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Research Paper

Landscape fragmentation constrains bumblebee nutritional ecology and foraging dynamics

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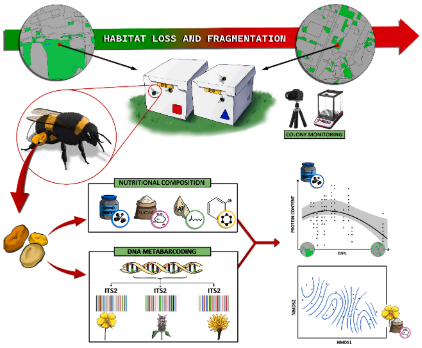
HIGHLIGHTS

- Habitat fragmentation decreases the nutritional quality of resources collected by bumblebees.
- Proteins, lipids and protein to lipid ratio of pollen were influenced by landscape configuration.
- Local plant species richness influenced protein and polyphenol content of pollen.
- Longer foraging trips were recorded in areas with reduced green cover.
- Specific plant communities composition was linked to pollen nutritional features.

GRAPHICAL ABSTRACT



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ABSTRACT

Habitat fragmentation is modifying landscapes and the distribution of floral resources, possibly shaping pollinator resource acquisition, which is an issue of global concern for pollinator health and urbanization sustainability. Here, in different urban parks contrasting in terms of local features and surrounding urban matrix, 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 trip length 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 longer foraging time in smaller green areas, showing that urban green area fragmentation limits nutritional resource accessibility. However, flower local richness improved the collection of beneficial nutrients as proteins and polyphenols, thus potentially rescuing negative landscape effects. This study illuminates the link between landscape and local features and the nutritional ecology of pollinators, a key aspect for understanding pollinator foraging dynamics. The findings of the study can provide valuable guidelines for policy makers and stakeholders involved in the management and ecological restoration planning for urban green areas and even for outlining mitigation measures in urban contexts.

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1. 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, Grass, Belavadi, & Tscharntke, 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 community structure and their interactions (Grass, Jauker, Steffan-Dewenter, Tscharntke, & Jauker, 2018) with important implications for pollinators nutritional ecology and for biotic components that directly and indirectly describe services connected to pollinators like the pollination ecosystem services and cultural services (e.g., Granata et al., 2023; Gervais, Courtois, Fournier, & Bélisle, 2020; Theodorou et al., 2020).

The fragmentation of green areas in landscapes may also shape several aspects that influence the nutritional ecology of pollinators (Hülsmann, von Wehrden, Klein, & Leonhardt, 2015; Winfree, Bartomeus, & Cariveau, 2011), such as the availability in terms of richness and abundance of floral resources (Potts et al., 2010) and their spatial distribution (Matteson, Grace, & Minor, 2013). For instance, fragmentation can result in an uneven 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). The main outcome of this scenario is the limitation of pollinators' food choices which can lead to their inability to satisfy their nutritional demands (Theodorou 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 sites in a landscape characterized by a lower degree of habitat fragmentation and an even distribution of resources 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., 2016). 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, could act synergically, ultimately jeopardizing urban pollinators and their services to the ecosystems.

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, Schürch, & Ratnieks, 2014). Indeed, bumblebee fitness is symmetric to the seasonal distribution of flower resources and nutrients: for instance, late-season shortages are associated with fewer bees the following year (Timberlake, Vaughan, Baude, & Memmott, 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, Farrell, Patch, Grozinger, & Tooker, 2018). These factors interact with each other, as 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, Hughes, Derwent, & Stout, 2002) and a reduction in colony fitness in highly urbanized areas (Theodorou et al., 2022). These negative effects on colony performance can be mainly ascribed to an unbalanced intake 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, Hilpert, & Leonhardt, 2017; Nicolson, Neves, Human, & Pirk, 2018).

