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## Original article

# Non-linear effects of landscape on pollination service and plant species richness in a peri-urban territory with urban and agricultural land use

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## ABSTRACT

Pollination contributes to both human food security and the reproduction of the majority of wild plant species, but pollinators are facing a rapid decline, a major cause of which is habitat conversion and degradation due to human activities. Urbanization is one of the major types of habitat conversion, but its influence on pollination has been surprisingly mixed, ranging from markedly negative to strongly positive effects. One hypothesis proposed to explain these discrepancies is that pollinator responses to urbanization are highly dependent on the non-urban control habitat, with negative effects when the controls are natural or semi-natural areas but positive when they are intensive agricultural areas. It was also proposed that the pollination response along an agricultural-to-urban gradient is non-linear, with maximum pollination observed at an intermediate level of urbanization due to increased environmental heterogeneity. To test these two hypotheses, we selected a group of 38 sites in a peri-urban area near Paris, France, using a semi-stratified sampling strategy that ensured that all three of the urban, agricultural and semi-natural gradients were maximized. We then estimated pollination using two approaches: we evaluated the pollination success of *Lotus corniculatus*, a strictly entomogamous self-sterile plant species pollinated mainly by bees, and we measured the species richness of entomogamous and non-entomogamous plants, the difference in their response being expected to relate to the pollination service provided by the overall pollinator community. We found that in our study area, pollination success of *L. corniculatus* responds positively to the agricultural to urban gradient but not to the semi-natural to urban gradient. The diversity of both entomogamous and non-entomogamous plants is highest at sites surrounded by intermediate proportions of urban and agricultural areas. In addition, high proportions of urban areas have a negative effect on the diversity of non-entomogamous but not entomogamous plant species, suggesting that pollinators are able to partially buffer entomogamous plant species against the negative effect of urban development. Our results show the importance of urban areas in pollination conservation plans and demonstrate that the interaction between different anthropogenic land-use is an important factor for understanding pollination.

## 1. Introduction

Pollination's importance to both humanity and biodiversity has been increasingly demonstrated over the past few decades. First of all, more than 85 % of all Angiosperms currently depend, at least partially, on pollinators to reproduce (Ollerton et al., 2011). Additionally, pollinators provide a crucial ecosystem service by increasing or stabilizing the yield of approximately 75 % of crop-plant species globally and about 35 % of global crop production depend on them (Klein et al., 2007). Pollination service is currently under threat across the globe due to

human activity (Goulson et al., 2015) with serious consequences for both wild plant species (Fontaine et al., 2006) and agricultural productivity (Garibaldi et al., 2013; Reilly et al., 2020; Deguines et al., 2014). One of the major driver of pollinator declines is the conversion and degradation of habitats related to human activities and in particular urbanization (Potts et al., 2010).

During urbanization, beneficial habitats are replaced with impervious anthropogenic surfaces, floral resources change in favor of more exotic plants (Walker et al., 2009; Fukase and Simons, 2016) and their flowering peaks happen earlier in the season due to urban heat (Fisogni

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et al., 2020), high amounts of pesticide are frequently used in private gardens (Muratet and Fontaine, 2015) and connectivity between urban green areas (mostly parks and private gardens, Serret et al., 2014) and with the semi-natural areas surrounding the city decreases (Pellissier et al., 2012). All these factors tend to decrease pollination levels and urbanization is therefore considered by many authors to be highly detrimental to pollinators (e.g. Cardoso and Gonçalves et al., 2018; Lagucki et al., 2017). However, other researchers found very different results and suggest that on the contrary, cities can act as refuge and be an opportunity for conserving pollinators (e.g. Hall et al. 2015; Baldock, 2020; Theodorou et al., 2020). In their recent review of the literature to identify the drivers of urban pollinator populations and pollination, Wenzel et al. (2020) hypothesize that the results of studies on the effect of urbanization are so contrasted because of three main factors.

First, they argue that the responses of pollinators to urbanization are highly dependent on the naturalness of the non-urban control habitat (Wenzel et al., 2020). The effects of urbanization are usually found to be negative when urban areas are compared to natural or semi-natural areas (e.g. Hostetler and McIntyre, 2001; Verboven et al., 2014). On the opposite, modern conventional agriculture usually puts great pressure on pollination, with large open monoculture fields, reduced floral resources throughout the season, regular ploughing that reduces nesting opportunities, and pesticides that reduce pollinator survival and impact their behavior (Garibaldi et al., 2013; Varah et al., 2020). When urban areas are compared to conventional, intensive agricultural areas, the effect of urbanization may thus be positive for pollinators (e.g. Baldock et al., 2015; Theodorou et al., 2020). Interestingly, it has furthermore been hypothesized that the effect of intermediate levels of urbanization could be positive (Banaszak-Cibicka et al., 2018; Wenzel et al., 2020), i. e. that areas with intermediate levels of urban land use could be more favorable than areas with a majority of either urban or agricultural land-use. The hypothesis is that an intermediate level of urbanization could create land mosaics increasing environmental heterogeneity, which would increase niche diversity and thus insect pollinator diversity (Zerbe et al., 2003).

