orchards. Exploring weed floral phenotypes in more detail by considering supplementary floral traits such as scents or colours and by studying weed pollinators could also help to understand the differences we discovered between the flowers of weeds and grassland species flowers (Junker & Parachnowitsch, 2015). Moreover, studying plant-pollinator trait matching could help to better understand these results (Goulnik et al., 2021). At last, these observed discrepancies could be related to our datasets, limited in the number of species and not necessarily representative of the two floras being compared.

In this study, we tested the flower economics spectrum developed by Roddy et al. (2021) by exploring the covariations between flower size, flower longevity and FMA. We hypothesised that weeds were among the species that invest comparatively little in floral structures, contrary to species tested by Roddy et al. (2021). We expected that all traits would covary positively and that it would be possible to distinguish species with a high investment in floral structures from species with less investment, which defines low-cost floral strategies. Flower longevity and floral mass area (FMA) covaried positively, as expected (Figure 2). This confirmed that FMA is linked to the maintenance cost of a flower, even in low-cost flowers such as those of weed species. This relationship has already been tested for orchid species with costly flowers, but hardly so for species of other families (Zhang et al., 2017). This relationship partly confirms the FES proposed by Roddy et al. (2021): longer-lived flowers have higher carbon costs, even in species producing low-cost flowers such as weeds. We did not find any other relationship among FES traits. However, the species studied here, being weeds and from Mediterranean ecosystems (Teixido & Valladares, 2014), can be considered as species with fairly small flowers compared with the 20 species tested by Roddy et al (2021) (*Illicium* spp., *Rhododendron* spp., *Magnolia* spp.). This could explain why we did not observe the trade-off between FMA and flower size predicted by Roddy et al. (2021). Another explanation could be that there is actually no trade-off between these two traits.

In a second step, our study aimed to extend the FES to resource-related traits, which are traits that represent significant costs for plants. Flower size was found to be associated with pollen volume, indicating that species with a high investment in the morphological construction of petals also produce more pollen. The two main food sources for insects, nectar and pollen (Pernal & Currie, 2001), marginally covaried positively in our weed species, which was not the case in the grassland species studied by Goulnik et al. (2020). However, using the data of Hicks et al. (2016) on the nectar and pollen resources of 75 meadow plants, we also found a positive relationship between pollen volume and nectar sugar content. Our results seem to indicate that plants can invest in both pollen and nectar at the same time. This positive relationship, which is not limited to weed species, may be due to pollinator selection of plant species that produce both a large volume of pollen and abundant sugar resources, both being known as complementary resources for pollinators. This stresses the need to add to the FES framework plant productions used as resources by pollinators, even though it should be considered that many environmental and biotic factors can bear on nectar-linked traits (Parachnowitsch et al., 2019).

The independence of nectar or pollen nutrient-related traits with morphological traits could be due to different selective pressures happening at the same time: hot temperatures and dry conditions favour small and short-lived flowers (Teixido et al., 2016), pollinators favour larger and more rewarding flowers (Rowe et al., 2020) whereas nectar robbers also have an important role in nectar evolution (Irwin et al., 2004). Finally, it seemed crucial to understand whether, and how, these floral strategies were related to leaf traits in order to understand and describe global plant strategies by including reproductive traits.

4.3. Floral weed strategies reflect CSR strategies

Are the floral weed strategies observed in our study linked to the already known plant strategies such as Grime's CSR, i.e. competitive, ruderal and stress-tolerant, strategies (Grime, 1974; MacLaren et al., 2020; Pierce et al., 2017) or to the global spectrum of plants' form and function (Díaz et al., 2016)? As in E-Vojtkó et al. (2022) our results reveal a significant and strong positive relationship between leaf area and flower size ($r = 0.74$, $p = 0.0004$). Lambrecht & Dawson (2007) also previously found that, at the plant scale, total leaf area and visual cues floral traits (i.e. flower area and reproductive height) were positively correlated. This highly significant relationship was confirmed in our study at the organ scale. This could indicate that certain floral traits, such as flower size and flower height, could be integrated into the first axis of form and function of the plant spectrum (Díaz et al., 2016) in order to describe plant reproduction ability in relation to plant size. We also identified a trend of a positive relationship between leaf mass area and floral mass area, indicating a relationship between plant investment in vegetative and floral parts, both traits being related to the lifespan of the respective organs (Roddy et al., 2021; Westoby et al., 2002). However, flower longevity and leaf life span were not correlated, this pattern still needs to be investigated. Finally, nitrogen and C/N ratio of leaf and pollen are two independent dimensions of the weed phenotype for the studied species while flower size and leaf size were positively correlated. As did E-Vojtkó et al. (2022) we found a positive relationship between floral and leaf sizes but also a link between LMA and FMA, traits that are linked to organ production costs. Consequently, we cannot conclude that floral and leaf phenotypes are independent in weed species.

