






## RESEARCH ARTICLE

# City climate and landscape structure shape pollinators, nectar and transported pollen along a gradient of urbanization

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**Funding information**

Regione Lombardia, Grant/Award Number: POR FESR 2014-2020; Italian Ministry of Universities and Research (MUR), PONRI FSE REACT-EU 2014-2020 - "Azione IV.4 - Dottorati e contratti di ricerca su tematiche dell'innovazione, Azione IV.6 - Contratti di ricerca su tematiche Green"; Open Access Funding provided by Università degli Studi di Milano-Bicocca within the CRUI-CARE Agreement.

**Handling Editor:** Péter Batáry

**Abstract**

1. Urbanization gradients influence both landscape and climate and provide opportunity for understanding how plants and pollinators respond to artificially driven environmental transitions, a relevant aspect for the ecosystem service of pollination.
2. Here, we investigated several aspects of pollination along an urbanization gradient in landscape and climate. We quantified wild hoverfly and bee abundances with trapping, standing crop of nectar with spectrophotometer, and the pollen transported by flower visitors with DNA metabarcoding, in 40 independent sites from semi-natural to built-up areas in Northern Italy. Direct and indirect effects were fitted considering landscape and climate variables.
3. Linear and nonlinear relationships were detected along the urbanization gradient. Pollinator abundances increased quadratically and peaked at 22% of impervious cover with an 81% growth, and they decreased with green-patch distance by 37% and urban park largeness by 60%. This indicates that pollinators are more abundant at intermediate levels of urbanization. Climatically, pollinators diminished by up to 46% in areas with low spring–summer temperature seasonality: urban areas likely posing thermic stress. Furthermore, the sugar mass available in nectar increased by 61% with impervious cover and by 79% with precipitations, indicating that city nectars were less consumed or flowers more productive. Furthermore, the species richness of pollen decreased by 32% in highly urbanized areas, and contained a high incidence of exotic plants, hinting for anthropized, simplified plant communities.
4. *Synthesis and applications.* Urbanization influences pollinator abundances, nectar resources and transported pollen in direct and indirect ways. Pollinators are negatively affected by a thermally harsh climate in highly urbanized areas with isolated green areas and large parks. Suburban landscapes demonstrated the highest pollinator presence. In the city core, flowers contained more nectary sugar in association with more precipitations, while pollinators collected pollen from a small number of plants, mainly exotic. These findings highlight the strong

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influence of urban landscape and climate on pollinators and plants, showing that cities are heterogenous realities. Patterns from this study will serve as basis for pollinator-friendly planning, mitigation and management of urban landscapes.

#### KEYWORDS

habitat disturbance gradient, landscape ecology, multi-trophic interactions, plant–pollinator interactions, plant nectar and pollen rewards, pollen identification with DNA HTS High-throughput sequencing, temperature and precipitation climatic gradient, urban biodiversity conservation

## 1 | INTRODUCTION

Given the environmental change caused by cemented and built-up surfaces, urban areas are often considered as a separate macrohabitat for animal and plant communities (Bolger et al., 2000; Faeth & Kane, 1978). Cities provide an artificial environment that creates an extreme transition (Lemoine-Rodríguez et al., 2020), causing several types of responses on biodiversity. These impacts affect a number of ecosystem processes, mainly by influencing changes in species interactions (Cohen et al., 2020; Geslin et al., 2013) comparable to disturbance events (Biella et al., 2020). As plants and pollinators play key roles in many ecosystem processes (Patel et al., 2020; Potts et al., 2016), it is of utmost importance to understand how urbanization gradients shape the aspects of pollination and pollinator ecology.

Urbanization can be described as a gradient, with different consequences for plants and pollinators. For instance, plant diversity is higher at moderate urbanization (McKinney, 2008), and sub-urban areas host higher wild bee and butterfly diversity than the city core (Banaszak-Cibicka & Żmihorski, 2020; Kurylo et al., 2020). Moreover, different pollinator types and life-history traits respond differently to urbanization (Wenzel et al., 2020). For instance, less Diptera: Syrphidae than Hymenoptera are expected to occur in cities (Persson et al., 2020). Within Hymenoptera, built environments may change the composition of bee assemblages, with a high occurrence of solitary and above-ground nesting bees (Wilson & Jamieson, 2019), while filtering big species out (Buchholz & Egerer, 2020). Furthermore, fragment isolation may play a role, as a study found poorer pollinator assemblages in more isolated urban green areas (Tonietto et al., 2011). All these aspects highlight the need to further explore how pollinators respond to structural differences in urbanized landscapes.