Second, the effects of urbanization on pollinators and pollination is also dependent on the level of urbanization, with positive response of pollinators in the low density urban areas characterized by a high proportion of urban green spaces, whereas negative response were observed for high density urbanization with high proportion of impervious areas (e.g. Theodorou et al., 2016; Lagucki et al., 2017; Martins et al., 2017). Noteworthy, in an already densely urbanized country like France, urbanization currently takes place mainly in the form of peri-urbanization (Vallès, 2018). This "urban sprawl" that characterize peri-urban territories leads to low-density residential urbanization that generally takes place around pre-existing urban centers on former agricultural land. Interestingly, it seems possible that this process of peri-urbanization, often considered negative in geography or ecology but which replaces agricultural areas with low-density urban areas, may have relatively positive results for pollinators. Finally, another factor explaining the varied results of urban pollinator studies is the highly contrasting responses to urbanization gradients among different pollinator taxa, with for example Diptera and Lepidoptera showing lower species richness in urban areas, whereas the reverse is true for Hymenoptera and especially bees (Reviewed in Senapati et al., 2017; Hall et al., 2017; Levé et al., 2019; Baldock, 2020; Theodorou et al., 2020).

While our understanding of the effect of urbanization on pollinators and pollination has progressed very significantly in recent years, several issues remain to be clarified. First, to the best of our knowledge, comparisons between urban and agricultural areas on the one hand, and between urban and semi-natural areas on the other, have only been carried out separately until now. It would therefore be very interesting to study the response of pollinators to both urban to agricultural and urban to semi-natural gradients in an integrative way, within the same study area. Second, while it has been hypothesized that the response of pollinators to urbanization might be non-linear, and most positive for an

intermediate level of urbanization associated with greater environmental heterogeneity, we believe this has not been tested yet.

In order to elucidate these two questions, we chose as our study area a peri-urban territory located near Paris, France, which was historically composed of agricultural land but which has undergone strong peri-urbanization in recent years. We then developed an innovative sampling design to select a set of 38 sampling points with maximized variance in urban, agricultural, and semi-natural land use. Because different orders of insects respond very differently to urbanization, we chose to measure pollination holistically, using two complementary measures. First, we measured the fruiting rate of birdsfoot trefoil, *Lotus corniculatus* L., a strictly entomogamous and self-sterile plant species that is primarily pollinated by bees (Ollerton et al., 1998; Zaninotto et al., 2021). This first measure should allow us to estimate the pollination service provided by bees. Next, we studied the diversity of entomogamous wild plant species and compared it to the diversity of wild plants that do not rely on insect pollination. The difference in response of these two groups of plants is expected to be related to the pollination service provided by the overall pollinator community. We then combined principal component analysis of the land use categories and generalized linear models to test the following two hypotheses in our study area: (1) while the agricultural-urban gradient will benefit pollination, the semi-natural-urban gradient will have a negative effect; (2) the pollination response along the agricultural-urban gradient will be non-linear, with maximum pollination observed at an intermediate level of urbanization due to increased environmental heterogeneity.

