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Original article

Vegetation density is the main driver of insect species richness and diversity in small private urban front gardens

Joeri Morpurgo [a,b,*], Margot A. Huurdeman [b], J. Gerard B. Oostermeijer [b], Roy P. Remme [a]

[a] Department of Environmental Biology, Institute of Environmental Sciences, Leiden University, Einsteinweg 2, Leiden 2333 CC, the Netherlands
[b] Institute for Biodiversity and Ecosystem Dynamics, Department of Evolution and Population Biology, University of Amsterdam, the Netherlands

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ABSTRACT

Urbanisation changes natural ecosystems and vegetation to urban green spaces, and causes insect communities to experience novel challenges for survival. New evidence suggests that urban green spaces, no matter how small, can provide meaningful habitats for insects. Information on design and management of small gardens ($<6\ m^2$) in dense urban areas is still scarce. In particular, it is hardly known which garden designs provide most benefits to insects. We surveyed 65 small urban façade gardens ($\mu=1.7m^2$) in Amsterdam and The Hague in The Netherlands and measured various garden attributes that are expected to be relevant for general, flower-visiting and herbivorous insect species richness and diversity. Plant coverage and richness were the strongest predictors of insect biodiversity and species richness. We found no support for associations with native plants or garden size.

Synthesis and applications: To strengthen insect biodiversity in the urban environment, we recommend future design of urban green spaces to focus on maximising coverage and richness of vegetation. Although there are advantages to using native species, we acknowledge that garden owners often prefer exotic species. Some of these can also affect insect diversity and abundances positively.

1. Introduction

Insects are essential for urban ecosystem functioning, health, and for supporting ecosystem services beneficial to humans. The economic value generated by insects has been estimated to be worth billions (Losey and Vaughan, 2006; Ngo et al., 2017). In the urban environment, increasing insect biodiversity positively affects ecosystem functioning and human well-being through processes such as pollination of flowers, nutrient cycling, supporting water regulation through soil-bioturbation, and as very important components of many trophic networks (Buchholz and Egerer, 2020; Belovsky and Slade, 2000; Drager et al., 2016; Eggleton, 2020). Flower-visiting insects are, for example, indispensable for pollination and therefore help sustain plant and insect populations throughout the urban and peri-urban environment (Eggleton, 2020). Herbivorous insects, sometimes considered pests by homeowners, are important to ecosystem functioning by making plant resources available for detritivores which in turn feed the soil. This trophic cascade from herbivorous insects to soil nutrients is highly important for plant diversity and ecosystem health (Belovsky and Slade, 2000). Despite the importance of insects to humans and ecosystems, their numbers are dwindling at alarming rates (Hallmann et al. 2017). With the decline of insects, many of the important ecosystem services we depend on, as well as biodiversity at large, will further destabilise and decrease (Wagner et al., 2021).

During the process of urbanisation, construction changes the natural landscape drastically and plays a key part in reducing and changing the local biodiversity (Güneralp & Seto, 2013). Urbanisation mostly affects natural vegetation through processes of fragmentation, degradation or complete removal. The remnant semi-natural areas are constituted by urban green spaces (UGS), which are often more heterogeneous and composed of different vegetation compared to the original habitat (Yang et al., 2021). Consequently, the process of urbanisation has been shown to substantially reduce the abundance and species richness of several arthropod taxa, with butterflies showing the largest decline of 85 % in abundance (Piano et al., 2020). Consequently, new UGS installed can be colonized by species that are able to adapt to these different habitats and environmental conditions. Several studies have now shown that these UGS have high levels of biodiversity and are colonized and inhabited by endangered, rare and important species (Boakes et al., 2024; Ives et al., 2016; Jokimäki et al., 2018). Interestingly, the colonizing biodiversity

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* Correspondence to: Environmental Biology Department, Institute of Environmental Sciences, CML, Leiden University, Leiden, the Netherlands.
E-mail address: joeri.morpurgo@gmail.com (J. Morpurgo).

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tends to be relatively similar across the globe and different from their local counter parts (Lokatis and Jeschke, 2022). Hence, it should be realized that urban biological communities are novel, and often differ from those observed in nature reserves (Kowarik, 2011).