Cities directly impact local climates (Kuttler, 2008), likely triggering species physiological responses, even in plants and pollinators. Urban climate is usually warmer, with lower relative humidity and higher precipitations than the surroundings (Kuttler, 2008). The urban heat island effect determines high temperatures and it decreases temperature seasonality, having low variation daily and across seasons (Marando et al., 2019). For instance, warmer cities impact plant physiology and phenology, triggering earlier flowering (Fisogni et al., 2020; Neil & Wu, 2006). Even pollinator physiology can be affected (Hamblin et al., 2018): bees inhabiting city cores have high thermic stress (Burdine & McCluney, 2019). It is likely that the climatic impact of

cities on plant and pollinator physiology are directly connected to diversity and abundances of those assemblages (Chown & Duffy, 2015; Diamond et al., 2015). This is exemplified by studies showing that the climatic features could affect some families of bees even more than landscape alteration (Kammerer et al., 2021). Therefore, it seems relevant to describe the responses of plants and pollinators not only as a function of landscape alone but also by urban climatic variation.

In this study, we evaluated the effects of urbanization on several aspects of pollination and pollinator ecology, which are also relevant for ecosystem functioning and services (Biella, Akter, et al., 2019; Patel et al., 2020), namely pollinator abundances, flower nectar resources and transported pollen. We surveyed along a gradient of increasing urbanization in Northern Italy, a region characterized by a high proportion of impervious cover (i.e. water resistant built-up surfaces) and remarkable climatic shift due to urban areas (Perini & Magliocco, 2014). To address a mechanistic understanding of how an artificial gradient shapes pollination ecology and to connect local surveys to the structure of the surrounding area, we characterized landscape composition, its configuration and the climate by hypothesizing that landscape and climate could interplay by posing direct and indirect effects (Fenoglio et al., 2021).

Firstly, we measured pollinator abundance as an indicator of habitat suitability (Bartholomée et al., 2020), and hypothesized that along the urbanization gradient pollinators may be dependent on landscape and local climate. The landscape could affect pollinators by the distribution and accessibility of suitable areas measured here as the isolation of green spaces used for foraging (Steffan-Dewenter & Tschardtke, 1999). Within the highly urbanized areas, we also tested the role of city park size in order to further highlight the relationship with patch size, as larger areas might serve as refugia for larger populations (Baldock et al., 2019). In addition, temperature variation along the urbanization gradient could impact flower visiting organisms and also determine their local abundance (Burdine & McCluney, 2019; Hamblin et al., 2018) by affecting pollinator physiology (Colinet et al., 2015). In this scenario, impervious cover describes the urbanization gradient and we expected an indirect effect mediated by the other variables named above.

Secondly, we characterized the availability of nectar sugar mass, because nectar constitutes one of the main resources collected by flower visitors (Hicks et al., 2016). This reward depends on the secretion rate and thus to plant physiology and environment, and its amount is partly determined by pollinator foraging rate (Corbet, 2003).

Regarding the landscape, we hypothesized that the available nectar quantity could depend on the size and shape of green areas because bigger patches may host richer communities (Collins et al., 2009), described as the edge density (ED) as it also accounts for shapes, it uses both area and perimeter of patches and favours comparisons among landscapes (McGarigal, 2015; Soifer et al., 2021). In addition, plant productivity may depend on the local climate, especially precipitations and the length of the thermally suitable season for growing, parameters that vary with urbanization and that could impact nectar production (Mueller et al., 2020; Zipper et al., 2016). The impervious cover is expected to have indirect effects through the other factors.

Thirdly, we considered the pollen carried by flower visitors and we obtained the number of plant species visited by pollinators from the transported pollen, that is an important component of the total pollination rate (Bosch et al., 2009). Here, we considered pollinators as passive samplers of flowering plants given the difficulty posed by complex urban structures (e.g. tall buildings, balconies and private gardens) that impede traditional survey techniques. We described the transported pollen richness along the urbanization gradient described by the impervious cover and we also expected an influence by green-patch size indicated by the ED, as it may determine local plant diversity (Collins et al., 2009). We did not analyse climatic variables in this case as in anthropogenic areas pollen availability could be primarily influenced by management (Aronson et al., 2017).