## 2. Materials & methods

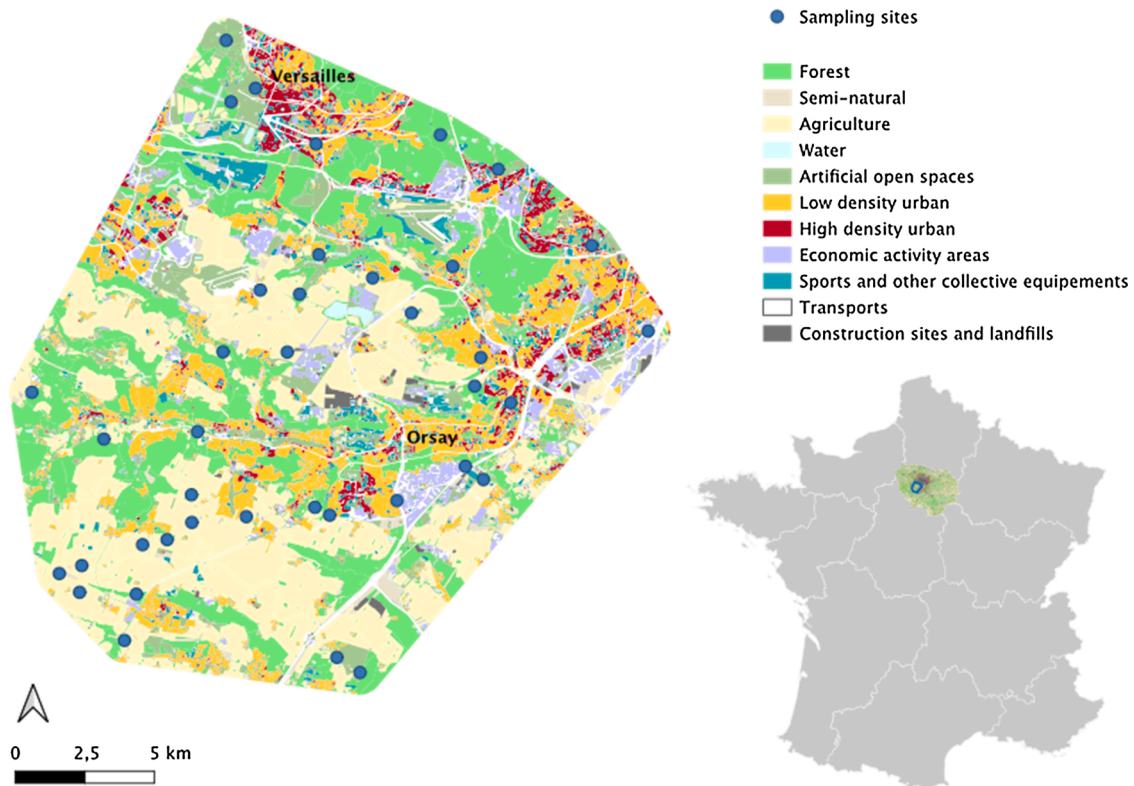
### 2.1. Study area

The study area is centered on the Saclay and Limours uplands, located in the junction zone between the Parisian agglomeration and the large plains that surround it (Fig. 1). Until very recently, the territory had a mainly agricultural vocation but the ongoing development of the Paris Saclay University scientific and technological pole considerably increases the urban hold on the territory. At the same time, a natural, agricultural and forest protection zone of more than 4,000 ha has been created, perpetuating the agricultural use of the land on the plateau. The study area thus presents major challenges in terms of the coexistence of urban and agricultural areas and biodiversity in a context of urbanization.

### 2.2. Selection of sampling sites

The sampling locations in this study were selected in 2016 using a semi-stratified sampling that maximized the triple gradient of urban, agricultural and semi-natural areas among our sampling sites (see a detailed description in Supplementary Material). We used the 2012 edition of the MOS (Mode d'Occupation des Sols) cartographic database for general land use in Ile-de-France produced by the IAU (Institut d'Aménagement et d'Urbanisme de la Région d'Ile-de-France). The MOS covers the Ile-de-France region and is made from regional digital orthophotographs of 15 cm resolution acquired from IGN, completed by Pleiades images of 50 cm resolution. For the selection of sampling sites, we used the MOS version with 11 land-use categories when generating initial random points and five categories when assigning landscape context for semi-stratified sampling (Table S1).

First, to standardize the local context, we generated 1000 random points (Fig. S1) located within open habitats characterized by a mostly herbaceous vegetation (MOS categories 'Semi-natural' and 'Artificial Open Spaces'), which are the most favorable for plants and pollinators in the study area. We then extracted the relative surface of each of the five MOS categories (Forest, Agriculture, Water, Artificial Open Spaces and Urban) in a 300 m buffers around the random points. This buffer size was chosen because it seemed a good compromise between the spatial



**Fig. 1.** Location of the study area in France and land use in Ile-de-France. Location of the sampling sites, represented by the blue dots, and land use in the study area (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

scales that are relevant for different taxonomic groups of pollinators (Desaegher et al., 2018; Theodorou et al., 2020). The five categories information was simplified into our three categories of interest: Agriculture, Urban (combining the MOS categories ‘Urban’ and ‘Artificial Open Spaces’), and Other (combining the MOS categories ‘Forest and ‘Water’) and was used to assess the landscape context of the 1000 random points (Fig. S1). We then used a semi-stratified sampling procedure to select a 40 points subsample maximizing the triple gradient of urban, agricultural, and semi-natural land use (Fig. S2). We used a geographic information system (QGIS) to analyze land use data. The stratified sampling procedure was implemented with R. We kept only 38 (Fig. 1) of the initial 40 sites because recent land-use changes had rendered two of them impervious. These 38 locations are hereafter our sampling sites.

### 2.3. Landscape analysis around the sites

For the purposes of our analysis, we have re-examined the landscape context in a 300 m buffer around the 38 sampling points (Fig. S3) using the 2017 edition of the MOS, which is the most recent available. We have chosen to base our analysis on the MOS version with 47 categories, which we have grouped into seven major items as described in Table 1, to be the most relevant to pollinator ecology. For this new classification, we also used independent data sources regarding the areas classified in the MOS as being prairies or parks, to take into account that some of these areas have very low levels of maintenance, which makes them more comparable to semi-natural areas. We used the land use cartography produced by the consortium Theia (2017), as well as the inventories of remarkable vegetation produced by the Conservatoires Botaniques d’Île de France. If the land-use assessment was conflictual between sources, we re-assessed the land-use using aerial Google Earth photographs and field-site visits. This led to the reclassification of some prairies and urban green areas polygons to the semi-natural category in our seven categories classification (Table 1). In summary, semi-natural

**Table 1**

Land use categories considered when assessing the landscape context in a 300 m buffer around the sampling sites.