A key driver for biodiversity across the globe is the area of available habitat (e.g. Brooks et al., 2002; Fahrig, 2013). This premise holds for cities, where substantial evidence showed that increasing amounts of habitat, through gardens or public UGS, enhances urban biodiversity (Beninde et al., 2016; Majewska & Altizer, 2018). The general mechanism used to explain the enhanced biodiversity is that increasingly larger UGS contain increased amounts of plant diversity, which allow for increased animal biodiversity (Delahay et al., 2023). Indeed, meta-analysis shows that garden size drives insect diversity, although the analysis was limited to studies that cover larger gardens (6.1 m^2 – 70 000 m^2; Majewska and Altizer, 2020). To our knowledge, the smallest garden sizes in which insects were studied that focus on insect were in urban grasslands, using plots of flowering plants ranging from 1 to 100 m^2 and showing a positive correlation between area and insect flower-visitor diversity (Blaauw & Isaacs, 2014). Considering that a substantial amount of the UGS in cities are relatively small, they may contribute strongly to the urban biodiversity (Baker et al., 2018; Davies et al., 2009). With the increasingly limited space in the dense urban environment (Vergnes et al., 2014; Haaland and van Den Bosch, 2015), not large garden size, but rather the area of vegetation, and thus habitat, maybe a more mechanistic and manageable driver than garden size, but this has not been properly investigated. With the increasingly dense urban environment, gardens are likely to become smaller, which in The Netherlands façade gardens are a common strip-like small garden type in front of homes. Importantly, at the very small spatial scale (<6 m^2) of façade gardens in urbanised areas, garden size and plant coverage are to our knowledge rarely studied in tandem as a potentially important drivers of biodiversity.

In general, garden design is thought to be an important driver of urban insect biodiversity. An ecologically preferred design choice is that the inclusion of native plant species provides greater benefits to biodiversity than exotic species (Schlaepfer et al., 2011). The key mechanism explaining this benefit stems from a perceived mismatch between the traits of native fauna and exotic or ornamental plant species. This can for example lead to bees being unable to retrieve nectar from flowers that are shaped differently than native counterparts (Cohen et al., 2022). For herbivorous insects, exotic plant species may simply be less edible compared to native plants. This difference could be due to a lack of co-evolved traits that help to deal with the potentially different physical or biochemical resistance of exotic plant species (Costan et al., 2022; Elton, 2020; i.e. the enemy-release hypothesis). A study on floral resources and bee communities reported that, indeed, increasing proportions of native plants in gardens were associated with an increase in species richness and abundance of specialist bees (Tavares Brancher et al., 2023). Similarly, a study on backyard gardens reports that native plants in combination with local and landscape characteristics may be important for protecting and harbouring bee communities (Pardee & Philpott, 2014). However, there is a lack of evidence to support this narrative across a wider array of insect taxa. Salisbury et al. (2015) found that in addition to native species, some exotic species can play an important role in garden design by providing abundant resources to specialistic taxa and by extending the flowering season. These studies suggest that certain design features of gardens attract and support biodiversity better than others. Therefore, it is urgent to understand what design features of urban gardens are favoured by insect communities in cities. Especially given that this information can be used by policymakers and citizens, as they seem willing to support wildlife, so that we can support insects from cities across the globe (Davies et al., 2009).

In this study, we aim to understand how the design of very small urban façade gardens (<6 m^2) is related to general, flower-visiting and herbivorous insect diversity. These façade gardens are small green strips directly at the street-facing front of houses, often created and managed by the inhabitants by removing one or several sidewalk tiles. The ultimate goal is to identify easily adjustable design aspects of façade gardens that increase insect diversity. A better understanding of how individual aspects of garden design impact insect diversity will better inform policymakers and citizens on how to design insect-friendly gardens. To assess their impact, we measured several design attributes of façade gardens and related these to the insects found in the gardens.

Based on the considerations presented above, we hypothesized that garden size would be positively correlated with species richness and diversity. We hypothesized that this is also true for the plant coverage and species richness in the façade gardens. In addition, we expected that the proportion of native plant species in the gardens will positively affect insect diversity. We also expected flower-visiting insects to respond positively with the presence and abundance of flowers. Finally, as (micro)climate also affects the activity of insects, the exposure to the sun (Cardinal position) is also expected to have a significant impact.

2. Methods

2.1. Selection of gardens

In 2019, we surveyed insects and vegetation of façade gardens (n = 65; Appendix 1) in the Dutch cities of Amsterdam (52∘21’33.1”N 4∘54’33.5”E) and The Hague (52∘04’57.0”N 4∘17’40.3”E). Both these cities have roughly the same climate, as the cities are 51 km apart from each other, with a national average 851 mm of precipitation and 10.5°C over the past 30 years (KNMI, 2023). Amsterdam is a larger city (21930 ha) and The Hague is approximately half the size (9813 ha). Both cities are classified as extremely urbanised, but The Hague has a higher population density of 6827 individuals per square kilometre than Amsterdam, with 4880 individuals per square kilometre (Centraal Bureau voor Statistiek, 2023).

