



Original article

Pollination success of *Lotus corniculatus* (L.) in an urban context

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ABSTRACT

Most anthropogenic activities are known to have deleterious effects on pollinator communities. However, little is known about the influence of urbanization on pollination ecosystem services.

Here, we assessed the pollination service on *Lotus corniculatus* (L.), a self-sterile, strictly entogamous Fabaceae commonly observed in urban and suburban areas. We assessed the pollination success of artificial *Lotus corniculatus* populations at three levels: at large scale, along an urbanization gradient; at intermediate scale, based on landscape fragmentation within a 250 m radius and at local scale based on floral resource abundance and local habitat type.

The main findings were that the pollination success, when assessed with the number of fruit produced per inflorescence, was lower in urban areas than in suburban ones, and was negatively affected by the number of impervious spaces in the neighborhood. The relationship between the number of fruits and the distance to the nearest impervious space was either positive or negative, depending on the gray/green ratio (low vs. high). Finally, on a local scale, floral resource abundance had a negative effect on pollination success when *L. corniculatus* populations were located in paved courtyards, and a positive one when they were located in parks.

Pollination success seems to be explained by two intertwined gradients: landscape fragmentation estimated by the number of impervious spaces in a 250 m radius around *L. corniculatus* populations, and the behavior of bumblebees toward birdsfoot trefoil and floral displays, which appears to differ depending on whether a neighborhood is densely or sparsely urbanized. An abundance of attracting floral resources seems to enhance pollination success for *L. corniculatus* if it is not too isolated from other green spaces.

These results have important implications for the sustainability of pollination success in towns by identifying local and landscape factors that influence reproductive success of a common plant.

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1. Introduction

Urban green spaces are believed to make an important contribution to sustainable development within cities. However, they are often small, isolated, strictly managed and embedded in a hostile urban matrix (Bastin and Thomas, 1999). They are therefore often poorly suitable for maintaining plant and animal populations (Farhig, 2003). Moreover, highly fragmented landscapes found in cities negatively affect plant communities (Bascompte et al., 2002) and animal species living in interaction with them (Fischer and Lindenmayer, 2007), especially pollinator communities (Fontaine et al., 2006).

Ecosystem services play a key role in improving the quality of life in towns and cities. One crucial service is pollination, which is

needed not only to sustain urban ecosystems (Bolund & Hunhammar, 1999), but also to allow vegetable and ornamental plant production. For almost 80% of flowering plant species, this service is dependent on animals (Buchmann and Nabhan, 1996; Ollerton et al., 2011). In urban areas, pollinators can be affected by fragmentation in different ways: a lack of resources in each space, due to their small size (Goulson et al., 2005) and a lack of suitable habitats at landscape scales (Winfree et al., 2009; Williams et al., 2010). As a consequence, in cities, pollinator populations need to adapt their foraging behavior to maintain a sufficient net energetic gain. Along an urbanization gradient in Stockholm, Arhné et al. (2009) found that bumblebee diversity in allotment gardens was negatively correlated to urbanization intensity. In fact, pollinators tend to fly long distances to find suitable vegetation patches which they forage extensively, visiting many plants and many inflorescences per plant (Goverde et al., 2002; Rusterholz and Baur, 2010). Thus they usually neglect isolated or small unattractive patches (Goverde et al., 2002; Cheptou and Avedaño, 2006) in

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which, consequently, plant species have reduced reproductive success. Moreover, bumblebee and bee abundance could be driven by more local effects, such as local flower abundance (Tommasi et al., 2004; Ahrné et al., 2009; Kearns and Oliveras, 2009; Lazaro and Totland, 2010).

To our knowledge, the pollination success (i.e. the number of fruits and seeds produced per plant) has rarely been assessed in an urban context and natural (versus controlled) conditions. Van Rossum (2010) showed that the seed production of *Centaurea jacea* was higher in urban than in rural areas, mainly because of agricultural use of land outside the city. Dunley et al. (2009) and Cussans et al. (2010) assessed the influence of landscape fragmentation on pollination in suburban contexts but no papers reported studies on pollination qualities within cities.