Land Use Category	Description
Forest	Areas classified as forest by the MOS 2017
Agriculture	Areas classified as cultivated by the MOS 2017, including cultivated prairies.
Semi-natural	Areas classified as semi-natural by the MOS 2017, as well as the prairies and UGA (see category UGA below) that are hosting remarkable plant assemblages or identified as biodiversity reservoirs at the regional level according to the Conservatoire Botanique.
Water	Areas classified as water by the MOS 2017
UGA (Urban Green Areas)	Areas classified as UGA by the MOS 2017, with the exception of areas deemed as of high conservation interest at the regional scale (see category semi-natural)
Low density urban	Areas classified as low density urban by the MOS 2017
High density urban	Areas classified as high density urban and impervious by the MOS 2017

areas in our classification include areas composed of herbaceous vegetation (and possibly isolated shrubs or trees) which are also characterized by a low level of maintenance e.g., annual mowing, extensive grazing, or brush clearing, but no tilling or intensive use of fertilizers or herbicides (Norderhaug and Johansen, 2011; Peeters et al., 2014). This land use category is expected to be the most favorable for pollinators in our study territory.

The landscape context within a 300 m buffer were used to quantify the compositional heterogeneity at each sampling point, using the Shannon–Wiener index ( $H_{SW} = -\sum p_i \cdot \ln p_i$ ) and the Gini–Simpson index ( $H_{GS} = 1 - \sum p_i^2$ ) where  $p_i$  is the proportion of each of the seven land use categories.

We estimated the correlations between the relative surface of the 7 land-use categories using the Spearman correlation. We found that some categories were strongly correlated and we therefore performed a



Principal Component Analysis (PCA) to reduce the landscape metrics to their relevant dimensions. This analysis was used to identify two landscapes gradients, from agricultural to urban areas (PCA axis 1) and from urban to semi-natural areas (PCA axis 2), which we used as our explanatory variables in subsequent analyses. Note that these two explanatory variables are quantitative and not qualitative: sites are characterized by their position on these two gradients, but not as being entirely urban, agricultural or semi-natural.

#### 2.4. Vascular plants species richness and pollination mode

For each of the 38 sampling sites, we estimated the number of vascular plant species twice a year in June and July, in 2018 and 2019. We surveyed a 10 m<sup>2</sup> plot at each sampling site, which correspond to the area adopted by other programs, e.g., in France, Vigie-flore (Martin et al., 2019). This area is relatively educed compared to the area needed to fully characterize plant communities but the accumulation curves of preliminary assessments in 2017 indicated an overall good representation of vascular plants present at each site. Plants were determined to the maximal taxonomic resolution possible on-site. We standardized species taxonomic nomenclature with the taxonomical reference TAXREF V5.0 (<https://inpn.mnhn.fr/programme/referentiel-taxonomique-taxref>), which is the one used by Cettia, the Ile-de-France naturalist database where we contributed our data (<https://cettia-idf.fr/>).

We collected information on the mode of pollination of each species from several databases: the BiolFlor database on biological and ecological traits of the German flora (Klotz et al., 2002), the LEDA database of life-history traits of the Northwest European flora (Kleyer et al., 2008), the TRY global database of plant traits (Kattge et al., 2011). Pollination mode was coded as a binary trait: plant species were considered to be insect-pollinated (hereafter entomogamous species) or pollinated through other vectors (mainly wind-pollinated plants, hereafter non-entomogamous species). This allowed us to obtain four estimates, two in 2018 and two in 2019, of the number of entomogamous and non-entomogamous species for each of the 38 sampling sites.

#### 2.5. Pollination service based on the fructification rates of *L. corniculatus*

We assessed the pollination service on *L. corniculatus* following the methodology of Pellissier et al. (2012). In brief, we left pots of greenhouse-grown *L. corniculatus* for a 15-day period at each of our study sites. The pots were then returned to the greenhouse and the number of fruits per inflorescence was counted for each inflorescence of each plant. Because in this species flowers must be pollinated to develop into fruits, the number of fruits per inflorescence is an estimate of the efficiency of the pollination service for *L. corniculatus*.

Measurements were performed in 2019 for a subset of 25 of the 38 sites previously described that were close enough to road access that it was relatively easy to set up plant pots and then come and water the plants. The birdsfoot trefoil, *L. corniculatus* (L.) (Fabaceae), is an herbaceous perennial plant native to grasslands in temperate Eurasia and North Africa, which is also widely used as a crop in grasslands and intercropping. *L. corniculatus* is a self-incompatible (Miri and Bubar, 1966; Seavey and Bawa, 1986), strictly entomogamous species, mainly pollinated by bees, especially bumblebees and solitary bees of the genus *Megachile* (Ollerton and Lack, 1998; Zaninotto et al., 2021). Because *L. corniculatus* is frequently used as a crop, numerous cultivars are available. We chose the ‘Leo’ cultivar because both its number of flowers per inflorescence and its number of seeds per fruit are very homogeneous (Pellissier et al., 2012; Chateil and Porcher, 2015), allowing us to estimate pollination success by counting the numbers of fruits produced per inflorescence.