## 2 | MATERIALS AND METHODS

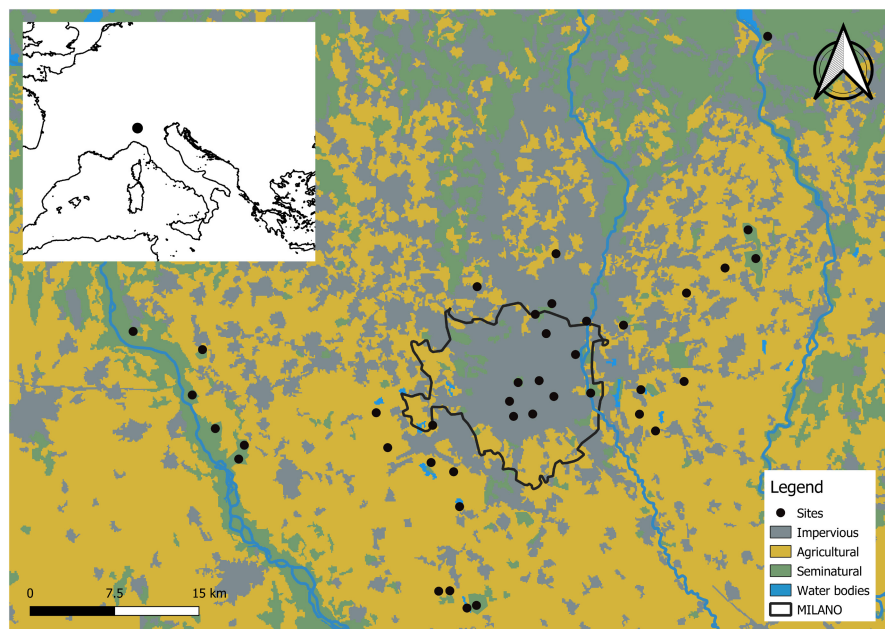
### 2.1 | Study area

Study sites were set in Northern Italy (Figure 1), a region that is occupied by urbanized surfaces (about 38% of the regional area), intensive agricultural environments (c. 53%) and natural forests, wet

habitats and semi-natural hay meadows (c. 9%) (Regione Lombardia and ERSAF, 2010). Study sites were selected randomly with a GIS software (QGIS 3.6.2) and were distributed in an area of 1,575 km<sup>2</sup> including the entire region of Milan and the urban parks of Milan city. We applied a minimum of 1 km distance between putative sites to assure the independency of samplings (Phillips et al., 2019), later confirmed by a non-significant autocorrelation analysis of each response variable based on locations with Moran's *I* tests ( $p > 0.05$ , if considering 10 neighbouring sites or considering all neighbours in a band of 100 km). We adjusted the exact sampling locations so that each would be located in either an urban park largely surrounded by 'impervious' surfaces (i.e. concrete, asphalt, buildings) or at the margins of agricultural fields with a varying quantity of surrounding impervious surface or in semi-natural hay meadows near forests (<1 km) with little amount of urbanization nearby (Figure S1). Overall, 40 sites were surveyed, across the entire urbanization gradient (Figure 1; Figure S1, 11 urban parks, 15 agriculture margins, 14 semi-natural hay meadows). Sampling permits were obtained when needed from local authorities.

### 2.2 | Landscape and local climate characterization

To characterize landscape composition, we measured the cover percentage of impervious surfaces, urban green areas and semi-natural lands (forests and hay meadows). To describe landscape configuration, we focused on green and semi-natural patches together and calculated the ED and the Euclidean nearest neighbour distance (ENN). ED measures the size of patches by considering the length of all edge segments per area unit and accounts for shape, while ENN describes the mean distance between patches in the landscape (McGarigal, 2015). For sites in recreational urban parks, we also calculated the size of the parks.



**FIGURE 1** Sampling sites. The distribution of sampling sites along a gradient of increasing urbanization in Northern Italy, with the Municipality of Milan, three major rivers and the main land uses of this region

Temperature and precipitation vary with urbanization (see Figures S2 and S3), we used 3 months' averages of hourly temperature at 2 m and hourly precipitation sum between February and July 2019. We calculated temperature seasonality as the coefficient of variation between spring and summer. Air temperature data were also used to calculate the growing season suitability (GSS) index, quantifying the length of the vegetative season that could impact the productivity of plant resources (Zipper et al., 2016). All variables were extracted from circular buffers of 1 km around the sampling sites; further methodological details are available in Appendix A1.

### 2.3 | Pollinator abundance

Sampling of pollinator abundances took place during the peak flowering period for the study area, from mid-May to mid-June 2019, in 36 sites. Passive sampling took place for 24 hours, with pan and sticky traps as complementary methods (details on traps are in Appendix A2). In each site, three sets of pan traps were placed 10 m apart from each other and five yellow sticky traps were placed at 5 m from the pan traps. In this study, we counted the total abundance of bees and hoverflies (Hymenoptera: Anthophila and Diptera: Syrphidae) following Bates et al. (2011). We did not count honeybees since their numerosity is only due to beehives in the vicinities. In the statistical analyses that followed, we kept wild bees and hoverflies together and evaluated their total abundance as they belong to the same guild of pollinators (see Figure S4).

### 2.4 | Nectar sugar quantification

Standing crop of sugar mass in the nectar was measured from mid-May to mid-June in 35 sites. The flowers of two or three most abundant herbaceous flowering species were selected after inspecting plant cover based on the number of stalks. We chose abundant plants as they should offer most of the local resources. Standing crop of nectar sugar mass is a measure of nectar quality available at a given time and it is a function of plant secretion and of pollinator visitation frequency (Corbet, 2003). The sugar mass per flower was quantified as explained in Appendix A2 and data for each given species were calculated by dividing the sugar mass by the number of washed flowers of a species processed at a site (Biella, Akter, et al., 2019).