The importance of a balanced intake of macronutrients and phytochemicals has been emphasized by several observations of different bee species showing clear food choices of floral resources to meet their nutritional demands (Kriesell et al., 2017; Liu, Zhang, Chai, & Yang, 2006; Ruedenauer, Spaethe, & Leonhardt, 2016; Vaudo, Patch, Mortensen, Tooker, & Grozinger, 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 in bees foraging choices, 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 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). In this case, we would also observe a tight association between the 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, Moonen, Prins, van Wieren, & van Langevelde, 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, pollen nutrients in the resources brought to the colony and the green area fragmentation, (iii) explore the potential association between the foraging behaviour in terms of trip duration and the landscape features of green areas. 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 conservation actions for pollinators in urban contexts.

2. Materials and methods

2.1. Study design and sampling

Study sites were chosen to represent a gradient of different green areas size and fragmentation within an urban landscape. The colonies were positioned in green areas accessible to the public for recreational purposes (e.g. urban parks) that were characterized by similar habitat features at the local scale and also representing the various types of urban green areas (e.g. allotments, parks, forested areas, grasslands, see also Appendix A1 Figure S1). 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, Parmentier, Pisman, de Graaf, & Smagghe, 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 (Fig. 1). Colonies were elevated from the ground and protected from rain and sun with wooden sheds covered with an insulating sheet (Fig. 1). Each colony was left at each site for at least 48 h. The sampling activities took place during the central phase of the colony life cycle, as the colonies were fully active in supplying the nest and sexuals were not seen emerging during the experiment. Most of the sites were sampled twice, with a month between samples and using a different pair of colonies between time replicates 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 48 h 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 sampled weekly over a month.

2.2. 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 (Fig. 1). We sampled pollen from on average 28.25 ± 9.78 workers for each colony on each date for a total of 1562 bumblebees and of 3076 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, and specifically in the foraging trip length, the colonies in all sites were monitored using video cameras (SuperEye RJ0090-UK, One-ThingCam^{TM}), for three hours on a single day, a length comparable to a previous study (Biella et al., 2019). Recordings were made approximately at the same time of the day at the different sites (9:00 a.m. – 12:00p.m.) to control for possible confounding effects related to intraday variation in the foraging behaviour of the colonies. The number of workers entering and leaving the colony was later counted from the videos. We calculated the ratio between the exits and the entrances of workers in intervals of 20 min as an index to estimate the foraging trip length (Biella et al., 2019); for instance, a higher number of exits compared to entrances per time unit is a proxy of longer foraging bouts, as in social foragers the nest exits rates depend on the rates of returning with food provisions (e.g. Gordon, Dektar, & Pinter-Wollman, 2013).

2.3. 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, corresponding 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,