We cultivated the plants in an insect-proof greenhouse with climate control (22 °C day / 18 °C night, lighting for 16 h per day). We sowed the seeds (provider “Semences du Puy”) between the end of January and mid-February 2019 in pots. Water retention granules (provider

“STOCKOSORB”) were added to the breeding ground in order to reduce the frequency of watering in the experimental sites. During the growth in the insect-proof greenhouse, the plants were regularly examined to check for the presence of fruits and we observed that all flowers wilted without producing any fruit, confirming the strict entomophily of the plants. We placed eight pots of plants per site on each of the 25 selected site, for a 15-day period between 27th May and 12th June 2019. Plants were returned to the greenhouse after the 15-day period and let for a period of 7–10 days to give the fruit time to develop. Then, within each pot, we counted the fructification rate, i.e. the number of fruits per inflorescence (including zero fruit) for each inflorescence, as well as the number of inflorescences per pot.

#### 2.6. Data analyses

All analyses were performed using R software version 3.5.1 (R Core Team, 2020). The numbers of entomogamous and non entomogamous plant species per sampling site were modelled using a GLMM with a Poisson error structure and a log link function, with sampling site and year as random effects, using the lme4 R package (lmer function). Similarly, the number of *L. corniculatus* fruits per inflorescence was modelled using a GLMM with a Poisson error structure and a log link-function. Site and pot were taken as random effects, with pot nested in site. The fructification data distribution was skewed towards zero, which we took into account by using a zero-inflation model from the glmmTMB R package (function glmmTMB). The tabmodel function from the DHARMa R package was used to present the results of the models. For the three models, we used the first two axes from the PCA of site landscape context (see Results below) as explanatory variables. Because we wanted to test the hypothesis that areas with intermediate levels of urban land use could be more favorable than areas with a majority of either urban or agricultural land-use, we added in the three models a quadratic term for the first PCA axis, which corresponds to the gradient from agricultural to urban lands (see Results below).

### 3. Results

#### 3.1. The triple gradient of “rural /semi-natural /urban” is well represented in the two main axes of the PCA analysis of the landscape context of the sampling sites

Performing a PCA on the landscape context in a 300 m buffer around the 38 sampling sites showed us that the two first axes represented both a relatively high proportion of the variance (28.7 % and 25.3 %, respectively), as well as relevant ecological dimensions (Fig. 2). The first axis identifies a gradient between agricultural land use and the three categories associated with the urban context: urban green areas and

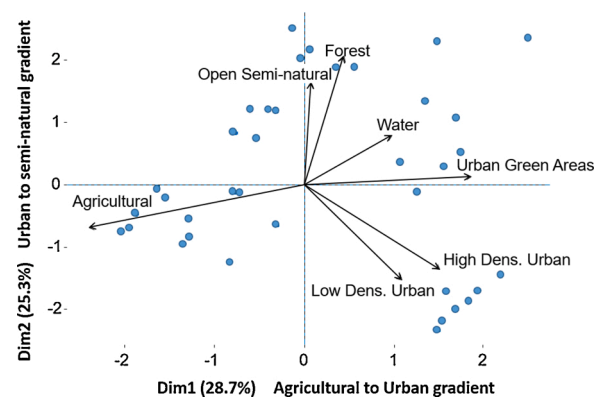


Fig. 2. PCA Biplot of landscape descriptors (labelled arrows) and sampling sites (blue dots) For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.

both low and high density urbanization. It therefore represents a gradient from agricultural to urban land use. The second axis is negatively correlated with both low and high density urbanization areas, and positively correlated with both forest and open semi-natural areas, and thus represents a gradient from urban to semi-natural areas. Among the 38 sampling sites, there is a high correlation between the proportions of forest and open semi-natural areas on the one hand, and between the proportions of low and high density urban areas on the other. These correlations are present and even higher among the initial 1000 random points within the study area that were used to select the 38 sampling sites (Fig. S1), and are therefore representative of the territory and not specific to our sampling sites.

Contrary to our expectations that intermediate levels of urban land use would be associated with increasing environmental heterogeneity, we found that our two estimators of landscape compositional heterogeneity, the Shannon–Wiener and the Gini–Simpson indices, were linearly positively correlated with the agricultural to urban gradient (Spearman’s rank correlation;  $S = 4474.7$ ,  $p$ -value = 0.0003). There were no relationships between the urban to semi-natural gradient and the two indices.