### 2.5 | Pollen richness with DNA metabarcoding

In each sampled site, insects foraging on flowers were actively sampled for 1 hr by hand-netting and then stored in sterile Eppendorf tubes filled with ethanol 70%. In the laboratory, we randomly chosen a subset of the sampled sites ( $N = 25$ ) and analysed the pollen from insect bodies with DNA metabarcoding

following the protocol of Biella, Tommasi, et al. (2019) and recommendations by Tommasi, Ferrari, et al. (2021). Details of the protocol and bioinformatic processing are reported in Appendix A3. For each site, the number of plant species found in the pollen of all flower visitors was used as an indication of pollen richness.

### 2.6 | Statistical analyses

Putative predictors were chosen based on the ecological hypotheses outlined above. We used a repeated K-fold cross-validation for choosing whether to fit linear or nonlinear (quadratic) models by selecting the lowest mean RMSE (root mean squared error) from 10 repetitions of  $K = 10$  (Table S1). To test collinear variables, we calculated the variance inflation factor (VIF) index and correlations from preliminary models (Table S2) with the R package *CAR* (Fox & Weisber, 2019). In the regression models listed below, predictors were square rooted to correct variable skewness and they were scaled to avoid different numerical ranges.

We analysed the effects of landscape composition and configuration, and the summer-to-spring temperature seasonality on pollinator abundances in a structural equation model (SEM) with the *SEMeff* package in R (Murphy, 2021), significances and standardized coefficient estimates were obtained from 999 bootstraps; correlations among predictors were accounted with the option *unique.eff*. To avoid high collinearity (Table S2), the proportion of impervious cover describing the urbanization gradient was fitted as an indirect effect on pollinators with a quadratic linear regression on the ENN and temperature seasonality. These two were fitted as direct effects on pollinator abundances with a GLM, where the ENN indicates the distance between patches used by pollinators and temperature seasonality indicates the potential for thermic stress. In addition, we analysed the relationship between pollinator abundances and recreational park size with a GLM with the subset of data from city parks (this predictor was log-transformed), the significance was obtained with likelihood-ratio tests. In all cases, a Poisson family was used for error distribution with a logarithm link function.

For the sugar mass per flower, we analysed the direct and indirect effects of landscape variables and urban climate in a SEM. To avoid high collinearity (Table S2), we fitted the indirect effect of the proportion of impervious cover as a quadratic linear regression on ED, mean summer precipitation and GSS. The direct effects by ED, the mean summer precipitation and the GSS were modelled on sugar mass in a GLMM, with a gamma error distribution and the logarithm as a link function, with plant species and site identities as random intercepts. While the impervious cover characterizes the urbanization, the other variables describe the impact on plant productivity as ED explains the role of patch size on the diversity of plant communities, and the mean summer precipitation and GSS measure the amount of natural watering and length of the favourable season.

We also analysed the effect of the urban landscape on the transported pollen richness. We used the total pollen richness for each site as response variable in a GLM with the proportion of impervious land and ED as predictors, a Poisson family for error distribution and a logarithm link function. Significance was tested with likelihood-ratio tests. These variables were used because impervious cover indicates the urbanization gradient and ED considers the role of patch size in hosting plant diversity, while we did not expect a contribution from seasonal climate. In addition, we investigated the connection between the geographical origin of plants and the landscape from the plant species of pollen transported. To do so, we used the fourth corner analysis to evaluate the relationship between plant incidence measured as the proportion of samples where a plant was found at a given site; plant origin as native of the sampled region, agricultural crop or exotic (Galasso et al., 2018); and site attributes as the proportion of impervious, semi-natural and urban green cover. The analysis was performed with ADE4 package in R (Thioulouse et al., 2018) by setting 999 permutations of sites and species values for testing significances.

### 3 | RESULTS

Abundances of pollinators associated positively and linearly with the seasonal variation of the mean temperatures between spring and summer (Table 1; Figure 2b), with the highest thermic seasonality in sites with medium to low impervious cover (see Figure S2). Specifically, pollinators increased by 46% across the range of temperature seasonality. Increasing green-patch ENN was associated

with a decline in pollinator abundance of 32% across the range of the variable (Figure 2c). Pollinator abundance was quadratically linked to impervious cover fitted with an indirect effect, increasing until a threshold value of 22% of impervious cover that corresponded to an 81% growth of pollinators, after which the relationship became negative (Figure 2d). In city parks, the relationship between pollinator abundances and park size was negative (Table 1; Figure S5), with a decline of 60% over the range of the studied urban parks (0.02–0.68 km<sup>2</sup>).