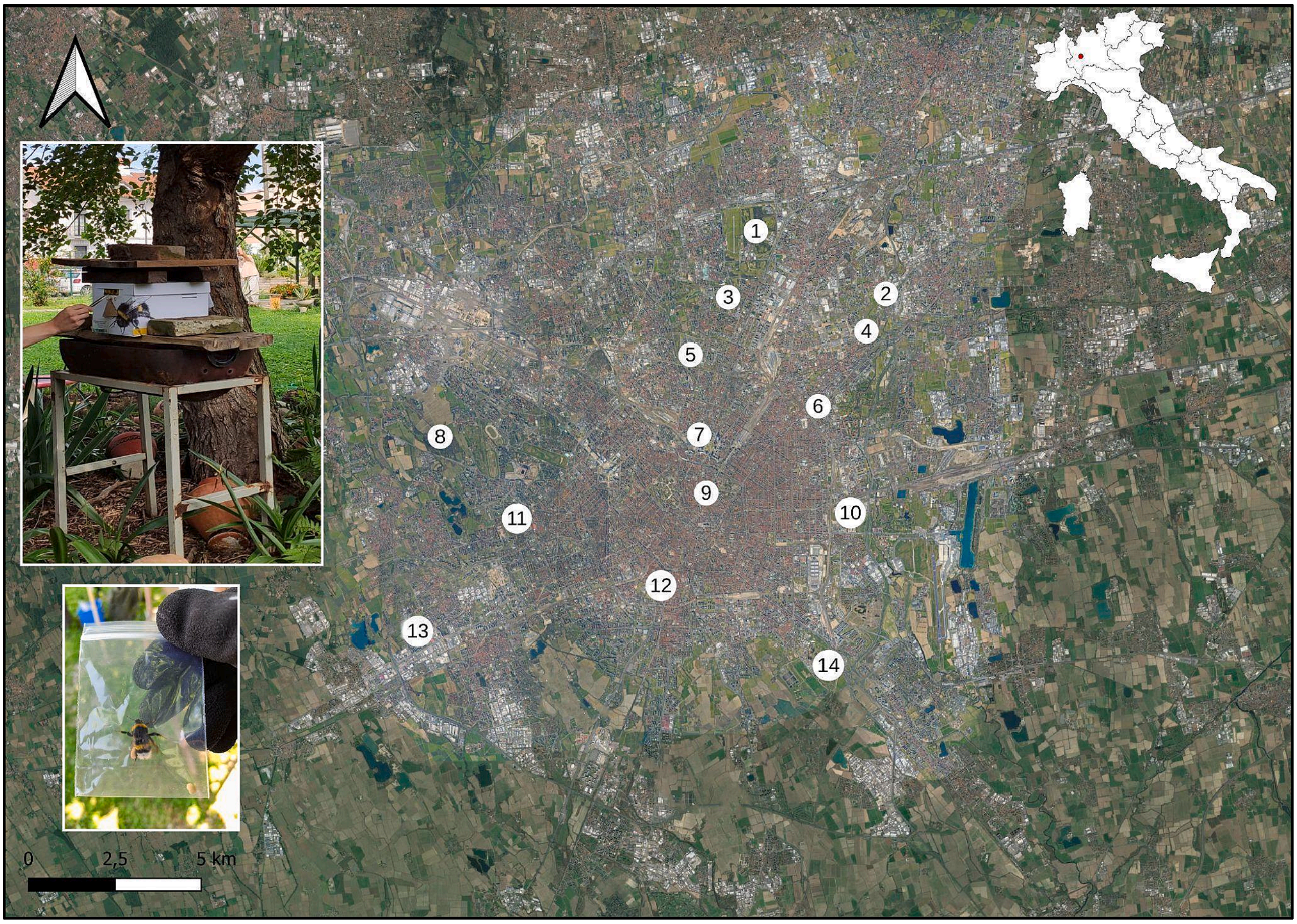

Fig. 1. Map of the study area in north Italy, showing the location of the experimental sites. The two insets show the setting of the colonies and a phase of the pollen sampling procedure.

and carbohydrates content with standard analytical protocols. Briefly, the extraction of proteins was carried out by using a basic solvent (0.1 M NaOH) and their subsequent quantification was performed by the Bradford assay. Lipids and carbohydrates were extracted by a protocol based on a mixture of solvents and their quantification was carried out through an assay based on the use of vanillin and anthrone, respectively (see Vaudo et al., 2016). Furthermore, pollen loads were analyzed for the antioxidant content, total phenol content, and flavonoid content by the DPPH (2,2-diphenyl-1-picrylhydrazyl), Folin-Ciocalteu and $AlCl_3$ (aluminium chloride) assays, by following the procedure reported in Pioltelli et al. (2024). Full details on the protocols adopted for the extraction and quantification of both macronutrients and secondary metabolites are reported in Appendix A1 (Text S1).

2.4. *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. The extraction of the DNA was conducted using the Qiagen© DNeasy® Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions (Full details on the wetlab DNA metabarcoding approach are reported in Appendix A1, Text S2). Briefly, the ITS2 DNA region was targeted and the library preparation and sequencing were conducted with Illumina MiSeq 600 V3 (2 × 300-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, Ferrari, Labra, Galimberti, & Biella, 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 A1, Text S2 for all additional details). The number of plant species found in the pollen samples was used as an indicator of pollen richness.