To investigate whether floral and leaf plant strategies are linked, we explored multi-traits relationships between CSR strategies and the floral strategies of weeds. The CSR-calculating tool of Pierce et al. (2017) confirmed that the 19 weed species studied here mainly follow ruderal-competitive strategies (Figure 4) (MacLaren et al., 2020) and that these strategies were reflected in the PC1. To our knowledge, this is the first study demonstrating that weed species with high ruderal scores produce cheaper but more numerous flowers, whereas weeds with high competitive scores produce fewer but costlier flowers (Figure 5). Using PCA axes and CSR strategies we showed that floral and leaf weed strategies are strongly related. Ruderal species cope with highly disturbed environments (such as crop fields) with a fast life cycle and low-cost leaf production (Fried et al., 2022). We demonstrated that this low-investment strategy also applies to flower production, but is counterbalanced by many flowers, maybe to rapidly attract pollinators with a greater blossom surface area. This assumption is backed by the finding that the production of flowers is associated with early flowering and with low seed mass ($r = -0.51$, $p = 0.027$, *data not shown*), which is consistent with the weed syndrome described by Bourgeois et al. (2019). On the other hand, the competitive strategy is efficient for intercepting available resources, e.g. light or nutrients, when the ecosystem is only moderately disturbed, like in the mown inter-rows of perennial agroecosystems (Nicholls et al., 2013). Producing large, high-held, and rewarding flowers is also an efficient way to compete to attract pollinators (Caruso et al., 2019). In our study, competitive weeds were mainly found in mown habitats whereas ruderal weeds were abundant in tilled habitats, as observed by Fried et al. (2022). To cover the dietary needs of a wide range of pollinators, it seems essential to sustain a variety of floral resources by diversifying the methods of weed management in agroecosystems (Balfour & Ratnieks, 2022; Bretagnolle & Gaba, 2015). Since we found that floral traits are linked to CSR strategies, which are modified by agricultural practices (Kazakou et al., 2016), it is possible that weed management could also affect the available floral resources in agroecosystems. High-intensity land use in grasslands is already known to shape floral resources by homogenising floral traits, inducing changes in flower colour, nectar tube depth or resource production (Goulnik et al., 2021). Diversifying agricultural practices at the landscape level to increase the functional diversity of weeds could contribute to diversify the flower resource for pollinators (Fründ et al., 2010) as well as provide the numerous other ecosystem services expected from weeds, such as producing food resources for livestock (Genty et al., 2023) and natural enemies (Serée et al., 2023) but also supporting processes contributing to soil fertility, such as decomposition (Bopp et al., 2022).

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Data archiving statement

Data available from the UMR ABSYS Dataverse: https://doi.org/10.18167/DVN1/6ZCRGN

Conflicts of Interest Statement

The authors have no conflict of interest to declare.

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Supporting information

Table S1. Percentage of Grime's CSR strategy for each species, according to Pierce et al.'s (2017) calculating method.

Species	%C	%S	%R	CSR strategy	Dominant CSR strategy
Arenaria serpyllifolia	5.9882	0	94.012	R	R
Carduus pycnocephalus	63.912	0	36.088	C/CR	C
Cerastium glomeratum	17.356	0	82.644	R/CR	R
Diplotaxis erucoides	42.051	0	57.949	CR	CR
Geranium dissectum	22.505	15.72	61.775	R/CSR	R
Geranium rotundifolium	31.374	0	68.626	R/CR	R
Malva sylvestris	40.367	12.126	47.506	CR/CSR	CR
Medicago arabica	32.492	0	67.508	R/CR	R
Medicago minima	17.651	0	82.349	R/CR	R
Picris hieracioides	43.091	0	56.909	CR	CR
Plantago lanceolata	37.104	0	62.896	R/CR	R
Ranunculus bulbosus	41.284	8.3758	50.34	CR	CR
Sanguisorba minor	31.913	0	68.087	R/CR	R
Senecio vulgaris	30.1	0	69.9	R/CR	R
Sherardia arvensis	0.1731	0	99.827	R	R
Torilis arvensis	51.527	0	48.473	CR	CR
Torilis nodosa	59.831	0	40.169	CR	CR
Trifolium campestre	11.206	10.969	77.825	R/CR	R
Veronica persica	13.762	0	86.238	R	R