Sugar mass per flower was linearly and significantly dependent on summer mean precipitation (Table 1, Figure 3a,b). It was also associated with the impervious cover fitted with an indirect effect (Figure 3c). Specifically, sugar mass increased by 79% with precipitations and by 61% across the range of impervious cover. However, it was not significantly dependent on green area ED or GSS.

The transported pollen richness showed a linear negative relationship with the impervious cover, and specifically by 32.5% across the range of the variable, and it was not significantly dependent on green area ED (Table 1; Figure 4). Most of the species in the pollen transported by pollinators were native to the region (66.1%). The incidence of exotic plants in the pollen samples was significantly higher at sites with higher cover of urban green areas (Table 2).

### 4 | DISCUSSION

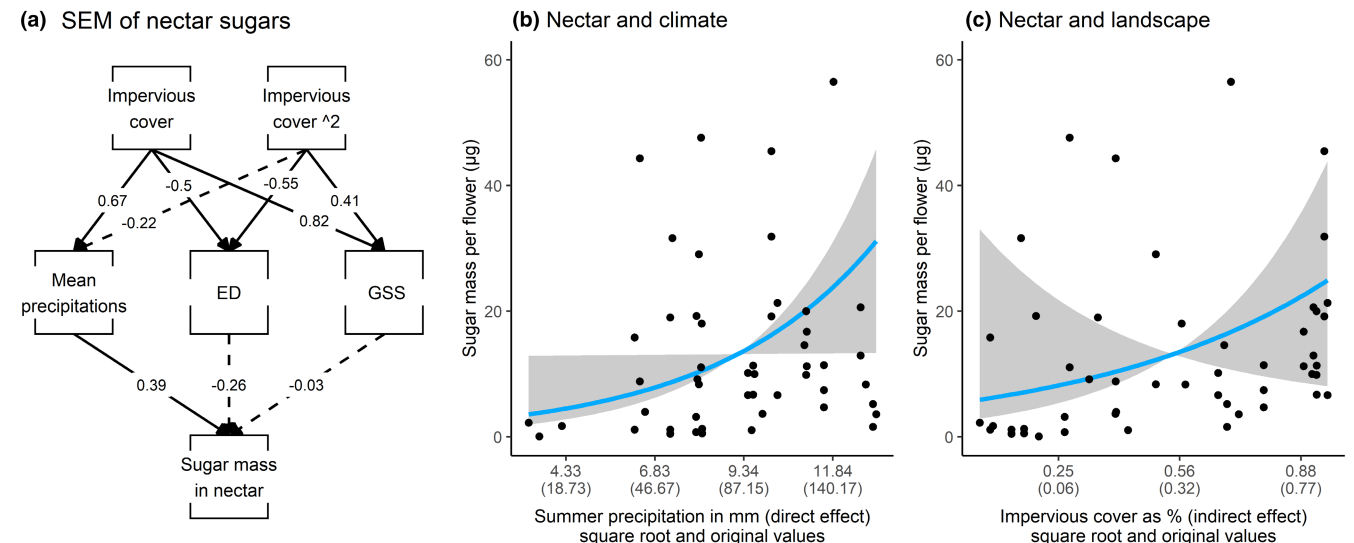
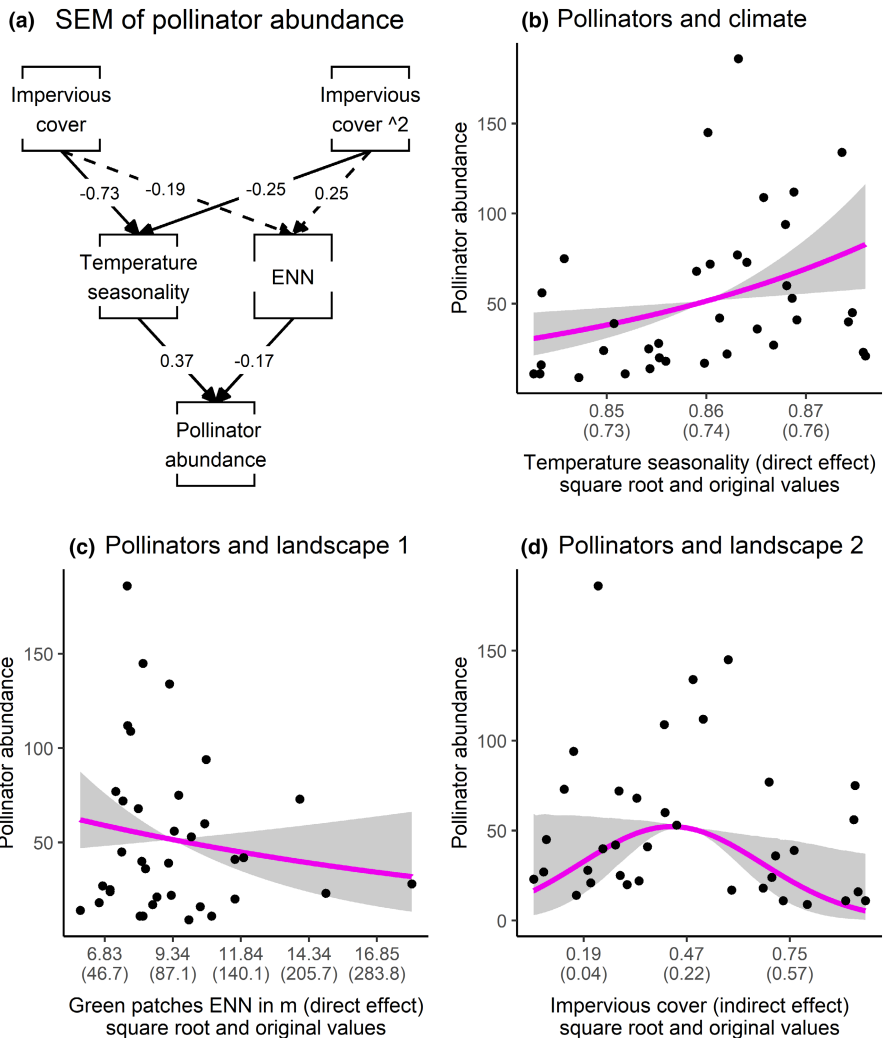
Along the gradient of urbanization, climate and landscape impacted pollinator abundance. At a landscape level, impervious cover had