In this study, we aimed to analyze relationships between urbanization and pollination services in the Parisian agglomeration (France). For that purpose, we used small, artificial populations of *Lotus corniculatus* (L.), a strictly entomophilous species that requires the intervention of insects, *Bombus* spp., to produce fruits and seeds (Ollerton, 1993). We located these populations in different urban conditions within the Paris region. Eight *L. corniculatus* populations were placed in two different habitats of a densely urbanized inner Paris area (parks and paved courtyards) and 14 were placed in lawns in the less densely urbanized peri-urban fringes of Paris. Thus, we used both a gradient and a habitat approach with the aim of answering the following questions:

1. Does pollination service differ in more or less intensely urbanized landscapes; i.e. how many fruits and seeds are produced by *L. corniculatus* plants in different urban conditions?
2. How do land-use patterns in the immediate neighborhood influence their reproductive success?
3. When lotus pots are placed near wild or ornamental patches of vegetation, does local floral abundance influence *L. corniculatus* pollination success? And if so, in what way?

2. Materials and methods

2.1. Study species

Lotus corniculatus (L.) (Fabaceae) is an herbaceous, perennial species growing in heaths and grasslands across Europe, Asia and Northern Africa. Regeneration is realized mainly by seeds. Birdsfoot trefoil is strictly entomophilous, being mainly pollinated by *Bombus* species (Jones and Turkington, 1986; Proctor et al., 1996 Hennig and Ghazoul, 2011). Pressure exerted on the keel causes the staminal column to act as a piston, allowing pollen to be deposited on the ventral surface of the bumblebees as they forage flowers. Self-pollination under normal circumstances is extremely rare (Ollerton, 1993; Ollerton and Lack, 1998). The birdsfoot trefoil is widely used as a crop plant, and numerous cultivars are available. We used the 'Leo' cultivar, in order to obtain homogeneous population. This variety exhibit a restricted variability in fruits and seed production (resp. 5.3 ± 0.35 fruits per inflorescence and 12.3 ± 1.63 seeds per fruit, Sandha et al., 1977). Most of the inflorescences produced by our plants harbored 6 flowers (pers. obs.).

2.2. Study sites

We studied 22 artificial populations of *Lotus corniculatus* individuals ('Leo' cultivar, sowed in February 2009). Each population consisted of three pots, containing four or five (depending of the

success of plantation) *L. corniculatus* individuals. The mean number of inflorescences per pot was 17.4 ± 2.4 . Before placing pots in late June 2009, we always checked that no wild *Lotus corniculatus* populations were visible in the surrounding to avoid a size effect on our estimation of reproductive success.

2.2.1. Peri-urban area

Fourteen populations were placed in the urban fringe of Paris, at a distance of 3–26 km from Paris center (Fig. 1) in industrial fields that are inaccessible to the public, always in lawns.

2.2.2. Urban core

In order to measure the influence of immediate surroundings on the pollination success in a highly urbanized area, we chose eight other populations within Paris, close to the Jardin des Plantes (Fig. 1). In this highly urbanized landscape, populations were placed in two different 'immediate-surrounding' environments: four populations were located in urban parks and four in paved courtyards surrounded by buildings.

2.3. Pollination success assessment

Fruits were collected at the end of July 2009 after visually checking for their maturity, the number of fruits per inflorescence and the number of seeds per fruit were counted and used to estimate pollination success (Cussans et al., 2010). As the cultivar used is known to exhibit few variability in flower display and seed production (Sandha et al., 1977), the number of fruits per inflorescence and the number of seed per fruit were considered good proxies of the reproductive success.

2.4. Landscape data

Dramstad et al. (2003) showed that bumblebees increase their use of flower resources when they are more than 100 m from their nest; we thus calculated landscape composition within this range, i.e. within a 250 m radius of each *L. corniculatus* population. Landscape composition was calculated from IAURIF Land Use Pattern (LUP) data (2003). The LUP classes were grouped in order to distinguish (1) green spaces with herbaceous vegetation (parks, pasture and allotment gardens), (2) impervious spaces (houses, industrial spaces, railway and road borders) and (3) others (forest, arable land and water spaces). This last category was not analyzed due to its very low prevalence in the study area. As LUP data did not take into account roads less than 25 m wide, we added small streets from the IGN Road Database (IGN ROUTE 500[®], 2009) that were also considered as impervious spaces. Using Arcgis 9.2 (ESRI) software, we calculated (1) distances between each population and the next impervious space. Within each 250 m radius around populations, we also calculated (2) the number of green spaces, (3) the number of impervious spaces, (4) the gray-on-green ratio i.e. the total surface occupied by impervious spaces divided by the total area occupied by green spaces.

2.5. Data analysis

Statistical analysis was performed using R software 2.10 (R Development Core Team, 2009), the ade4 package (Dray and Dufour, 2007) and the MASS package (Venables and Ripley, 2002).