2.5. *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 areas, by assigning to the original level and sublevel of land-use classification that defined polygons dominated by green patches (detailed information in Appendix A1 Text S3 and Appendix A1 Figure S1). Using QGIS 3.10.11 we computed a buffer of a 1 km radius around each site as this distance is above the mean foraging distance observed for bumblebees in urban landscapes (Conflitti et al., 2022) and to evaluate the landscape features of the surrounding urban green areas. Three fragmentation landscape metrics were calculated using the package *landscapemetrics* (Hesselbarth, Sciaini, With, Wiegand, & Nowosad, 2019) in R ver 4.2.0 (R Core Team, 2022). In detail, we quantified the percentage of green area cover (% Green Cover), the mean Euclidean nearest neighbor distance (ENN) that measures the mean distance to the nearest neighbouring patch of the same type, and the contagion index (CI) that is based on cell adjacencies and describes the probability of two random cells belonging to the same class, as indexes of area size and 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 and crossing the main types of vegetation; at least 100 m^2 of green areas were carefully investigated.

2.6. *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 to quadratic terms was evaluated through the AIC criterion (with a threshold of $\Delta AIC > 2$, Zuur, Ieno, Walker, Saveliev, & Smith, 2009, reported in Table 1) and by visual inspection of variable boxplots and scatterplots. These and the following regression analyses were performed with *glmmTMB* package in R (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 with presence/absence data (Appendix A1, 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.

Table 1

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

Response variable	Model covariates	B_i	χ2	*p*-value
Proteins	% Green cover	−0.529	2.526	0.11
	ENN	1.019	13.975	**<0.001**
	I(ENN)ˆ2	−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)ˆ2	−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
P:L ratio	% Green cover	0.075	0.11	0.74
	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
P:C ratio	% Green cover	−0.212	0.246	0.62
	ENN	−0.076	2.05	0.15
	CI	0.0381	0.813	0.37
	log(Number of flowering species)	−0.035	0.109	0.74
Antioxidants	% Green cover	−0.096	0.65	0.42
	ENN	0.09	0.931	0.33
	CI	0.069	0.019	0.89
	log(Number of flowering species)	0.195	0.643	0.42
Polyphenols	% 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**
Flavonoids	% 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
Exits/Entrances	% Green cover	−1.115	9.562	**0.002**
	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

3. Results

3.1. Pollen nutritional properties and foraging dynamics

The overall mean content of macronutrients of the pollen load dry weight were protein 14.72 % (±4.33 %), lipid 4.67 % (±1.44 %) and carbohydrates 30.48 % (±7.25 %). The mean P:L ratio was 3.43 (±1.38).

Pollen nutritional content varied significantly in response to the size 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), except for a case showing low protein concentration although it was the richest in terms of flowering species. Lipids concentration was quadratically related to 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).

Foraging dynamics indicated significantly longer foraging bouts in association with a decrease in the amount of green cover at study sites (Fig. 2f, Table 1), and it followed the separate trends of entrances and exits per time unit in relation to the green cover (reported in Appendix A1 Fig. S2). Colony weight did not vary significantly during the sampling season with only a slight reduction at the end of the sampling season in a panel of colonies (Appendix A1, Table S2, Fig. S3a).

3.2. Pollen species richness and composition

At least 50 species were identified in the pollen pellets. The most abundant species was *Trifolium repens*, detected in more than 50 % of the samples, followed by *Tilia* sp. (46.6 %), *Rubus* sp. (32.7 %), and *Trifolium pratense* (19.1 %), a full list of species identified and their occurrence rate in the pollen samples is reported in Appendix A1, Table S3. The pollen richness did not vary significantly in response to any of the three landscape metrics investigated and the richness of flowering species (Appendix A1, Table S4) or along the sampling season (Appendix A1, Table S2, Figure S3b). Despite this, the RQL fourth corner analysis indicated that the pollen species composition was significantly related to the amount of green cover, but not to the ENN and CI indexes (Appendix A1, Table S5, Figure S4), while no significant correlation was found between plant geographical origin (exotic/native species) and landscape fragmentation (Appendix A1, Table S6, Figure S5).