**TABLE 1** Estimated direct and indirect relationships of pollinator abundances, nectar sugar mass available and pollen species richness carried by pollinators with landscape and climatic variables. Significances are from likelihood-ratio tests, or bootstrapping for structural equation models (SEMs), and they are highlighted in bold when <0.05. For each indirect variable, the coefficients are obtained as a total of the products of the coefficients being along each causal pathway. ENN indicates the Euclidean nearest neighbour distance of the green and semi-natural areas and ED is their edge density, growing season suitability index is indicated with GSS

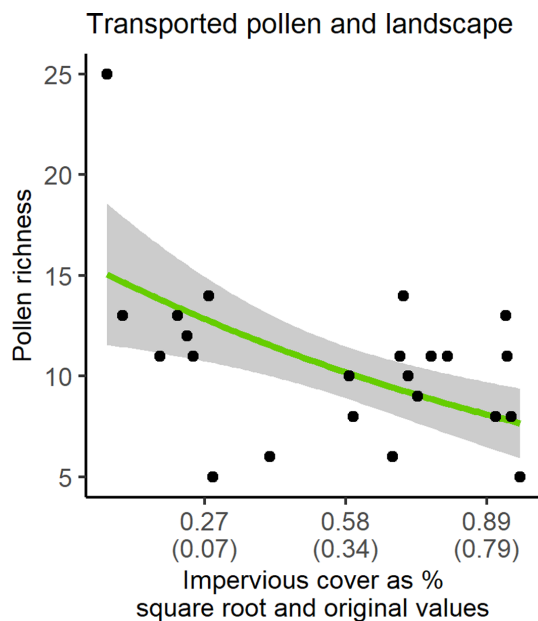
Response	Model type	Predictor	Coefficient estimate ( $B_i$ )	Significance $p$	Degree of freedoms; $\chi^2$
Pollinator Abundances	Urbanization landscape and climate (SEM)	Impervious cover (indirect)	First degree = -0.24	<b>&lt;0.05</b>	
			Second degree = -0.13	<b>&lt;0.05</b>	
		ENN (direct)	-0.17	<b>&lt;0.05</b>	
		Temperature seasonality (direct)	0.37	<b>&lt;0.05</b>	
Pollinator Abundances	Urban parks (GLM)	Recreational park size	-0.53	<b>&lt;0.001</b>	1; 81.47
Nectar sugar mass	Urbanization landscape and climate model (SEM)	Impervious cover (indirect)	First degree = -0.36	<b>&lt;0.05</b>	
			Second degree = -0.04	>0.05	
		Summer precipitation (direct)	0.39	<b>&lt;0.05</b>	
		ED (direct)	-0.26	>0.05	
		GSS (direct)	-0.03	>0.05	
Pollen richness	Urbanization landscape (GLM)	Impervious cover	-0.23	<b>&lt;0.001</b>	1; 11.29
		ED	-0.11	>0.05	1; 2.50



**FIGURE 2** Pollinator abundances along an urbanization gradient. (a) Structural equation model (SEM) with the effects on pollinator abundance, including standardized coefficients and dashed lines when non-significant. Prediction lines, grey confidence intervals and data points of pollinators with (b) temperature seasonality between spring and summer, (c) the 'ENN', mean distances of green and natural patches and (d) impervious cover as a percentage of buffer area. Predictors were square rooted, untransformed values are in parenthesis. Statistical outputs are reported in [Table 1](#)