2.5.1. Urban gradient scale

Using the eight populations located within the highly urbanized area and the fourteen populations located in the peri-urban fringe, the simple relationship between broad scale landscape (urban vs peri-urban) and pollination success (i.e. the number of fruits per

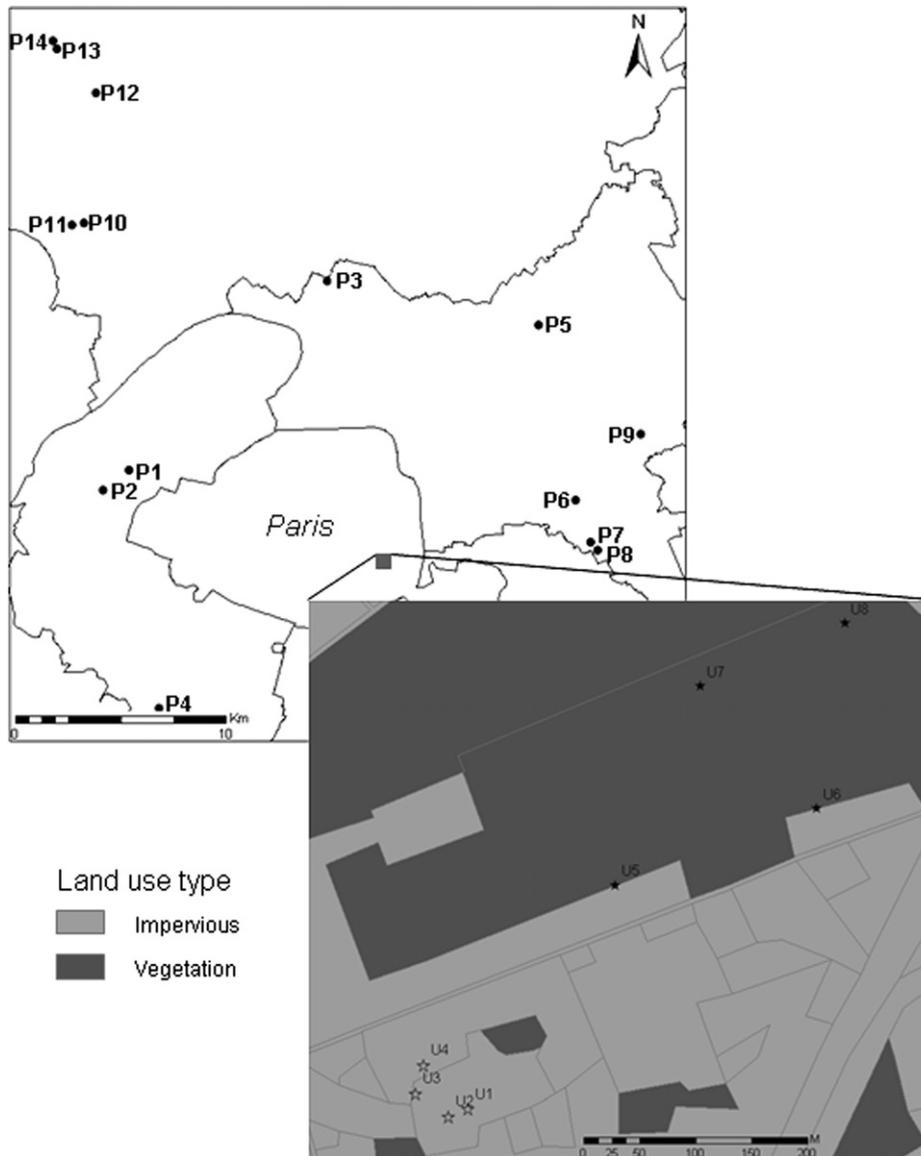


Fig. 1. Locations selected for the setting of the *L. corniculatus* populations. Circles: peri-urban populations, open stars: urban populations located in paved courtyards, plain stars: urban populations located in parks.

inflorescence and the number of seeds per fruit) was assessed using ANOVAs.

2.5.2. Landscape scale

At first, an exploratory principal component analysis (PCA) was carried out to describe gradient derived from the above-defined landscape data. Green and impervious surfaces and the number of spaces were included as a measure of landscape fragmentation and composition. Distances between the *Lotus corniculatus* populations and the next green or impervious surface were used to describe immediate landscape structure. The gray/green ratio was used as a measure of the degree of urbanization.