Appendix S2

Figure S1. Plot of correlations between visual cues and resource availability floral traits. A. Reproductive height and floral area (Spearman’s r = 0.55, p = 0.035). B. Total number of floral units and floral area (Spearman’s r = - 0.61, p = 0.02). Notes: ns not significant; * p < 0.05; ** p < 0.01; *** p < 0.001.

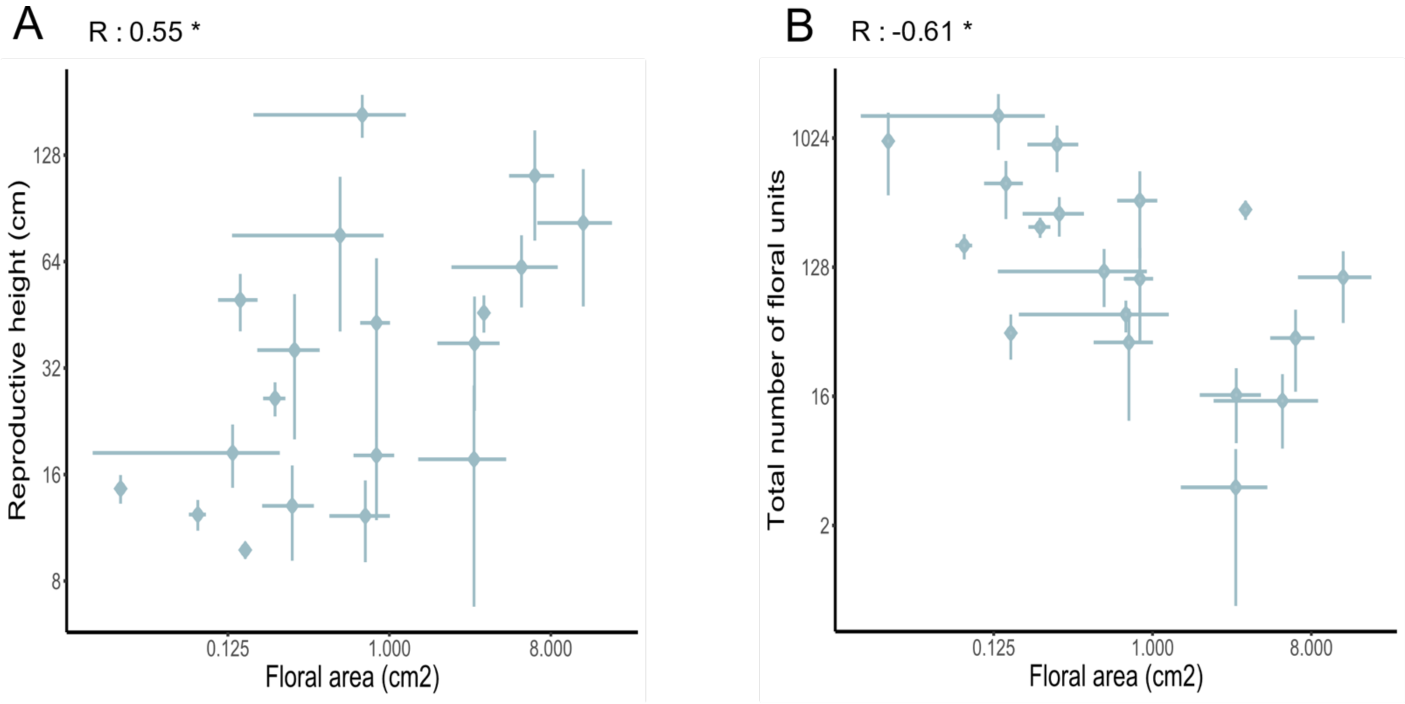

Figure S2. Plot of correlations between visual cues and resource availability floral traits and construction-related floral traits. A. Reproductive height and pollen volume (Spearman's r = 0.81, p = 0.001). B. Reproductive height and flower size (Spearman's r = 0.74, p = 0.004). C. Floral area and pollen volume (Spearman's r = 0.76, p = 0.004). D. Floral area and flower size (r = 0.82, p < 0.001). Notes: ns not significant; * p < 0.05; ** p < 0.01; *** p < 0.001.