**FIGURE 3** Sugar mass in nectars along an urbanization gradient. (a) Structural equation model (SEM) with the effects on sugar mass (available standing crop) per flower, including standardized coefficients and dashed lines when non-significant. Prediction lines, grey confidence intervals and data points of sugars with (b) mean summer precipitation and (c) impervious cover as a percentage of buffer area. Predictors were square rooted, untransformed values are in parenthesis. Statistical outputs are in [Table 1](#). ED is the edge density of green and natural patches; growing season suitability index is indicated with GSS



**FIGURE 4** Plant species richness in pollen on flower visitors along an urbanization gradient. The relationship between pollen species richness for each site and impervious cover measured as surface percentage, in circular buffers, with prediction line, grey confidence intervals and data points. This variable was square rooted, untransformed values are in parenthesis, the statistical outputs are indicated in [Table 1](#)

**TABLE 2** Relationships between the landscape composition and the origin of plant species in the pollen (i.e. 'Native', 'Crops' or 'Exotic'), estimated from the frequency of plant presence on pollinators of each site. The statistical significance  $p$  is indicated in bold when below 0.05, or it is underlined for marginally significant cases with  $p$  between 0.05 and 0.1

Land use cover	Plant origin	Fourth corner statistic $r$	$p$ -value
Green areas	Exotic	0.203	<b>0.025</b>
Green areas	Native	-0.156	0.115
Green areas	Crop	-0.036	0.696
Impervious	Exotic	0.139	0.205
Impervious	Native	-0.076	0.499
Impervious	Crop	-0.074	0.432
Semi-natural	Exotic	-0.194	<u>0.077</u>
Semi-natural	Native	0.188	<u>0.091</u>
Semi-natural	Crop	-0.025	0.77

an indirect effect mediated by temperature and isolation of green patches on pollinators. This relationship was quadratic as at low-to-medium impervious cover, pollinators were increasingly abundant with urbanization, but decreased when impervious surfaces were higher than 22%. This threshold is comparable with another study from North America where butterfly abundance decreased when more than 25% of impervious cover occurred (Kurylo et al., 2020). Thus, cities are not homogenous entities, but some parts of the urban

gradient may benefit pollinators (i.e. suburban areas) while the heavily urbanized city cores do not (Banaszak-Cibicka & Żmihorski, 2020; Buchholz & Egerer, 2020). Our study included sites covering the whole gradient of urbanization, to do so they were located in habitats with varying impervious cover and specifically in either semi-natural meadows, crop margins or urban matrix. It follows that each site could have been influenced by other local factors as different species pools and management (Sydenham et al., 2016).

Another landscape variable that directly affected pollinators was the isolation of green patches, with a negative linear relationship. This clearly indicates that the dispersion of green patches across a landscape may severely impact local pollinator abundances. This result recalls other studies showing that small- and medium-sized bees forage at close vicinities, for instance at a maximal distance of 150 m (Hofmann et al., 2020; Zurbuchen et al., 2010). However, these studies were conducted in open landscapes, but in an urban setting it may be reasonable to expect lower home ranges given the presence of vertical obstacles (Harrison & Winfree, 2015). Moreover, the size of city parks impacted pollinator abundances, as we recorded fewer pollinators with increasing park size. This result is comparable to what previously found in the United Kingdom and Germany (Baldock et al., 2019; Daniels et al., 2020). This may be due to low habitat quality (Bates et al., 2011) or a low population size diluted over a large area (Holzschuh et al., 2016). In spite of all these relationships, local conditions may play an important role in mitigating negative landscape impacts when nesting possibility and flowering resources are high (Delaney et al., 2020; Tommasi, Biella, et al., 2021).

Temperatures also varied along the artificial gradient and specifically their seasonal variation. Consequently, pollinator abundances increased linearly and directly with a rising temperature seasonality between spring and summer. This result indicates that pollinators are less abundant in sites where the climate is less variable between those seasons, and it contradicts previous ideas suggesting a link between a stable urban climate and pollinators (Baldock, 2020). This finding is corroborated by a previous physiological study showing that wild bees are affected by a high temperature where the impervious cover is high (Burdine & McCluney, 2019). Furthermore, another study showed that bees avoid warmer areas in cities (Hamblin et al., 2018) and that warming may also reduce foraging activities (Kühnel & Blüthgen, 2015). All together, these studies and our research indicate that pollinators may be sensitive to the harsh urban climate.