In order to determine pollination service drivers in spaces with different levels of urbanization, a general linear model (GLM) integrating a Poisson distribution and a log-link was used on fruit count data. This GLM included (1) gray/green ratio, (2) number of green and (3) impervious spaces and (4) the distance to the nearest impervious surface. The distances were log-transformed prior to

analysis. The gray/green ratio was used instead of proportions of green and impervious surfaces to avoid colinearity issues in the GLM (these two variables were retained in the above-described PCA to provide additional information about the gradient being considered). The interaction effects between the gray/green ratio and the number of green and impervious spaces were included. After being fitted, a downward stepwise model selection using AIC was applied in order to select the best linear combination of variables to explain pollination success.

2.5.3. Local scale

Using data that had been collected only in highly urbanized landscapes, we examined the effect of local variables on the number of fruits produced per inflorescence using GLM, assuming a Poisson distribution and a log-link. Local variables we analyzed were the type of habitat that the pots were located in (urban park or paved courtyard) and the abundance of insect-attracting flowers in the immediate vicinity of the pots, ranging on a scale from 1-to-no-flowers to 3-to-many flowers.

3. Results

3.1. Urban gradient scale

L. corniculatus populations placed in the peri-urban area produced on average more fruits per inflorescence than those placed in urban core (Fig. 2, $F = 13.48$, $p < 0.001$). This difference was not found for the mean number of seeds produced per fruit (Fig. 2, $F = 2.50$, $p = 0.114$).

3.2. Landscape scale

The number of impervious and green spaces ranged from 10 to 56 and 5 to 21 respectively in the pre-defined radii around the pots. *L. corniculatus* pots were never located further than 61 m from an impervious space (Table 1). The first two axes of the PCA carried out on landscape data accounted for respectively 47.8% and 25.4% of the total inertia. The populations were positioned along the first axis on an impervious area gradient, ranging from low to high gray/green ratio. Populations were then positioned along a fragmentation gradient, with numerous populations situated in both vegetated and impervious spaces as opposed to populations located far from impervious spaces (Fig. 3).

After the model selection, the fitted values were positively correlated with the observed fruit set values ($r = 0.25$, $t_{157} = 3.19$, $p = 0.002$). The number of impervious spaces within a 250 m radius were negatively correlated to pollination success of *L. corniculatus* populations (Fig. 4, $\text{Chi}^2 = 6.46$, $p = 0.01$), regardless of the gray/green ratio within the buffer radius. The interaction effect of the gray/green ratio and the distance to the next impervious patch was also significant ($\text{Chi}^2 = 4.25$, $p = 0.04$); hence the pollination success based on these two variables exhibited more complexity (Fig. 5). When the distance to the impervious surface is short, the

gray/green ratio appeared to barely influence pollination performance. As the distance to the nearest impervious patch increased, the gray/green ratio had an increasingly positive effect on pollination success. When we considered the distance to impervious patches at different gray/green ratio values, a different pattern appeared. For low gray/green ratios, the distance positively influenced the fruit set whereas this influence became negative as the gray/green ratio increased (Fig. 5).

3.3. Local scale

The fitted values of the local model were positively correlated with the observed fruit set values ($r = 0.35$, $t_{172} = 4.84$, $p < 0.001$). The number of fruits produced per inflorescence was always higher in parks than in paved courtyards (Fig. 6). The interaction between local floral resource abundance and habitat was significant ($\text{Chi}^2 = 4.43$, $p = 0.03$) with a positive influence of floral resource abundance around *L. corniculatus* pots in urban parks and a negative one in paved courtyards (Fig. 6).

4. Discussion

Based on seed and fruit production, it appeared that pollination service was rather low in the anthropogenic environment studied either in the urban core or in the peri-urban area. The number of fruits per inflorescence was inferior to those observed in more natural environments for the same birdsfoot trefoil variety (in average 5.3 fruits per inflorescence in Sandha et al., 1977 vs. 3.1 in the peri-urban area and 2.6 in the urban core). The number of seeds per fruit was also inferior (in average 12.3 seeds per fruit in Sandha et al., 1977 vs. 9.9 in the peri-urban area and 9.5 in the urban core). *Lotus corniculatus* individuals require 12 to 25 visits per flower to attain the maximum seed set (i.e. the fecundation of every ovules in

