

Landscape fragmentation constrains bumblebee nutritional ecology and foraging dynamics

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Abstract

Habitat fragmentation is modifying landscapes and the distribution of floral resources, possibly shaping also pollinator resource acquisition. Here, using urban parks as field laboratories for the dramatic contrast around, we aimed to clarify how fragmentation and local flower availability shape bumblebee foraging dynamics by characterizing several components: the nutritional content and plant composition of collected pollen pellets, the foraging rate and the plant-nutrition association along a fragmentation gradient. We found mostly negative linear or non-linear relationships between nutritional quality and fragmentation, tight plant composition-nutrition associations interpretable as low access to alternative resources, and shorter foraging time in smaller green areas, showing behavioral limits by the landscape. Thus, fragmentation can constrain all aspects of bumblebee foraging by compromising resource accessibility. This study illuminates the link between landscape features and the nutritional ecology of pollinators, a key aspect for understanding pollinator foraging dynamics and even for outlining mitigation measures in urban contexts.

INTRODUCTION

The increase in the impervious cover associated with urbanization leads to the worldwide loss and fragmentation of suitable habitats that provide nesting and food resources to pollinators (Biella et al. 2022), which may impact the way pollinators forage. These changes in landscape composition and configuration inevitably result in lower connectivity between green patches (Wenzel et al. 2020). Along with the decline in connectivity, the size reduction of green fragments can decrease their quality intended as their potential to sustain local populations of pollinators (Fahrig 2003). These conditions affect both the plant and pollinator communities structure and their interactions (Grass et al. 2018) with important implications for pollinator’s nutritional ecology and for the related ecosystem service as well (Gervais et al. 2020; Theodorou et al. 2020). The fragmentation of green areas in landscapes may shape multiple aspects that influence the nutritional ecology of pollinators (Hülsmann et al. 2015; Winfree et al. 2011), such as the availability in terms of richness and abundance of floral resources (Potts et al. 2010) and their spatial distribution (Matteson et al. 2013). For instance, fragmentation can lead to the dishomogeneous distribution of plant resources to pollinators, as indicated by the linear decrease of pollen diversity collected by pollinators across a gradient of green areas fragmented by urbanization (Biella et al. 2022). Furthermore, fragmentation can directly influence the foraging behavior of pollinators (Gervais et al. 2020). According to the optimal foraging theory, pollinators will forage closer to their nesting in a landscape characterized by a lower degree of habitat fragmentation and an even distribution of resources in order to reduce their energetic expenditure (Goulson 1999). This was confirmed by a study showing that landscapes with higher green coverage were associated with shorter foraging distances and trip duration in several bumblebee species (Redhead et al. 2015). Therefore, the spatial

limitations imposed by landscape configuration on pollinator foraging behaviour, coupled with the consequent decline in the availability and quality of the resources, can act synergically, ultimately jeopardizing urban pollinators population conservation.

Eusocial pollinators, such as bumblebees, characterized by colony life cycles that last for several months (Crone & Williams 2016), are particularly susceptible to dishomogeneity in the nutritional landscape as they benefit from having continuous access to floral resources to sustain colony growth (Couvillon et al. 2014). Indeed, bumblebee fitness appears as symmetric to the seasonal distribution of flower resources and nutrients: for instance, late-season shortages are associated with fewer bees the following year (Timberlake et al. 2020). Moreover, local features (e.g., floral resources availability and quality) and landscape scale drivers (e.g., amount and fragmentation of green patches) are intimately related to bumblebee colony health, performance, and reproductive success (Theodorou et al. 2022; Vaudo et al. 2018). Previous studies on *Bombus terrestris* observed an increase in the colony growth rate and in the total number of workers at sites characterized by a higher diversity of floral resources (Goulson et al. 2002) and a reduction of colony fitness in highly urbanized areas (Theodorou et al. 2022). These negative effects on colony performance can be mainly ascribed to an unbalanced assumption of macronutrients (i.e., proteins, lipids, carbohydrates) and phytochemicals and especially to a low quality of the pollen provision that represents a primary food source for the larvae (Kriesell et al. 2017; Nicolson et al. 2018)