To analyse the relationships between the attributes of small gardens and insects, we studied small façade gardens, as they are both abundant in both cities and small in size/area (<6 m^2). These façade gardens are defined as small gardens directly in front of a house, facing the public street. Prior to our field work, we asked the owners for permission to capture and examine invertebrates in their garden by distributing leaflets door-to-door (Appendix 2). A façade garden was included in the study when (i) the homeowners granted permission, (ii) at least one plant was present in the garden, and (iii) the garden was situated within the spatial boundaries of the research area (Fig. 1, n = 65). This resulted in 50 sampling sites in Amsterdam and 15 in The Hague, which also generally had fewer façade gardens. Given the sample size difference between cities, we analysed the distribution of the predictors between cities using a t-test. We found that none of the predictors were statistically significantly different between cities ($p > 0.10$, Appendix 3). Finally, to avoid spatial or temporal autocorrelation, we visited the sites in random order within and among cities.

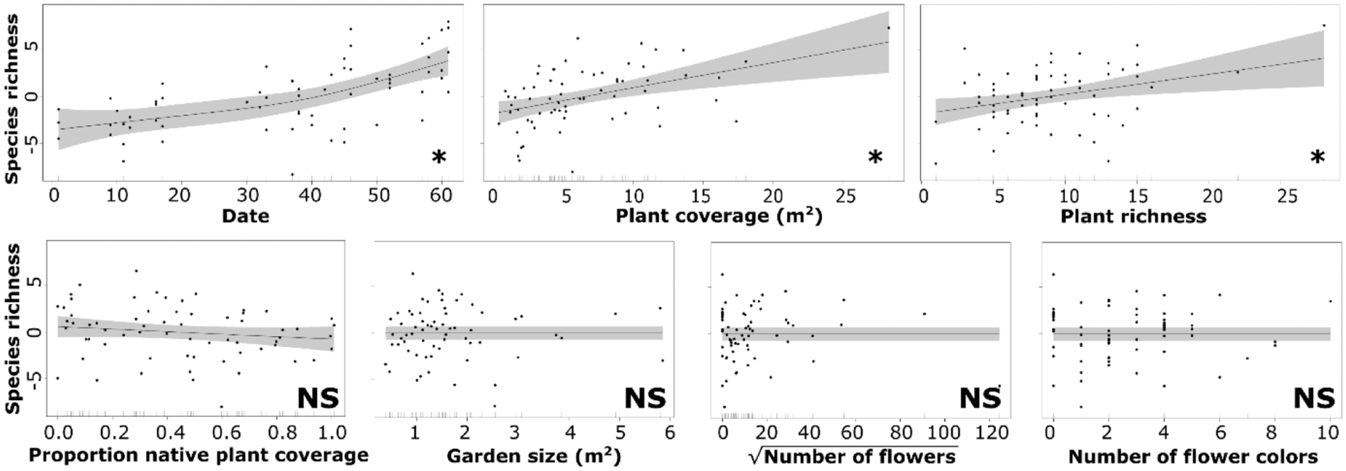
2.2. Garden features

We recorded information on several features of gardens that we thought could affect insect diversity (Table 1). The cardinal direction of the garden was included, as it impacts the amount of sunlight received. Subsequently, we time of survey, date, and the garden size in square metres.

2.3. Plant and vegetation surveys

Vegetation surveys were conducted several weeks before and directly after the insect survey, to allow for species-identifying features to emerge (i.e. flowers, leaves, etc.). All plants were identified to the species level where possible and otherwise to the best taxonomic depth possible. Plants were identified and classified as native or alien using the