The NMDS analysis revealed that nearly all nutritional classes were significantly correlated with the specific composition of the pollen pellets (Appendix A1, Table S7). Higher protein content was correlated with pellets dominated by species belonging mostly to the Fabaceae family (Fig. 3A) such as *Trifolium pratense and T. repens* that were also among the five most abundant species in our samples. Fabaceae species were furthermore characterized by intermediate levels of lipids (Fig. 3B), carbohydrates (Fig. 3C) and phytochemicals (Fig. 3D, E, F) such as in the case of *Melilotus officinalis* and *Medicago* sp.. Among the other most abundant species, the presence of *Rubus* sp. and *Tilia* sp. was associated with intermediate concentration of all the nutritional classes investigated, thus indicating that despite their high occurrence they were not the major determinants of nutritional variations in the pollen pellets.

4. Discussion

In this study, we investigated how habitat fragmentation could shape the foraging dynamics and nutritional intakes of a bumblebee species across a gradient of urban green area size and fragmentation. By setting a field study in urban landscapes where green patches of different sizes, isolation, and with varying 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 trip length.

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

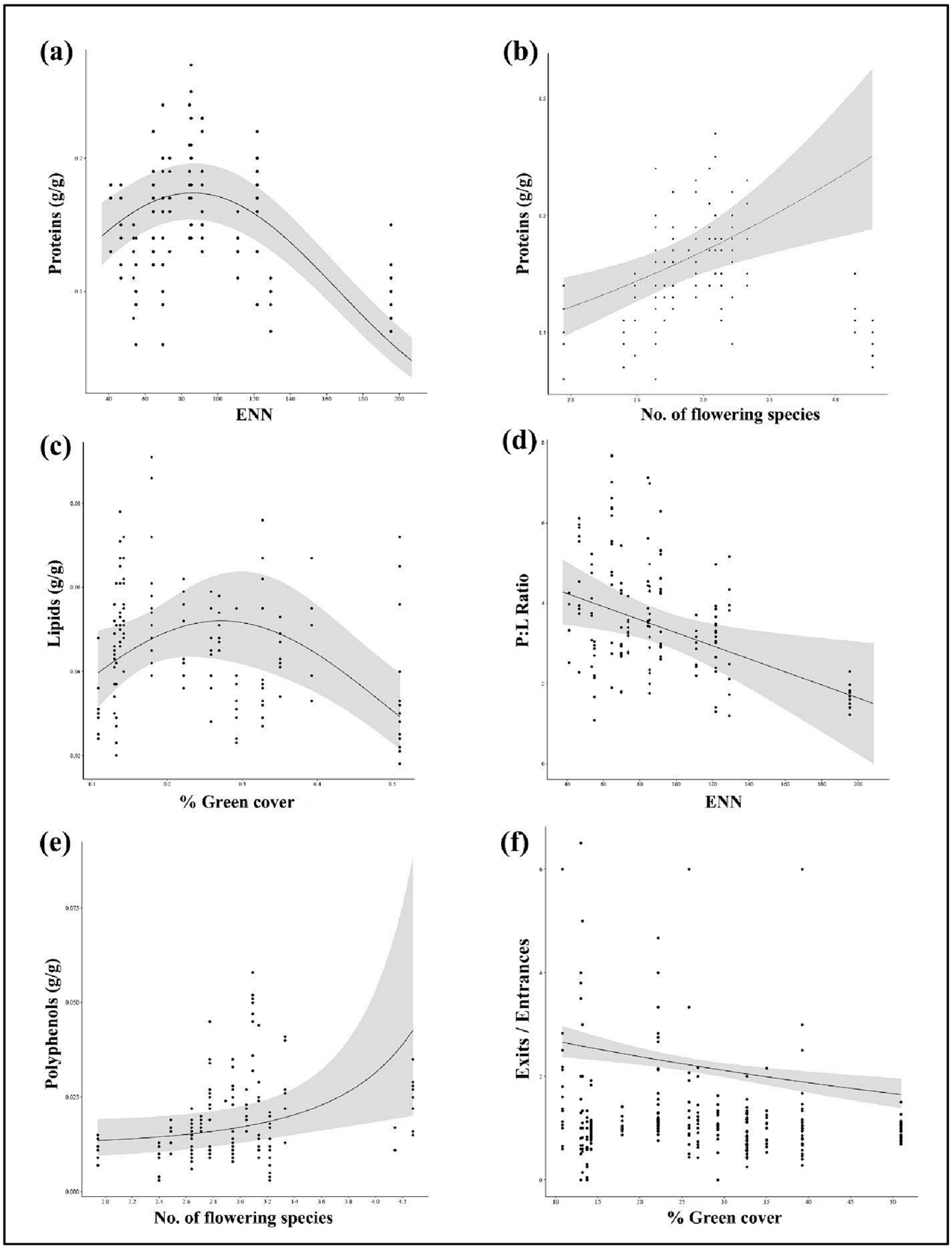

Fig. 2. Plots showing the variation of pollen loads nutritional content and trip length in response to landscape metrics and the local richness of flowering species. (a) Quadratic non-linear relationship between protein content in response to the ENN; (b) linear positive