The landscape and climate along the urbanization gradient impacted the nectar, one of the resources pollinators usually collect. The indirect effect of impervious cover and the direct impact of the rainfall positively associated with the standing crop of sugar mass available in the nectar of locally abundant plants, with a higher sugar mass available in urbanized areas than in non-urban sites. This result could be due to either higher secretion rate by plants or due to lower consumption by pollinators in cities (Corbet, 2003). The latter possibility seems reasonable given a lower pollinator abundance in the city core that may translate into a lower consumption rate. The former seems relevant because cities are more rainy (see Figure S3),

and thus urban plants could have an increased nectar productivity as implied by the positively linear relationship between rainfall and nectar sugar mass. This result is even corroborated by controlled experiments where more nectar sugar mass is found in plants watered more (Mueller et al., 2020). That cities may host significant amounts of nectar resources is particularly relevant for pollinator feeding (Tew et al., 2021). However, nectar availability could vary with plant phenology and the nectar pattern we observed might change when different plants flower due to seasonal phenology (Hicks et al., 2016). Plant phenology might even cause seasonal gaps of nectar resources with severe implications for pollinators (Timberlake et al., 2019), and thus our results should be interpreted within the time frame of our investigation.

In addition to the described patterns in pollinator abundance and nectar, a negative linear relationship was detected between the impervious cover and the richness of plant species found in the pollen collected by pollinators. This means that the pollen from fewer plant species were transported by the pollinators during their foraging trips in highly urbanized sites. As pollen diversity on flower visitor bodies often reflects the local flowering plant diversity (Biella, Tommasi, et al., 2019; Bosch et al., 2009), this result reveals that urban parks of the study area are not offering as diverse plant resources as areas outside the city. This result could be connected to the low plant diversity usually found in highly urbanized areas (McKinney, 2008). Interestingly, we detected a higher incidence of non-native pollen in sites with a higher cover of urban green areas. This indicates that the urbanization deeply shaped the foraging patterns of pollinators, which more frequently visited exotic flowers, possibly due to higher availability of exotic flowers in cities (Staab et al., 2020). It could be a concern that pollinators of urban areas carried less pollen richness dominated by non-native species, because it may even affect plant reproduction (Cohen et al., 2020).

In this study, the urbanization gradient set important scenarios for understanding how plant and pollinators respond to habitat alteration and environmental transitions of landscape and climatic features. We detected that several landscape and climatic facets of the artificial gradient shaped pollinator abundances, pollen species richness transported by flower visitors and sugar mass available in nectar, in linear and nonlinear ways. These aspects could have effects on plant reproduction by pollen, and on pollinator survival and nutrition. Importantly this study clarifies that suburban areas, generally characterized by impervious surfaces at medium-low density and green patches of low isolation, host a high pollinator abundance. It is important to note that pollinator abundances are often correlated with species richness (Vereecken et al., 2021), and thus it could be expected to find similar patterns when considering also pollinator richness. However, highly urbanized areas provide nectars richer in available sugars, while the pollen transported was less rich of plant species and frequently with non-native plants, compared to less urbanized areas. As the gradient is human-driven, future actions could modify the responses observed in this study. In particular, managing green areas incorporating practices that are more pollinator-friendly

will likely increase pollinator abundances and their activity (Turo & Gardiner, 2019). Thus, increasing the suitability of existing and future urban landscapes for plants and pollinators is a priority, given the relevance played for ecosystem services and even for human health (Smith et al., 2015).

## ACKNOWLEDGEMENTS

The authors thank authorities for the sampling permits, and Giulia Agostinetto, Davide Magnani, Carola Miuccio, Aidana Nurtaza, Isabel Rondi and Andrea Tapparo for their technical help, and Kathryn Harrold for linguistic revision. This survey was funded by the PIGNOLETTO project (co-financed with the resources of POR FESR 2014-2020, European regional development fund with the contribution of resources from the European Union, Italy and the Lombardy Region) and by the Italian Ministry of Universities and Research (with resources from the PONRI FSE REACT-EU 2014-2020 – “Azione IV.4 - Dottorati e contratti di ricerca su tematiche dell'innovazione, Azione IV.6 - Contratti di ricerca su tematiche Green”). Open Access Funding provided by Università degli Studi di Milano-Bicocca within the CRUI-CARE Agreement.

## CONFLICT OF INTEREST

The authors have declared that no competing interests exist.

## AUTHORS' CONTRIBUTIONS

P.B., M.L. and A.G. conceived the ideas and designed methodology; P.B., N.T., E.P., L.G. collected the data; P.B. analyzed the data; P.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via figshare <https://doi.org/10.6084/m9.figshare.19410476> (Biella et al., 2022).

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**How to cite this article:** Biella, P., Tommasi, N., Guzzetti, L., Pioltelli, E., Labra, M. & Galimberti, A. (2022). City climate and landscape structure shape pollinators, nectar and transported pollen along a gradient of urbanization. *Journal of Applied Ecology*, 59, 1586–1595. <https://doi.org/10.1111/1365-2664.14168>