A) Species richness of all insects



B) Shannon diversity of all insects

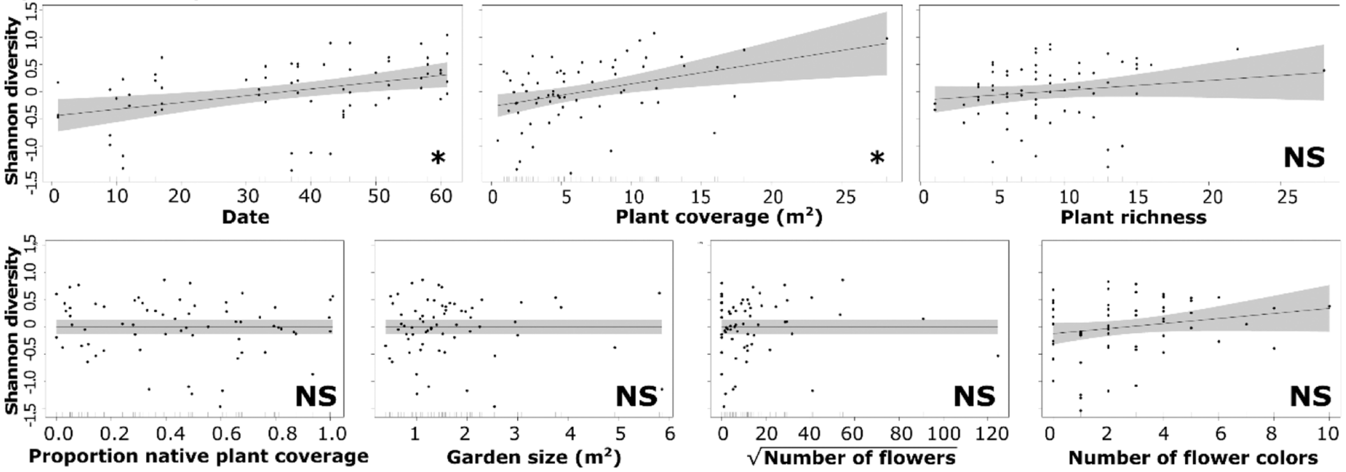


Fig. 1. Smooths of seven predictor variables in the Generalized Additive Models predicting A) Species richness and B) Shannon diversity of all captured insects. Predictor panels are supplied with either a * indicating a p-value < 0.05, or NS indicating a non-significant relationship.

guidelines from the 'Heukels' Flora van Nederland (Heukels and Van der Meijden, 2005). Species absent from the 'Heukels', such as several cultivars or exotic species, were identified using Pl@ntNet (Affouard et al., 2023).

For each plant species, we measured both cover and counted the number of flowers (Table 1). For every species, per individual we measured the total coverage by tapeline and summed the coverages of all individuals. The number of flowers per plant was counted for species with less than 100 flowers, while it was estimated for species with more than 100 flowers by counting the number of flowers in a cluster and then multiplying it by the total number of clusters. Finally, we also counted the number of easily distinguishable flower colors visible to the human eye (e.g. red, blue, but also dark blue or light blue).

2.4. *Insect survey*

Insect surveys were performed from April until June 2019 between 09:00 and 17:00, excluding only rainy days. Surveys were based on a single sampling effort of 15 minutes, during which insects were thoroughly searched on the aboveground parts of plants by two researchers simultaneously. Observed insects were captured using 50 ml falcon tubes and visually identified after the survey. A butterfly net and larger containers were also considered, yet none of the observed insects were too large to capture in a 50 ml falcon tube. Sampling with tubes was facilitated by the strip-like shape of the façade gardens, which can be a few meters wide but are often only 30 — 90 cm deep. For plant identification or insect sampling, we thus never needed to step into a garden.

Species were directly identified in the field using Chinery (2007) and released after the survey. Unidentified species were euthanized with ethyl acetate and identified in the lab using additional literature and the app ObsIdentify (Albouy and Richard, 2019; Ball and Morris, 2015; Van Veen, 2010). If an organism could not be identified to species level, the best taxonomic resolution was assigned, and with similar looking species they were assigned to a morphotype comprised of morphologically identical organisms.

2.5. *Statistical analysis*

All statistical analysis were performed in the software R (R Core Team, 2023). We employed six separate statistical models to link garden design features to aboveground insect diversity. To investigate the relationships more comprehensively, we created separate models predicting either species richness or Shannon diversity for: I) all observed insects, II) only flower-visiting insects, and III) only herbivorous insects. These categories were made to infer if all observed insects were affected in the same way (including non-flower visitor and non-herbivores), or whether flower-visiting or herbivorous taxa are affected by different garden features. We chose to use Generalised Additive Models (GAM) as they allow for non-linear relationships accounting for seasonality of insect richness and diversity, while favouring linear ones (Wood et al.,

Table 1

Summary of potential predictor variables of the response variables insect abundance and diversity. The predictor variables attempted to capture attributes of small gardens (size, flowers, plant coverage), climate, and temporality.