The importance of a balanced assumption of macronutrients and phytochemicals has been emphasized by evidence from several bees showing clear food choices of floral resources to meet their nutritional demands (Kriesell et al. 2017; Liu et al. 2006; Ruedenauer et al. 2016; Somme et al. 2015; Vaudo et al. 2016). Pollen macronutrients play a key role in this food choice as indicated by experiments showing that *B. terrestris* and *B. impatiens* workers can regulate their protein and lipid intake preferring pollen with higher protein concentration while avoiding provisions too rich in lipids (Vaudo et al. 2016). Beyond single nutrient concentrations, the ratios of macronutrients are also pivotal to describing bees foraging behavior, such as the protein:lipid ratio (P:L) (Vaudo et al., 2016). However, most of these studies were either in laboratory-controlled conditions or across permeable landscapes (such as semi-natural to agricultural areas); still, little is known about the pollinators nutritional ecology across a gradient of severe fragmentation where green areas are dispersed in highly inhospitable, cemented zones.

Here, we developed a field-based study to clarify how the amount and fragmentation of green areas of urban landscapes and the local availability of flower resources shape the foraging dynamics and the nutritional intake of a social pollinator. Two main expectations could be drawn regarding how bumblebee foraging could respond to fragmented landscapes. First, patchy dispersed green areas could decrease the nutritional quality of the pollen brought to the colony if plant species diversity at foraging sites is low. This is supported by a scenario in which the foragers encounter strong spatial constraints in patch distribution and quality that prevent access to equally profitable resources across landscapes (Barraquand & Benhamou, 2008; Ritchie 1998). In this case, we would also observe a tight association between plant taxonomic composition of pollen pellets and the chemical profiles of collected resources, indicating little use of alternative plant sources (Biella et al. 2019). Secondly, bumblebee colony behavior in terms of the rate of workers leaving the nest for foraging could reflect the heterogeneous distribution of resources, for instance by foraging longer in areas with dispersed resources by maximizing quantity over quality or increasing searching time (Jha & Kremen 2013; Weterings et al. 2018). It is also important to notice that the foraging frequency of bee workers reflects the foraging effort of a colony needing resources (e.g., Biella et al 2019, Pernal & Currie 2001). To test these expectations we aimed to (i) characterize the chemical composition of pollen pellets and their specific plant composition in landscapes of varying fragmentation (size, isolation of green areas), (ii) evaluate the association between plant composition and pollen nutrients in the resources brought to the colony, (iii) describe changes in the frequency of foraging to search for behavioral adjustments to the fragmented landscape. This study highlights the performance of varying fragmented landscapes in sustaining pollinators by evaluating several components that ultimately determine pollinator nutritional ecology: food preferences in terms of chemistry and diversity of collected flower resources and colony behavioral responses as foraging rate. Our study provides an empirical and multicomponent characterization of how landscape

and local features interact in shaping the nutritional ecology of key pollinators, that could even be used as a basis for outlining reinforcement measures for pollinators in urban contexts.

MATERIALS AND METHODS

Study design and sampling

Study sites were chosen in order to represent a gradient of different green areas size and fragmentation within an urban landscape, although all sites were the same type of habitat, namely green areas accessible to the public for recreational purposes (e.g., urban parks). The mean distance between sites was 2.5 km (min. = 1.2 km; max. = 4.3 km) to avoid spatial non-independence as this distance is above the usual foraging range observed for the selected pollinator model *Bombus terrestris* (Redhead et al. 2016; Wolf & Moritz, 2008). This species is common in Europe and can be easily found in different habitats (Polce et al. 2018), even in urban areas (Banaszak-Cibicka & Żmihorski 2012; Meeus et al. 2021). A pair of commercial colonies of this species (acquired from Bioplanet, Forlì-Cesena, Italy) was placed at each of 14 sites in different parts of the city of Milan, in Northern Italy (Figure 1). Colonies were elevated from the ground and protected from rain and sun with wooden sheds covered with an insulating sheet (Figure 1). Each colony was left at each site for at least 48 hours. Most of the sites were sampled twice, at a month time of distance using a different colony set and only if the plant community was very different from the previous sampling round (after a detailed visual investigation); Thus, the final number of sampling events was 29 and the samplings lasted from May 27th to July 30th 2020.