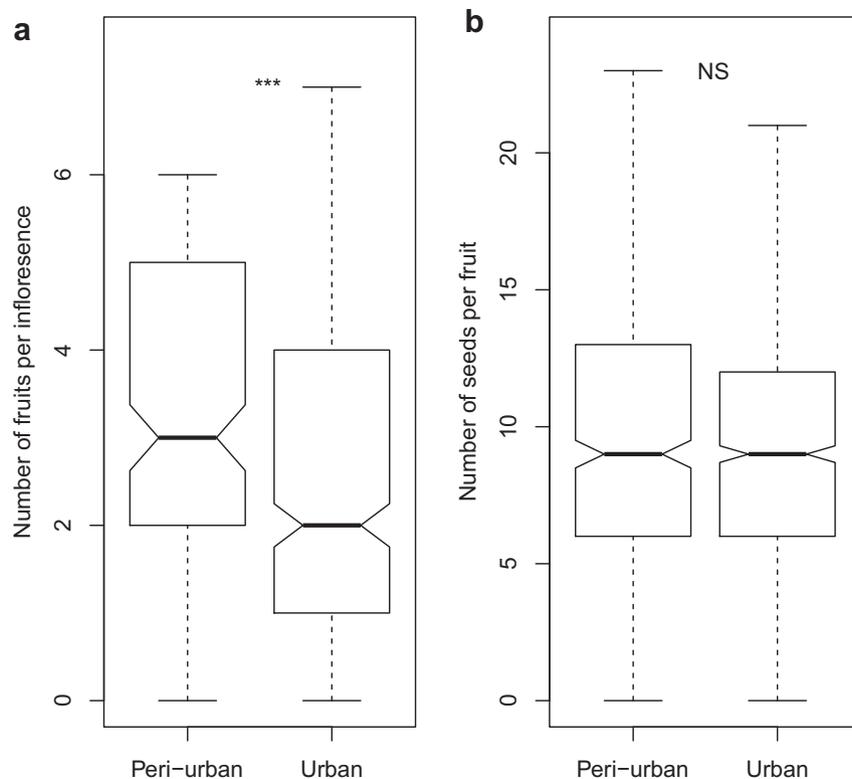


Fig. 2. Boxplots of the numbers of (a) fruits per infrutescence and (b) seeds per fruits, according to the urbanization level. Significant differences between means are indicated (***: $p < 0.001$, NS: $p > 0.05$).

Table 1Values of the metrics measured in 250 m wide radii, around each *L. corniculatus* population in peri-urban area.

Sites	Impervious surface area (in ha)	Green surface area (in ha)	Number of impervious patches	Number of green patches	Gray/Green ratio	Distance to the nearest impervious patch	Number of fruits per inflorescence (mean \pm s.d.)	Number of seeds per fruits (mean \pm s.d.)
P1	14.77 \pm 1.62	2.95 \pm 0.09	56	15	5	18.22	2.07 \pm 1.44	5.68 \pm 3.18
P2	13.79 \pm 0.2	6.94 \pm 0.43	15	11	1.99	11.35	1.00 \pm 1.15	5.67 \pm 6.28
P3	9.1 \pm 0.32	13.16 \pm 0.12	18	21	0.69	60.58	2.71 \pm 1.11	6.36 \pm 3.29
P4	18.09 \pm 0.29	1.65 \pm 1.08	31	6	10.93	0.33	3.50 \pm 1.77	7.96 \pm 2.92
P5	13.74 \pm 0.37	9.15 \pm 0.37	25	14	1.5	25.96	3.29 \pm 2.05	10.66 \pm 5.9
P6	8.65 \pm 2.51	8.12 \pm 1.15	20	14	1.07	7.85	1.40 \pm 1.67	13.88 \pm 10.33
P7	11.02 \pm 1.65	4.86 \pm 0.99	31	21	2.27	10.31	4.00 \pm 1.65	12.40 \pm 4.46
P8	13.85 \pm 0.37	6.65 \pm 0.17	29	14	2.08	7.51	0.50 \pm 0.58	2.00 \pm 2.45
P9	11.48 \pm 0.27	6.71 \pm 0.24	35	16	1.71	16.67	3.13 \pm 2.03	7.23 \pm 4.36
P10	13.08 \pm 1.44	2.14 \pm 0.31	12	5	6.1	28.52	2.97 \pm 1.53	9.40 \pm 4.19
P11	11.51 \pm 0.52	8.31 \pm 0.44	31	21	1.38	9.42	1.67 \pm 2.89	8.86 \pm 8.38
P12	8.53 \pm 0.33	7.72 \pm 0.71	21	17	1.11	7.46	4.33 \pm 0.98	13.02 \pm 4.89
P13	6.65 \pm 0.53	7.37 \pm 0.28	15	14	0.9	52.32	4.67 \pm 1.23	13.43 \pm 6.39
P14	9.84 \pm 0.5	6.89 \pm 0.42	10	9	1.43	8.1	3.93 \pm 1.75	7.86 \pm 4.24

the flower) (Morse, 1958; Jones and Turkington, 1986), it seems that it was hardly the case in our experiment.