### 3.2. Number of entomogamous plants species

The number of entomogamous plants species per site varied from one to 23, averaging at 10.18 species per site. We modelled this number of entomogamous plant species per site with a GLMM, using the two first axes from the PCA as well as the observation date (June or July) as explanatory variables and the year and site ID as random effects. We found that the agricultural to urban axis has a quadratic, negative effect on the number of entomogamous plants (Table 2): while very agricultural landscapes do not have a different number of entomogamous plants from more urbanized landscapes, landscapes with an intermediate proportion of urban areas present a significantly higher number of entomogamous plants (Fig. 3). We also observed a negative effect of the date of the observation on the number of entomogamous plants, meaning that we observed more species in our first observations, in June, than in our second, in July.

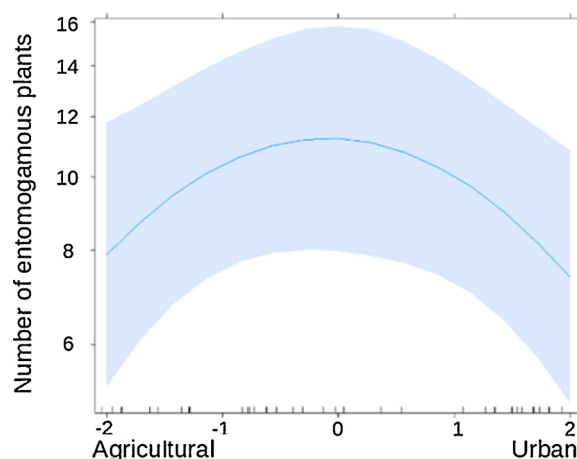
### 3.3. Number of non entomogamous plants species

The number of non entomogamous plants species per site varied from one to 17, averaging 6.58. We modelled the number of non entomogamous plant species on each site as previously with a GLMM, using the two first axes from the PCA as well as the observation date (June or July) as explanatory variables and the year and site ID as random effects. We observed both a negative linear and a quadratic effect of the agricultural to urban gradient on the number of non entomogamous plants; we also observed a positive effect of the urban to semi-natural gradient and a negative effect of the date (Table 3; Fig. 4). Sites with a high proportion of urban areas have significantly lower non-entomogamous species richness than all other site types: those with either a high proportion of agricultural or semi-natural areas, and those with an

**Table 2**

Result of the GLMM performed on the number of entomogamous plant species. The model used a Poisson error structure with a log link function. Data include 151 observations, made on 38 sites over two years.

Random effects	Variance		Std. dev.	
Site	0.130		0.361	
Year	0.036		0.191	
Fixed effects	Estimate	Std. error	Z value	Pz(> z )
Agricultural to urban gradient	-0.017	0.046	-0.370	0.711
Urban to semi-natural gradient	-0.105	0.056	-1.842	0.065
Agricultural to urban gradient <sup>2</sup>	-0.097	0.046	-2.081	0.037 *
Date	-0.004	0.001	-2.142	0.032 *



**Fig. 3.** Relationship between the agricultural to urban axis of the PCA and the number of entomogamous plant species. Predictions obtained with the R package ‘effects’.

**Table 3**

Results of the GLMM performed on the number of non entomogamous plant species. The model used a Poisson error structure with a log link function. Data include 151 observations made on 38 sites over two years.

Random effects	Variance		Std. dev.	
Site	0.028		0.170	
Year	0.031		0.176	
Fixed effects	Estimate	Std. error	Z value	Pr(> z )
Agricultural to urban gradient	-0.102	0.031	-3.209	0.001 **
Urban to semi-natural gradient	0.097	0.038	2.513	0.011 *
Agricultural to urban gradient <sup>2</sup>	-0.060	0.030	-1.981	0.047 *
Date	-0.006	0.002	-2.921	0.003 **

intermediate proportion of agricultural and urban areas.

### 3.4. The pollination service on *Lotus corniculatus*

For the birdsfoot trefoil data, the fructification rate, i.e. the number of fruits per inflorescence, ranged from zero to eight fruits, with an average of 1.53. We modelled this number of fruits per inflorescence with a GLMM, using the two first axes from the PCA as explanatory variables and the pot and sampling site as random effects. The distribution was skewed towards zero, which we accounted for using a zero-inflated model. We found that a higher proportion of agricultural areas negatively affects the fructification rate, whereas a higher proportion of urban areas has a positive effect (Table 4; Fig. 5). We did not detect a significant nonlinear effect of the agricultural to urban gradient but, because we were only able to use 25 sites for the *L. corniculatus* experiment, statistical power may be lacking to detect such an effect. There was no significant effect of the urban to semi-natural gradient.