To evaluate if 48h time was representative or robust against possible bumblebee life cycle variations, we measured the weight of bumblebee colonies and the plant richness of the pollen transported in a subset of 4 sites that were weekly sampled over a month.

Sampling of pollen loads and field data collection

Pollen loads were sampled from foragers just before entering their colonies after the foraging bouts. To collect pollen and avoid contamination, single workers were gently and individually placed in clean small plastic bags and the pollen pellets were detached from the corbiculae by gentle pressure on the pellets with tweezers. We sampled pollen from on average 28.25 ± 9.78 workers for each colony on each date, thus yielding a total of 3124 pellets weighing on average 19 mg (± 14) (dry weight). Samples were stored on ice on the field and then conserved at -80°C until analysis.

To test for variations in the foraging behavior of the colonies, the colonies in all sites were monitored using video cameras for three hours on a single day (SuperEye RJ0090-UK, OneThingCamTM), a time comparable to a previous study (Biella et al. 2019). The number of workers entering and leaving the colony was later counted. We calculated the ratio between the egress and ingress of workers in intervals of 20 minutes as an index to estimate the foraging rate (Biella et al. 2019); for instance, a higher number of egress compared to ingress per time units is a proxy of longer foraging bouts.

Phytochemical analysis

Individual pollen pellets sampled from the same colony were pooled to gain a total of about 4 replicates (mean = 3.7 ± 0.9) for each sampling date which corresponded to 7.78 ± 1.70 pollen pellets each. Aggregated pools were freeze-dried and ground into a fine powder using a TissueLyser (Qiagen, Germany). Samples were analyzed for their protein, lipid, and carbohydrate content with the standard analytical protocols (Appendix S1, Text S1). Pollen was also analyzed for its antioxidants content, total phenol content and flavonoid content as described in Appendix S1 (Text S1).

Pollen genetic identification

Pollen plant composition was assessed with a DNA metabarcoding approach. DNA extraction and sequencing were performed on the same pooled samples used for the phytochemical analysis, following standard protocols (Appendix S1, Text S2). Briefly, the ITS2 DNA region was targeted, and the library preparation and sequencing were conducted with Illumina MiSeq 600 V3 ($2 \times 300\text{-bp}$ paired-end sequencing). The

obtained sequencing reads were processed with a standard bioinformatic pipeline to obtain ESVs (Exact Sequence Variants) to be assigned taxonomically using a curated genetic reference database. Following the recommendation provided by Tommasi et al. 2021, the resulting plant identities in the samples were filtered with ROC curves based on sequencing reads distribution to gain ecologically realistic plant assemblies (See Appendix S1, Text S2 for all additional details). The number of plant species found in the pollen samples was used as an indicator of pollen richness.

Landscape fragmentation and local metrics

We used the regional land use cartography (DUSAF 6.0 <https://www.dati.lombardia.it/Territorio/Dusaf-6-0-Uso-del-suolo-2018/7rae-fng6>) to obtain data on “Green cover”, by assigning to the original level and sub-level of land-use classification that defined polygons dominated by green patches (detailed information in Appendix S1 text S3). Using QGIS 3.10.11 we computed a buffer of 1 km radius around each site and three fragmentation landscape metrics were calculated using the package *landscapemetrics* (Hesselbarth et al., 2019) in R ver 4.2.0 (R CoreTeam 2022). In detail, we quantified the percentage of green area cover (% Green Cover), the mean Euclidean nearest neighbour distance (ENN) and the contagion index (CI) as indexes of fragmentation.

The local assemblage of flowering plant species around the colonies was recorded by counting the number of species during random inspection walks replicated three times at each site; at least 100 m² of green areas were carefully investigated.