The number of fruits produced per inflorescence was almost 1.5 times lower in the urban core than in the peri-urban area. Because cities are known for their low bumblebee abundances (Ahrné et al., 2009; Winfree et al., 2009), low pollination success was expected in urban areas. We showed a high range on seed production per fruit but contrary to what we expected, this range was not linked to an urbanization gradient when considering the landscape on a broad spatial scale (urban core vs. peri-urban). Nevertheless, if it seems reasonable to assume that the number of fruits is an exclusive but simple proxy for the presence/absence of pollinator visits to the plant (Ne'eman et al., 2010), the seed production, known to better reflect the pollen loads and pollen transfer efficiency, is also dependent on other parameters such as non-uniform pollination, resource limitation, architectural effects (Medrano et al., 2000) and local environmental conditions (Ne'man et al., 2010). Even if we try to place our populations in similar conditions (*i.e.* on lawn, with similar enlightenment and watering, growing medium) and with a unique, homogenous cultivar, we did not control all

environmental conditions and the sensitivity of seeds productions to local conditions could scramble the influence of urbanization on pollination. However, in self-incompatible, entomogamous species, particularly in when populations are small, the reproductive success is more dependent on pollination than on other factors (Oostermeijer and den Nijs, 2003). Thus, given the small size of our artificial populations, the absence of difference in seed production between peri-urban and urban landscape possibly resulted from a pollen limitation (Bierzuchudek, 1981), *i.e.*, too few pollen grains brought by pollinators to fertilize all the ovules, thus limiting the number of seeds set per fruit.

Therefore, even though the suboptimal pollen load occurring in our experiment was not sufficient to allow the setting of the maximum number of seeds it was likely to be sufficient to allow the formation of a fruit, thus making the fruit set a better indicator of pollinator visits and thus pollination service provided by pollinators than the seed set in the case of populations suffering a pollination limitation. To go further in explaining patterns observed the measurement of the forage behavior of pollinators in artificial plant population will be of primary importance to disentangle the

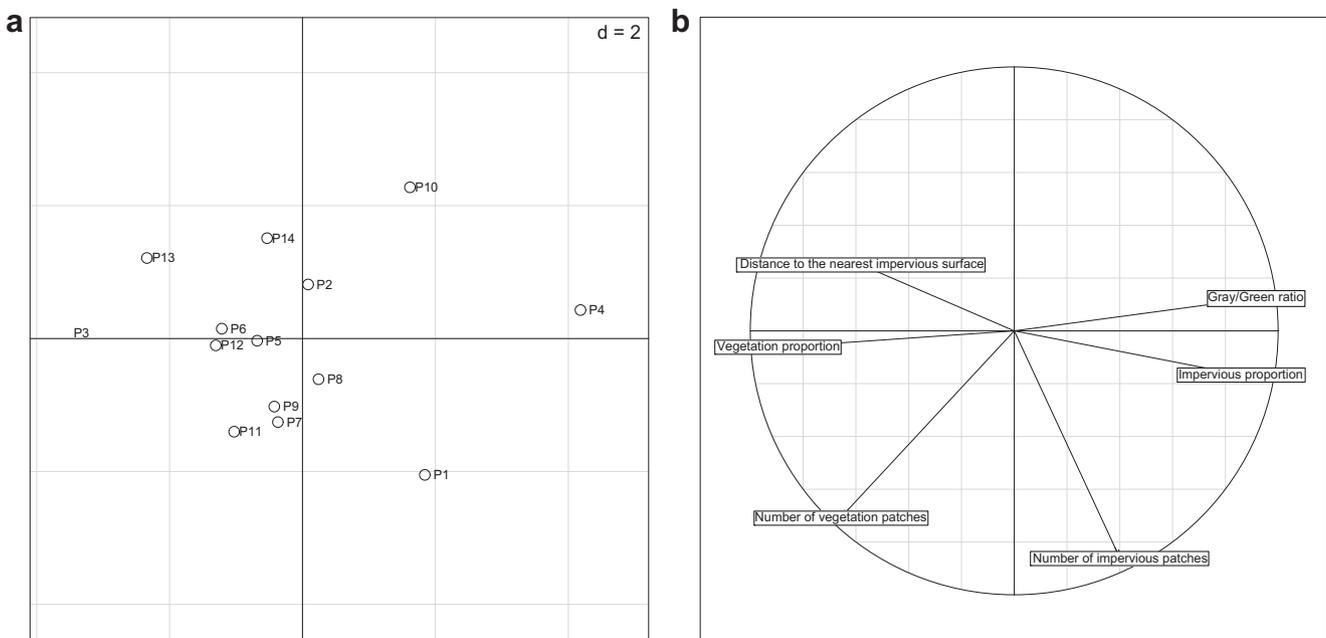


Fig. 3. Graphical interpretation of the PCA carried out on the landscape metrics data. (a) Factorial maps of the populations on PC1 and PC2 and (b) correlation diagram of landscape metrics on PC1-PC2.