relation between protein content and the number of flowering species at the sampling sites; (c) quadratic non-linear relationship between lipid concentration and the amount of green cover; (d) linear decrease of protein to lipid ratio in response to the increasing level of the ENN index; (e) increase in polyphenols concentration in response to increasing number of flowering species; (f) negative relation between the forager ratio of exits to entrances as a measure of trip length and the green cover. The black lines and grey areas indicate the prediction of the models and the confidence intervals (α = 95 %).

a scenario where spatial constraints prevent accessing profitable resources. If compared with previous studies (e.g., Moerman, Vanderplanck, Fournier, Jacquemart, & Michez, 2017; Vaudo et al., 2018), our results suggest a general impoverishment of diet quality where areas are more severely fragmented. However, in contrast with a recent study on *B. impatiens* where no nutritional content variations were found in the foraged pollen across green areas in agricultural landscapes that are permeable by foragers (Vaudo et al., 2018), our approach demonstrated that the urban matrix presents peculiar conditions imposing more severe hindrance to the foraging activity of insect pollinators. This is indicated by our results on the nutritional content of pollen pellets.

Some relationships between nutritional content and landscape features were non-linear, as in the case of protein and lipid contents displaying 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 typical of suburban areas can create favorable conditions for the thriving of pollinator populations (Banaszak-Cibicka &