Statistical analyses

The effects of landscape fragmentation and of the number of flowering species on the nutritional profile of pollen were tested by using (Generalized) Linear Mixed Models (LMMs/GLMMs) in R, with a binomial or beta distribution (based on the overdispersion parameters) distribution of the errors for variables of the percentages of protein, lipid, carbohydrate, antioxidant, phenol and flavonoid content. A Gaussian distribution was used for the protein:lipid ratio (P:L ratio) and protein:carbohydrates ratio (P:C). The models included the fragmentation metrics (percentage of green cover, ENN, CI) and the number of flowering species as fixed terms and the identity of the site, colony nested within the site, and week of the sampling as random effects. Collinearity among the four covariates was evaluated through the variance inflation factors (GVIF). The eventual transformation of the predictor variables was evaluated through the AIC criterion ($\Delta AIC > 2$, Zuur et al. 2009) and is reported in Table 1. The analyses were performed with *glmmTMB* (Brooks et al. 2023).

The relation between fragmentation metrics (cover, ENN, CI), the number of flowering species and the foraging rate was analyzed by using Gamma distributed GLMMs with the identity of site and colony (nested within site) as random effects.

The data on colony weight in time relative to the initial weight were analyzed by using Gamma distributed GLMMs with the ratio between the weight at a certain sampling replica and the initial weight as the response variable, the identity of site and colony (nested within the site) as random effects and the number of the sampling replica as the fixed effect.

Variations in pollen species richness in response to the fragmentation metrics (cover, ENN, CI) and to the number of flowering species recorded nearby the colony were evaluated through GLMMs with a Poisson distribution including the identity of site and colony (nested within site) and week of the sampling as the random effects. Furthermore, variations in time in the number of species foraged along the sampling season relative to the initial richness were evaluated by using Gamma distributed GLMMs with the ratio between the number of species at a certain sampling date and the initial number as the response variable, the identity of site and colony (nested within site) as random effects and the number of the sampling replica as the fixed effect.

To test an association between pollen nutrient profile and plant composition, a NDMS ordination analysis of the plant composition per site was performed and subsequently correlated to the nutrient profiles. We

analyzed community count data using sequencing reads as proxies of pollen abundances and Bray-Curtis dissimilarity index, as recent studies support the correlation between ESVs count on pollen species to microscopic pollen grain counts (e.g. Keller et al. 2015); however, to avoid the influence of differential read abundances among plants, the same type of analysis was repeated also with presence/absence data (Appendix S1, Table S1). We used the function *metaMDS* from the package “*vegan*” in R (Oksanen et al. 2022). Directional cosines between each NMDS vector and each of the nutritional variables considered were tested and their significance was evaluated with the *envfit* function of the package “*vegan*”.

To test whether species composition varied across the different aspects of habitat fragmentation and to assess the association between the geographical origin of the plants in the pollen and landscape fragmentation we used the RQL and Fourth Corner analysis. Community count data (i.e., number of sequencing reads) were used as indicators of pollen abundance. Plant origin as native or exotic/invasive was assigned according to Biella et al. 2022 and Galasso et al. 2018. The analysis was performed with “*ADE4*” package in R (Dray & Dufour 2007). To test if species composition varied across different habitats the function *manyglm* was used. To assess if species abundance variation in response to fragmentation was related to their geographical origin the trait by environment interaction term was calculated with the function *traitglm*. We set 999 permutations of sites and species values for testing significance.

RESULTS

Pollen nutrition and colony features

The mean content of macronutrients of the pollen load dry weight were protein 14.72% ($\pm$ 4.33%), lipid 4.67% ($\pm$ 1.44%) and carbohydrates 30.48% ($\pm$ 7.25%). The mean P:L ratio was 3.43 ($\pm$ 1.38). Pollen nutritional content varied significantly in response to the amount and fragmentation of green areas in the investigated urban gradient matrix (Table 1). Specifically, pollen protein content showed a quadratic non-linear relationship with ENN, peaking at intermediate levels (Fig. 2a) and a significant increase in response to the higher number of flowering species (Fig. 2b). Lipids concentration increased quadratically with the amount of green cover with a peak around 30% of green cover (Fig. 2c). The P:L ratio decreased significantly in response to an increase in the ENN (Fig. 2d). Total polyphenols content was significantly higher when more flowering species were present (Fig. 2e). Significantly longer foraging bouts were only associated with a decrease in the amount of green cover at study sites (Fig. 2f, Table 1). Colony weight did not vary significantly during the sampling season with only a slight reduction at the end of the sampling season (Appendix S1, Table S2, Fig. S1).