## 4. Discussion

### 4.1. Urban to semi-natural gradient: pollination service could reduce the impact of urbanization on entomogamous species richness

First, we observed that landscape variation along the urban to semi-natural gradient, ranging from a high proportion of impervious and residential areas to a predominance of forest and open semi-natural habitats, did not appear to affect the number of entomogamous plant species or the fruiting rate of bee-pollinated *L. corniculatus*. Because semi-natural areas are generally more favorable to pollinators than agricultural or urbanized areas (Wenzel et al., 2020), not detecting an

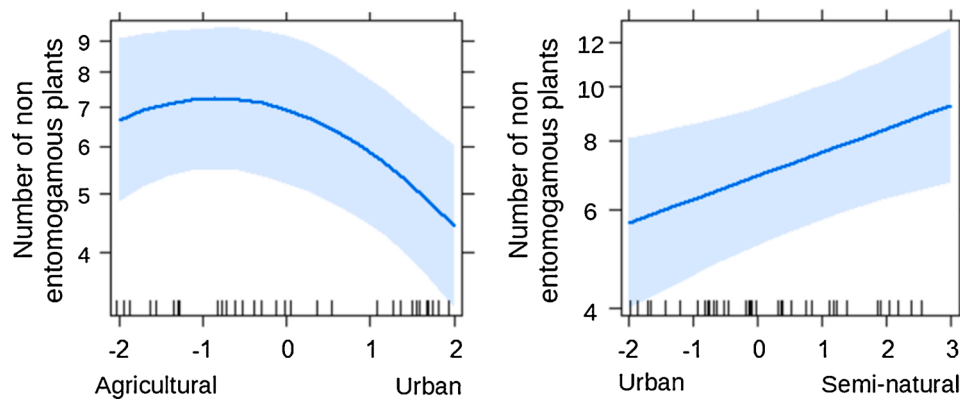


Fig. 4. Relationships between the agricultural to urban axis and the urban to semi-natural axis of the PCA and the number of non entomogamous plant species. Predictions obtained with the R package ‘effects’.

Table 4

Results of the GLMM performed on the number of fruits of the bird’s-foot trefoil. The model used a Poisson error distribution with a log link function and a zero-inflated model. The data include 1750 observations made on 25 sites (Site) in 168 pots (Pot:Site).

Random effects	Variance	Std. dev.		
Site	0.150	0.387		
Pot:Site	0.122	0.350		
Fixed effects	Estimate	Std. error	Z value	Pz(> z )
Agricultural to urban gradient	0.131	0.062	2.103	0.035 *
Urban to semi-natural gradient	-0.103	0.117	-0.879	0.379
Agricultural to urban gradient <sup>2</sup>	-0.073	0.082	-0.892	0.372
Zero-inflated model	Estimate	Std. error	Z value	Pr(> z )
Intercept	-1.033	0.087	-11.87	<2e-16 ***

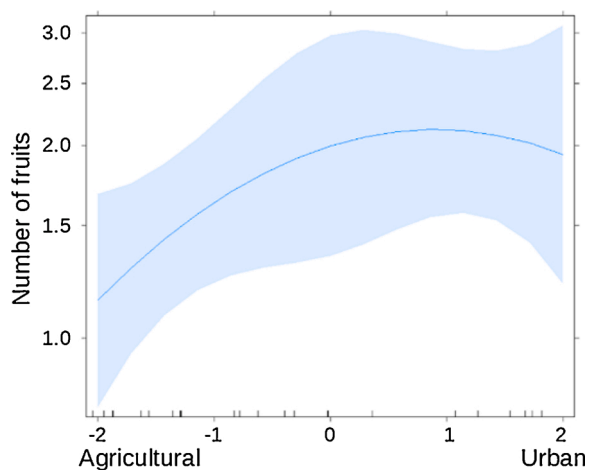


Fig. 5. Relationship between the agricultural to urban axis of the PCA and the number of fruits per inflorescence of *L. corniculatus*. Predictions obtained with the R package ‘effects’.

effect of this gradient on entomogamous plant diversity and the fruiting rate of *L. corniculatus* seems unexpected. However, this lack of impact can probably at least be partially explained by the fact that in our study area, sites with high values on the semi-natural gradient have either high proportions of semi-natural open environments or high proportions of forests (or both), but these two types of land cover do not necessarily have the same ecological consequences for pollination. Indeed, whereas numerous studies show an increase in pollinator diversity with increasing semi-natural habitats in general (including forests, managed

permanent grasslands and other open habitats; reviewed in Senapathi et al., 2017), the specific effect of forest cover seems much more contrasted. Within intensively managed agricultural landscapes, the presence of small forest patches leads to an increase in pollinator diversity (Farwig et al., 2009). However, in a more varied landscape, bee abundance and diversity have been shown to decrease with increasing forest cover in the surrounding landscape (Willem et al., 2018). Similarly, sites with low values on the semi-natural gradient have either high proportion of low density, residential, urban areas, or high proportions of high density urban and impervious areas (or both). The two different types of urban areas have also been shown to have contrasted effects for pollinators. Wenzel et al. (2020) showed that pollinators often showed positive responses to urban sprawl, i.e. moderate levels of urbanization with many green spaces, but showed decline in areas with high levels of urban densification. These contrasted effects of the land cover represented on both ends of the urban to semi-natural gradient could explain the lack of relationship that we observed between this axis and *L. corniculatus* pollination as well as entomogamous plant diversity. The association between the different categories that make up the urban to semi-natural PCA axis is observed at the scale of the entire study area and is not unique to the 38 sites studied (See Results). This seems to mean that, in this peri-urban study area, semi-natural areas are no more favorable for the pollination of *L. corniculatus* than urban areas. Note however that this result might not generalize to the pollination service to all entomogamous plant species. *L. corniculatus* is mainly pollinated by bees, especially bumblebees and solitary bees of the genus *Megachile* (Ollerton and Lack, 1998; Zaninotto et al., 2021) and it has been previously shown that Hymenoptera and especially bees are little affected by urbanization compared to other pollinator taxa like Diptera and Lepidoptera (Reviewed in Senapathi et al., 2017; Hall et al., 2017; Levé et al., 2019; Baldock, 2020; Theodorou et al., 2020). Thus, it is possible that if we had estimated the pollination service on several plant species, and particularly on species pollinated primarily by groups other than bees, a negative effect of landscape variation along the semi-natural to urban gradient would have been observed.