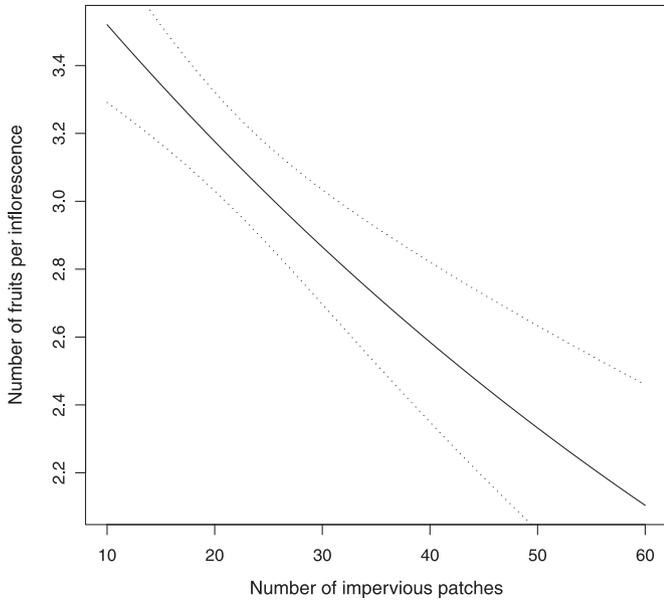


Fig. 4. Relationship between the number of impervious patches in a 250 m radius and the number of fruits, based on GLM prediction.

relative effects of pollen load and pollen transfer in the both above aspect of reproductive success in urbanized areas.

PCA carried out on peri-urban landscape data evidenced the existence of two intertwined gradients explaining pollination success. The number of fruits produced per inflorescence – and hence pollination success – decreased with the number of impervious patches within a 250 m radius of the *L. corniculatus* population, i.e. this number was a proxy for landscape fragmentation. This is concordant with the study carried out by Winfree et al.

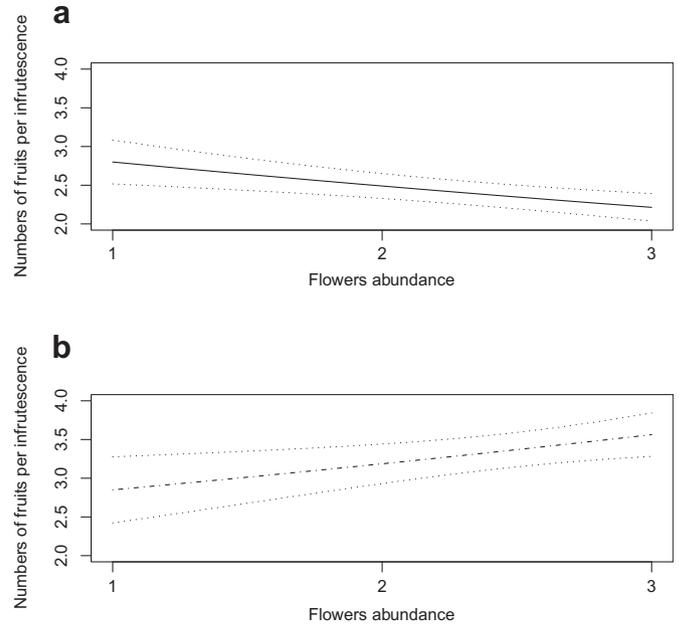


Fig. 6. Relationship between the abundance of floral resource and the number of fruits in *L. corniculatus* located in (a) paved courtyards and (b) urban gardens.

(2009), which showed that both bee abundance and species diversity were negatively affected by habitat loss and landscape fragmentation, especially in landscapes where very small natural areas remained. The decrease in pollination success of *L. corniculatus* was probably also linked to bee behavior in such fragmented landscapes. As the number of vegetation patches increased along with the number of impervious spaces, as shown in the landscape PCA, it was very likely that bees were more attracted by other floral resources and stayed longer in these other resource patches than in the relatively unattractive birdsfoot trefoil populations. In peri-urban areas, parks or gardens may be considered not only as abundant resource spaces for bumblebees, but also as distractions from other less attractive resources (Duncan et al., 2004).