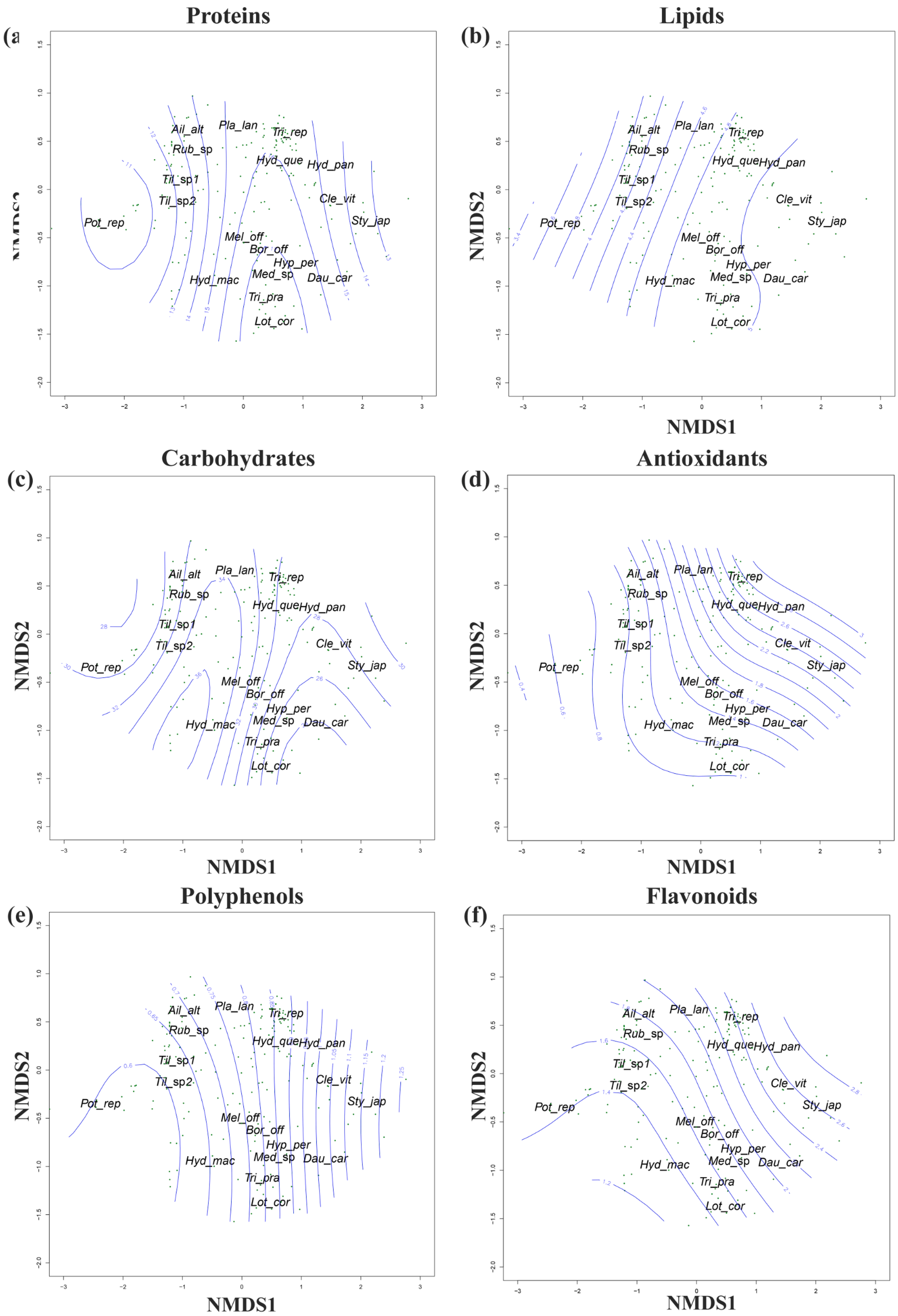

Fig. 3. Surface non-metric multidimensional scaling (NMDS) ordinations of pollen plant composition. Black names refer to acronyms of plant species and indicate the centroids of the samples dominated by those species (only the name of the most common species that covered more than 95 % of the total sequencing reads are reported here to improve plot readability, full names are in Appendix A1, Table S8). Contour lines indicate the nutrient contents that correlated with ordinal axes, which are interpreted as how each species in the community and the overall community composition correlates with the nutritional contents the pollen transported.

Żmihorski, 2020; Biella et al., 2022), and our results hint at 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 the variation in environmental features within different city realities (Ayers & Rehan, 2021). Indeed several studies demonstrated that different types of green areas are also different in how they support pollinators, the gardens being considered among the best areas (Baldock, Goddard, & Hicks, 2019), also for providing nectar nutritional resources (Tew et al., 2023) and our study clarifies that intermediate area fragmentation in the landscape could benefit the nutrition of pollinators.