Second, we found that, in contrast, non-entomogamous plants have significantly lower diversity in sites with low values along the urban to semi-natural gradient, whereas entomogamous plant species are not affected. Because the large majority of these non-entomogamous plant species are wind-pollinated, this could suggest that pollination service is more efficient than wind pollination in urbanized areas, i.e. that pollinators are able to partially buffer entomogamous plant species against the negative effect of urban development.

#### 4.2. Agricultural to urban gradient: Plant species richness is maximal for intermediate proportions of agricultural and urban areas

To test our hypothesis that pollination response along the



agricultural to urban gradient will be non-linear with maximum pollination observed at an intermediate level of urbanization, we used a quadratic term for the agricultural to urban gradient in the models investigating plant species richness and fruiting of *L. corniculatus*. We found that sites with a high proportion of urban areas and a low proportion of agricultural areas have significantly higher fruiting rate of *L. corniculatus*, a species mainly pollinated by bees, especially bumblebees and solitary bees of the genus *Megachile* (Ollerton and Lack, 1998; Zaninotto et al., 2021) and no significant quadratic effect was detected. This supports the theory, established by previous studies that urban areas can be hotspots for bees and pollination compared to intensive agricultural land, (Baldock, 2020; Hall et al., 2017; Theodorou et al., 2020; Levé et al., 2019). This result highlights the need to consider urban spaces when thinking of conservation of the pollination service.

On the other hand, we found a significant negative quadratic effect of the agricultural to urban gradient on both the number of entomogamous and non-entomogamous species, meaning that in our study area, plant diversities are maximal for sites with intermediate proportions of agricultural and urban areas. We did expect positive effects of this intermediate level of urbanization because of increased environmental heterogeneity, but we observed that in our study area, landscape heterogeneity is higher with high and not intermediate proportions of urban areas. The observed pattern must therefore have another explanation. In addition to the nonlinear effect, we observed that for non-entomogamous plants only, sites with a high proportion of agricultural areas had significantly more species than sites with a high proportion of urban areas. We thus observed both similarities and differences between the answers of entomogamous and non entomogamous species to this agricultural to urban gradient. Both groups of plants showed low levels of species richness in sites with high proportion of urban areas where bee pollination service is presumably high according both to our *L. corniculatus* results and the literature (Wenzel et al., 2020; Baldock, 2020). This suggests that this low plant species richness is probably not caused by a limited pollination service but by a factor that can influence both entomogamous and non entomogamous plant species. A possibility would be the level of management, in particular the frequency of mowing and the level of herbicides in the soil. The frequency of mowing has been showed to be a major factor reducing plant diversity in urban green spaces (Sehrt et al., 2020; Chollet et al., 2018; Aronson et al., 2017). Though we were not able to measure this frequency among our study sites, we expect it to be higher in urban green areas than in more rural sites. Regarding herbicides, their use in green spaces open to the public as well as on the roadway has been banned in France since 2017 for all municipalities. But as herbicides have traditionally been widely used in public and private urban green spaces (Aronson et al., 2017) and their persistence in the soil is frequently high (e.g. Curran, 2016), they could still have a negative influence on local plant diversity. In contrast, in our sites with high proportion of agricultural land, bee pollination service and entomogamous plant species richness are both low, whereas non entomogamous plant species richness remain high. These contrasted effects suggest that the lower entomogamous diversity in these agricultural sites may be due to a limited pollination service.

In conclusion, our hypothesis that urban and agricultural spaces could interact and create non-linear effects on pollination service and plant species richness seems verified for plant only, although it remains possible that we did not detect an existing nonlinear effect for *L. corniculatus* pollination service due to a lack of statistical power. The fact that this non-linear effect of the agricultural to urban is observed for both entomogamous and non-entomogamous plant species richness suggests, however, that it is not caused by a higher pollination service in sites with an intermediate proportion of agricultural and urban areas, but more likely by factors of a different nature for agricultural and urban environments, perhaps a higher intensity of management in urban areas and a reduced pollination service in agricultural areas.

## Declaration of Competing Interest

The authors report no declarations of interest.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ufug.2021.127454>.

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