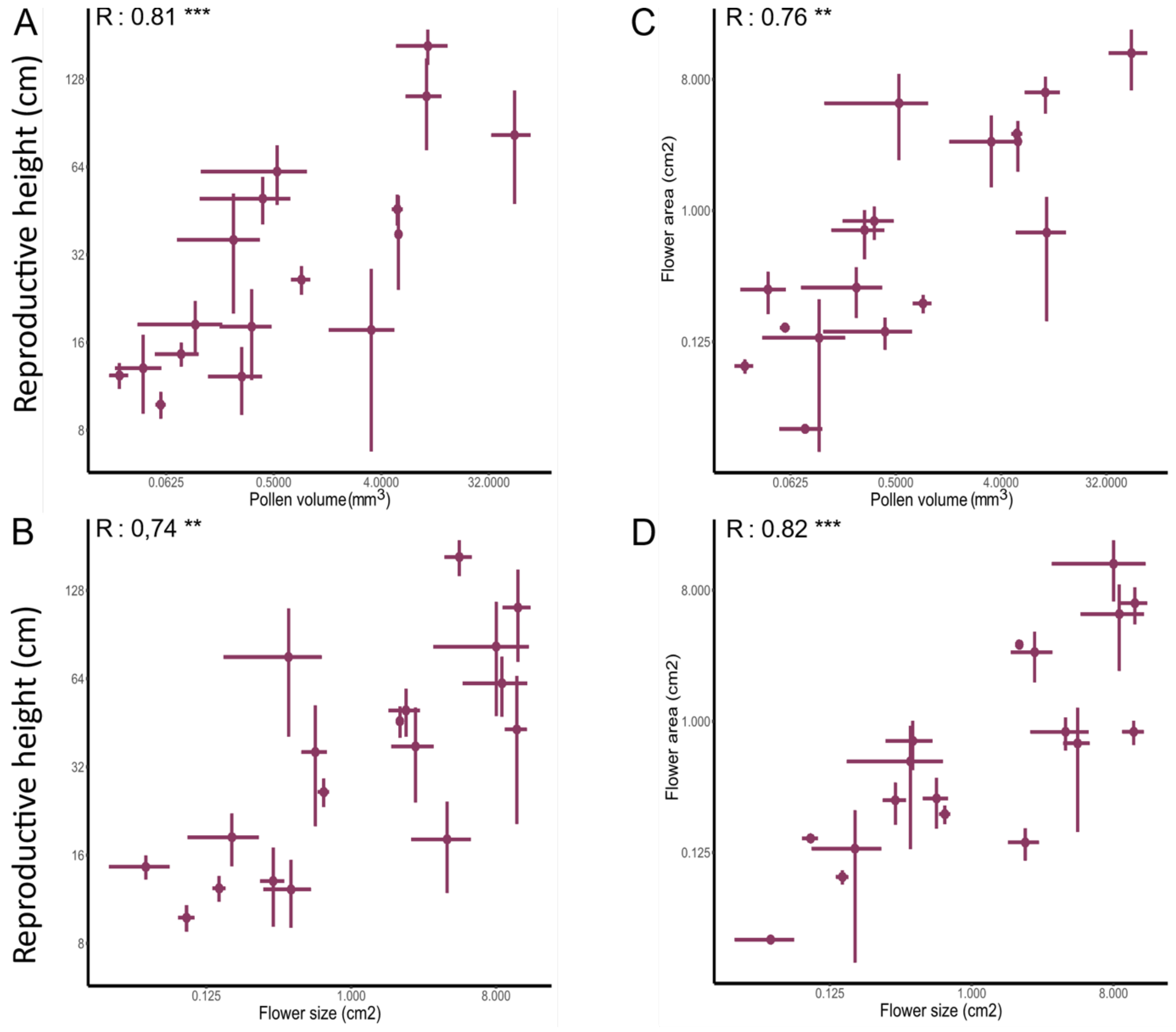

Figure S3. Plot of correlations between leaf traits and floral traits. A. Flower size and leaf area (Spearman's r = 0.74, p = 0.0004). B. Floral mass area and leaf mass area (Spearman's r = 0.47, p = 0.0636). C. Flower longevity and leaf life span (ns). Notes: ns not significant; * p < 0.05; ** p < 0.01; *** p < 0.001.