Pollen DNA metabarcoding

The transported pollen richness did not vary significantly in response to any of the three landscape metrics investigated neither to the richness of flowering species nor along the sampling season (Appendix S1, Table S2, Figure S3). The RQL fourth corner analysis indicated that the plant community composition was significantly related to the amount of green cover but not to the ENN and CI indexes (Appendix S1, Table S3, Figure S4) while no significant correlation was found between plant geographical origin and landscape fragmentation by the Fourth Corner Analysis (Appendix S1, Table S4, Figure S5).

The NMDS analysis revealed that nearly all nutritional classes were significantly correlated with the specific composition of the plant communities (Table 2). Higher protein content was correlated with communities dominated by species belonging mostly to the Fabaceae family (Fig. 3A), which were furthermore characterized by intermediate levels of lipids (Fig. 3B), carbohydrates (Fig. 3C) and phytochemicals (Fig. 3D, 3E, 3F).

DISCUSSION

In this study, we investigated how habitat fragmentation could shape the foraging dynamics and nutritional intakes of a bumblebee species. By setting a field-based experiment using urban landscapes as an open-air laboratory where green patches of different size, isolation and floral availability are interspersed in often

inhospitable concrete-dominated surfaces, we clarified how fragmentation could drive foraging for nest provisioning of a common pollinator. To address this topic we looked at: diet nutritional quality, plant composition and foraging rate.

Our results underline the significance of habitat fragmentation and local floral diversity in the nutritional composition of *B. terrestris* pollen pellets in terms of protein, lipid, polyphenol, and protein:lipid ratio. These findings support our initial hypothesis that fragmentation plays a key role in decreasing the quality of resources collected by pollinators in a scenario where spatial constraints prevent accessing profitable resources. If compared with previous studies (e.g., Moerman et al. 2017; Vaudo et al. 2018), our results suggest a general impoverishment of diet quality. In contrast with a recent study by Vaudo et al., 2018 on *B. impatiens* where no nutritional content variations were found in the foraged pollen across green areas in agricultural (thus permeable) landscapes, our approach demonstrated that the urban matrix presents peculiar conditions that could impose more severe hindrance to the foraging activity of insect pollinators. This is clearly indicated by our results on the nutritional content of pollen pellets. Although some relationships between nutritional content and landscape features were linear, both protein and lipid contents displayed quadratic responses, with higher concentrations observed at intermediate levels of green cover and distances between green patches. Numerous studies have already emphasized how intermediate levels of urbanization, for instance, those observed in suburban areas, can create favorable conditions for the thriving of pollinator populations (Banaszak-Cibicka & Żmihorski, 2020; Biella et al. 2022; Buchholz & Egerer, 2020), and our results hint for a link with their diet quality. This result further strengthens previous observations that for the understanding of pollinator dynamics, it is important to account for green areas heterogeneity and for the variation in environmental features within different city realities (Ayers and Rehan, 2021).

The adverse impact of extreme levels of habitat fragmentation becomes more pronounced when examining the P:L ratio, which exhibits a linear decrease at increasing ENN. Previous research has indicated that bumblebees tend to prefer a pollen diet rich in protein (Roulston et al. 2000) and that they are able to actively select for pollen provisions with a higher P:L ratio under optimal conditions (Vaudo et al. 2018; Russo et al. 2019). Therefore, considering that we analysed pollen pellets destined to larvae feeding, our observations indicate a possible deterioration in bumblebee nutritional balance at sites with high fragmentation. It should also be acknowledged that the decrease in the P:L ratio could lead to developmental problems and to a decrease in insects' reproductive fitness (Vaudo et al. 2018; Manning et al. 2007).