When the gray/green ratio was low, i.e. in less densely urbanized quarters, pollination success of *L. corniculatus* increased with the distance to the nearest impervious patch. In effect, when *L. corniculatus* populations were far from an impervious patch, they tended to be located in large vegetation spaces, known to be more attractive and more resourceful for social bees (Ågren, 1996). Moreover, when resource availability is high, bees increase their visitation rate to the patch but decrease the number of visits per flower (Waites and Ågren, 2004; Hegland and Boeke, 2006). Thus, in this case, given that bees visit the different plants in a given patch more or less randomly (as opposed to systematically), pollinators are more likely to forage on *L. corniculatus* by chance, all the more since this plant species is relatively unattractive in comparison to others.

By contrast, when the gray/green ratio was high, pollination success decreased with the distance to the nearest impervious patch. At such high gray/green ratio values, we assume that the landscape was fragmented and floral resources were spatially isolated. Thus pollinators would tend to forage longer in other, more appealing floral resources that were spatially isolated from *L. corniculatus* populations, and hence decreasing the latter's pollination success. Given the large and dense colonies formed by the natural populations of *Lotus corniculatus*, as opposed to our small sized artificial populations, one might argue that the variations observed might result from a size effect. However, even

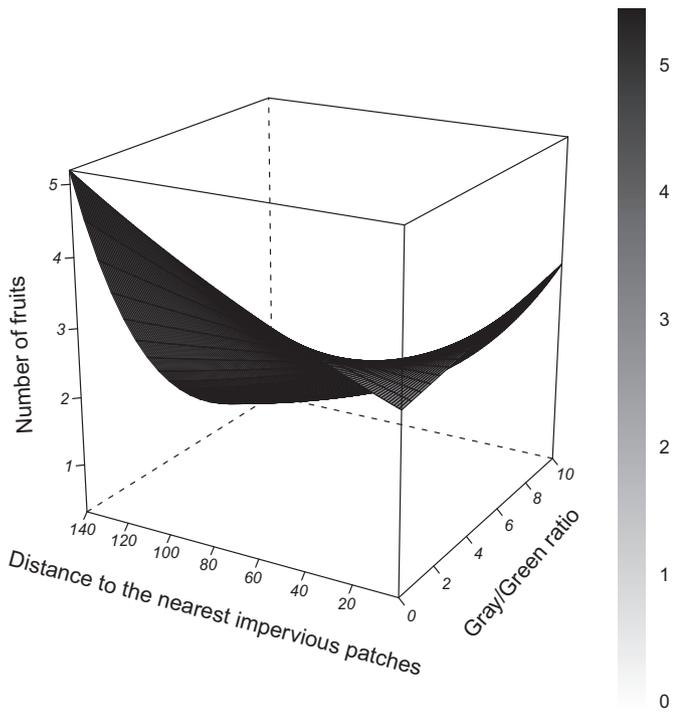


Fig. 5. Relationship between both the gray/green ratio and the distance to the nearest impervious patches in a 250 m radius and the number of fruits, based on GLM prediction.

though these populations were beyond the attractiveness threshold for the pollinators, their size was strictly controlled, thus the potential size effect was the same everywhere for all the individuals of our experimental design.

These assertions were verified at a local scale within the highly urbanized area. The amount of other foraging resources available around *L. corniculatus* populations was negatively linked to *L. corniculatus* pollination success when located in paved courtyards. The relation became positive when *L. corniculatus* populations were located in parks. Indeed, when local resources were very scarce, as in paved courtyards, the presence of appealing floral resources around *L. corniculatus* population apparently distracted bees from foraging on this unattractive plant (Rands and Whitney, 2010). By contrast, in parks, resources were more abundant and pollinators were therefore likely to visit more plants, thus enhancing the pollination success of *L. corniculatus* (McFrederick and LeBuhn, 2006). The two results above were consistent with those obtained on a larger landscape scale. Abundance of attracting floral resources is thus likely to act as a magnet resource, thus enhancing pollination success for every species in the patch if it is not too isolated from other green spaces.

Thus, on a large spatial scale – i.e., in urban and peri-urban environments – urbanization exerts a negative influence on pollination service, just as it does on the pollinator population. However, on a smaller scale, the relationship is probably not linear, thus emphasizing the need for studies linking pollinator population and pollination success at different spatial scales.

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