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, Cane, & Buchmann, 2000) and that they can actively select for pollen provisions with a higher P:L ratio under optimal conditions (Vaudo et al., 2018). Therefore, considering that we analysed pollen pellets destined for larvae feeding, our observations indicate a possible deterioration in bumblebee nutritional balance at urban sites with high fragmentation. It should also be acknowledged that the decrease in the P:L ratio could lead to developmental problems and a decrease in insect reproductive fitness (Vaudo et al., 2018; Manning, Rutkay, Eaton, & Dell, 2007). Indeed, more than the absolute intake of some nutrients, their relative proportion in the diet is vital for the health status of pollinators: deviations from the so-called "nutrient target" can lead to deficient growth (Vaudo et al., 2018) and also to compromised immune functions (Di Pasquale et al., 2013).

It is noteworthy that the local species richness of flowering plants was associated with the nutritional quality of the pollen collected, specifically in the polyphenol and protein contents. Concerning polyphenols, their relationship with plant richness were highly significant as this component has 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 (Đorđievski et al., 2023). Furthermore, experiments on *Apis mellifera* revealed a preference for sugar solutions containing polyphenols (Liu et al., 2006). In the case of the proteins, this relationship held true for all but one site that was characterized by a low pollen protein content despite being rich in terms of plant composition. Probably this extreme observation is related to the local plant community, that could have been dominated by species without a relevant nutritional content, where managers prioritized the aesthetic over the nutritional value of plants.

Overall, the relationships between proteins and polyphenols with local flower richness provide additional explanation to the link between pollinator richness and plant diversity, as documented in many studies (see Ollerton, 2017), and it is relevant also in the urban context (Rajbhandari, Matteson, Katz, LeBuhn, & Johnson, 2023). Our nutritional analysis showing responses to landscape fragmentation and 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. The link between plant species and pollen nutrient content could also be mediated by the plant composition of the pollen collected for feeding reasons. The analyses confirmed a tight association between pollen plant composition, nutritional profiles, and landscape, and no variation in pollen species richness along the fragmentation gradient. This result supports the hypothesis that fragmentation constrains 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). Furthermore, while the total number of species foraged remained consistent, the composition of the diet represents the main driver of the changes in pollen nutritional properties. 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, while the prevalence of native or exotic species in the pollen pellets was not an influential factor. This latter finding contrasts with previous studies showing the role of ornamental or exotic plants for feeding pollinators in urban contexts in comparison to non-urban areas (Biella et al., 2022; Staab, Pereira-Peixoto, & Klein, 2020; Tew, Memmott, & Vaughan, 2021). This discrepancy with the literature is probably because our study was entirely set in an urban context of quite similar habitats rather than comparing different habitats. Overall, our findings remark that plant species nutritional idiosyncrasies, other than plant origin, play a role in pollen resource selection by pollinators. Moreover, 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 trip length and 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, 2013; 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, 2013). 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, Steffan, & Tscharntke, 2006). Furthermore, changes in the foraging pattern could have implications for pollinator fitness (e.g. Kevan et al., 2009) and also for pollination service (Kremen et al., 2007).

5. Conclusion

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 be understood if programs 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. Alongside the management and creation of these conducive habitats, mitigation actions should also be directed towards enhancing the connectivity among green patches to increase accessibility to food resources for insect pollinators. This multifaceted approach integrating habitat presence, plant nutritional properties, area management, and connectivity in a pollinator-friendly way, will play a key role in safeguarding pollinators populations and their vital ecological contributions within urban environments.

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CRediT authorship contribution statement

E. Pioltelli: Writing – original draft, Visualization, Formal analysis, Data curation. **L. Guzzetti:** Formal analysis, Investigation, Writing – review & editing. **M. Ouled Larbi:** Investigation. **M. Labra:** Resources, Writing – review & editing. **A. Galimberti:** Investigation, Resources, Writing – review & editing. **P. Biella:** Conceptualization, Investigation, Methodology, Writing – review & editing.

Declaration of competing interest

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

Data availability

Data used in this article can be found online at https://doi.org/10.1016/j.landurbplan.2024.105075. Pollen raw sequencing reads from the DNA metabarcoding are available on NCBI (BioProject PRJNA1094568, at the link https://www.ncbi.nlm.nih.gov/sra/PRJNA1094568).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2024.105075.

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