Noteworthy, the local species richness of flowering plants was associated with the nutritional quality of the pollen collected, specifically in the protein and polyphenol contents. Polyphenols have been linked to numerous beneficial effects on bee health, including increased detoxification rates (Hýbl et al. 2021), improved memory retention (Riveros & Gronenberg, 2022), and mitigation of oxidative stress (Dordieviski et al. 2023). Furthermore, experiments on *Apis mellifera* revealed a preference for sugar solutions containing polyphenols (Liu et al. 2006). In this context previous studies documented that local flower richness has a beneficial effect and correlates positively with local pollinator richness has been documented (Ollerton 2017). Our nutritional analysis showing responses to landscape fragmentation and to local flowering richness further supports the existence of a link between diversity/abundance trends and the nutritional aspects of the diets provisioned by these insects. This could also be mediated by the plant composition of the pollen collected to feed the larvae. The analyses confirmed a tight association between pollen plant composition, the nutritional profiles, and landscape, and no variation in pollen species richness along the fragmentation gradient. This result supports the hypothesis that fragmentation constrains the access to profitable resources; otherwise, if foragers were highly adaptive, then alternative local resources of high quality or a higher species richness would have been collected even in fragmented landscapes and no plant composition-nutrient association would be found (Barraquand & Benhamou 2008, Biella et al. 2019; Ritchie 1998). Furthermore, the analyses suggest that while the overall number of species foraged remained consistent, the composition of the diet represents the main driver of the changes in the observed variation of pollen nutrition. In agreement with this, the fourth corner analysis confirmed that a landscape feature as the green area size shapes the specific composition of the collected pollen communities. However, this landscape influence was not reflected by the prevalence of native or exotic species in the pellets, indicating that plant species nutritional idiosyncrasies, other than plant

origin, play a role in resource selection of the foraged pollen. This latter finding is in contrast to previous studies that recorded the role of ornamental or exotic plants in pollen of an urbanization gradient and the role of garden plants for feeding pollinators in an urban context (Biella et al. 2022; Staab et al. 2020; Tew et al. 2021). This is probably because our study was entirely set in an urban context of quite similar habitats (i.e. urban parks) rather than comparing different urban ones. Overall, these findings highlight the complex relationships between landscape characteristics, plant community composition, and the nutritional resources available to bumblebees; leaving open the question of possible behavioral adjustments by foragers.

To answer this, we recorded workers leaving and returning the nests and found that the foraging effort by the colony, measured as the ratio between leaving and returning by time unit, showed a significant negative relationship with the amount of green cover surrounding the study sites. In other words, increasing green cover leads to shorter duration of the foraging trips. Indeed, as the foraging effort reflects the colony needs and the spatial accessibility of resources (Jha & Kremen 2012; Pernal & Currie 2001), longer trips were performed in landscapes with less green areas, as expected. In areas with less cover where patches are less profitable, a forager would forage longer, for instance for maximizing quantity over quality or due to high searching time for good resources (Weterings et al. 2018; Jha & Kremen 2012). Conversely, with a high green cover and according to the optimal foraging theory, pollinators will forage close to their nesting site in landscapes with evenly distributed resource patches to reduce searching costs and maximize foraging efficiency (Heinrich 1979). This difference in fragmentation causing differences in foraging efficiency could affect the fitness of the colonies as they are strongly influenced by foraging behavioral traits, including foraging trip duration (Westphal et al. 2006). Furthermore, changes in the foraging pattern as the one we observed in this study can impact how pollen is distributed across the landscape and ultimately results in an impairment of the pollination service (Kremen et al. 2007). In conclusion, this study clarified the role of fragmentation in shaping foraging dynamics when it comes to collecting resources for nest provision in a common bumblebee as *B. terrestris*. It also raises several warnings on the limited capacity of the urban nutritional landscape to sustain social pollinator populations. It is still to understand if reinforcement programmes aimed at increasing flower diversity in cities go along with the nutritional needs of pollinators and if such interventions will reverse the negative trends observed here with high urban fragmentation levels. Landscape-scale conservation efforts should prioritize the preservation and restoration of green habitats with suitable floral resources to support the foraging behavior and population persistence of bumblebees, especially in contexts threatened by high human-driven fragmentation.

Figures

Figure 1: Map of the study area in central north Italy, showing the position of the experimental sites. The two boxes showed the setting of the colonies and a phase of the pollen sampling procedure.

Figure 2: Graph showing the variation of pollen loads nutritional content and foraging rate in response to landscape metrics and richness of flowering species. (a) Variation of protein content in response to the ENN; (b) relation between protein content and the number of flowering species at the sampling sites; lipid concentration in relation to the amount of green cover is reported in (c) while the variation of protein to lipid ratio in (d). (e) shows the relation between the polyphenols concentration and the number of flowering species while in (f) is reported the relation of the variation in the foraging rate of the colony in response to the amount of green cover. The black lines and grey areas indicate the prediction of the model and its confidence intervals ($\alpha = 95\%$).

Figure 3: Surface non-metric multidimensional scaling (NMDS) ordinations of pollen plant communities are depicted in the figure. Black names indicate species centroids indicating samples dominated by these species (only the name of the most common species that covered more than 95 % of the total reads are reported). Blue contour lines indicate corresponding nutrient contents that correlated with ordinal axes, which are interpreted as how each species in the community (and the overall community composition) correlate with the nutritional contents the pollen transported. Full species name are reported in Appendix S1; Table S5.

Tables

Table 1: Output of the regression analyses of the nutritional content of pollen and of the foraging rate as a function of green cover and fragmentation and the number of flowering species. The regression coefficient (β_i), chi-square value (χ^2), and p -value are reported.

Response variable	Model covariates	B_i	χ^2	p -value
Proteins	% Green cover	-0.529	2.526	0.11
	ENN	1.019	13.975	<0.001
	I(ENN) ²	-1.412	15.237	<0.001
	CI	-0.051	2.415	0.12
	log(Number of flowering species)	0.017	6.55	0.01
Lipids	% Green cover	0.705	4.14	0.02
	I(% Green cover) ²	-0.792	5.571	0.04
	ENN	0.033	0.209	0.65
	CI	0.058	0.908	0.34
	log(Number of flowering species)	0.06	0.837	0.36
Carbohydrates	% Green cover	-0.05	0.408	0.52
	ENN	-0.022	0.1	0.75
	CI	-0.018	119	0.73
	log(Number of flowering species)	0.121	0.646	0.42
	% Green cover	0.075	0.11	0.74
P:L ratio	ENN	-0.644	4.756	0.03
	CI	0.279	1.839	0.17
	log(Number of flowering species)	0.088	0.0310	0.86
	% Green cover	-0.212	0.246	0.62
	ENN	-0.076	2.05	0.15
P:C ratio	CI	0.0381	0.813	0.37
	log(Number of flowering species)	-0.035	0.109	0.74
	% Green cover	-0.096	0.65	0.42
	ENN	0.09	0.931	0.33
	CI	0.069	0.019	0.89
Antioxidants	log(Number of flowering species)	0.195	0.643	0.42
	% Green cover	0.157	2.921	0.08
	ENN	-0.089	1.085	0.29
	CI	-0.037	0.372	0.54
	log(Number of flowering species)	0.562	7.613	0.006
Polyphenols	% Green cover	-0.092	0.874	0.35
	ENN	-0.03	0.099	0.75
	CI	-0.094	1.631	0.2
	log(Number of flowering species)	0.36	2.795	0.09
	% Green cover	-1.115	9.562	0.002
Egress/Ingress	ENN	-0.062	2.638	0.1
	CI	-0.029	0.751	0.39
	log(Number of flowering species)	-0.128	2.86	0.09

Table 2: NMDS output with the correlations between plant community data and nutritional content of the pollen foraged.

	NMDS1	NMDS2	r^2 Correlation	p -value
Proteins (g/g)	0.74	0.67	0.11	0.01
Lipids (g/g)	0.99	0.79	0.08	0.01

	NMDS1	NMDS2	r^2 Correlation	p -value
Carbohydrates (g/g)	-0.67	-0.74	0.05	0.01
P:L ratio	-0.27	0.96	0.02	0.22
P:C ratio	0.62	0.78	0.17	0.01
Antioxidants (g/g)	0.66	-0.75	0.22	0.01
Polyphenols (g/g)	0.92	0.38	0.16	0.01
Flavonoids (g/g)	0.92	-0.4	0.11	0.01

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