Variable	Definition and methods
Cardinal position	Categorical variable being North (n = 20), East (n = 11), South (n = 22), or West (n = 12). It indicates the direction the façade garden opposite of the building it is built against. This would be indicative of the amount of sunshine a garden would receive during the day.
Insect survey date	A numerical variable with the date of the insect survey. Starting the 4th of April and ending the 7th of June for a total of 60 survey days.
Plant coverage	A numerical variable describing the summed coverages of all plants growing in the garden. This means that a garden of 1 m^2 that has layered plant coverage could have a total coverage of >1 m^2. The observed values ranged from 0.44 — 28.24 m^2.
Plant species richness	A numerical variable of the number of plant species in a façade garden, with an observed range between 1 — 28. The average was 8.9 plant species in a garden, with a standard deviation of 4.68.
Garden size	A numerical variable describing the size or area of the garden in m^2. The garden sizes were between 0.39 — 5.9 m^2. The average garden size was 1.66 m^2, with a standard deviation of 1.14 m^2.
Proportion of coverage by native plant species	A numerical value between 0 — 1. It was calculated by dividing the summed coverage of native plant species by the total plant cover in the garden. The observed range was 0 — 1, with an average of 0.44.
Number of flowers	Numerical variable representing the number of flowers counted within a façade garden during a sampling event. The observed range is 0 — 15528.
Number of flower colors	Numerical variable describing the number of different flower colors in a façade garden. The observed range is 0 — 10, with an average of 2.65 colors per garden.
Proportion of coverage by evergreen plant species	A numerical value between 0 and 1. It was calculated by dividing the summed coverage of evergreen plant species by the total plant cover in the garden. The observed range was 0 — 0.87, with an average of 0.32.
Proportion of coverage by annual plant species	A numerical value between 0 and 1. It was calculated by dividing the summed coverage of annual plant species by the total plant cover in the garden. The observed range was 0 — 0.99, with an average of 0.16.

2017).

Considering the above, the mathematical formulation of the GAM for all insects and only flower-visiting insects was:

$$\begin{aligned} \mathit{Diversity} = {} & f(\mathit{Date}) + f(\mathit{Cardinal\ direction}) + f(\mathit{Plant\ richness}) \\ & + f(\mathit{Vegetation}) + f(\mathit{Garden\ size}) + f(\mathit{Native\ vegetation}) \\ & + f(\mathit{\#Flowers}) + f(\mathit{\#Flowercolors}) + \in \end{aligned}$$

For herbivores, we changed the terms that are flower-related to leaf-related traits. Therefore, the GAM for insect herbivores is:

$$\begin{aligned} \mathit{Diversity} = {} & f(\mathit{Date}) + f(\mathit{Cardinal\ direction}) + f(\mathit{Plant\ richness}) \\ & + f(\mathit{Vegetation}) + f(\mathit{Garden\ size}) + f(\mathit{Native\ vegetation}) \\ & + f(\mathit{Evergreen\ vegetation}) + f(\mathit{Annual\ vegetation}) + \in \end{aligned}$$

In all models, *diversity* represents either species richness or Shannon diversity index of either all insects captured, or solely flower-visiting or herbivorous insects. The term *Date* used a Gaussian Process smoothing that accounts for temporal autocorrelation, and relates to the number of days since the first insect survey. The *Cardinal direction* term uses a random effect to account for average differences in insect richness or diversity for gardens which face different directions, with North-facing gardens receiving least, and South-facing ones most sunlight. Finally, ∈ represents the unexplained error term of the model.

The other predictors are all modelled smooths using thin plate regression splines (TPRS) allowing for non-linear relationships (Wood, 2003). These splines effectively act as a model fitting step as the null space is also penalized slightly and the whole term can therefore be shrunk to zero (Wood, 2003). During the model fitting, several knots are used to smooth linear regression to a spline optimizing the restricted maximum likelihood (REML; Wood, 2017, p. 185). Effectively, this means that zero knots equals a linear regression, and every additional knot added allows for more smoothing. The advantage of the used TPRS approach is that knot number and position are based on the data instead of manual and hence subjective placement.

The terms that used the TPRS smooths are I) *vegetation,* representing the summed coverage of every species in a garden, II) *Plant richness*, representing the amount of unique species in a garden, III) *native vegetation,* the proportion of the summed native plant coverage in a garden, relative to that of exotic species, IV) the *number of flowers,* at the moment of sampling, and V) *the number of flower colors*, representing the number of visible flower colors at the sampling moment, VI) *evergreen vegetation*, and VII) *annual species* both as proportions of the summed total coverage of the vegetation.

The model diagnostics were visually inspected through assessing the autocorrelation function of the residuals, concurvity and the model residuals. No issues of concurvity (i.e. the non-linear variant of multicollinearity) or model fit were identified (Appendix 4 — 9).

3. Results

3.1. Data collection

Across the 65 studied façade gardens (Amsterdam (n = 50), The Hague (n = 15)) we found 235 plant and 154 insect species. The gardens had an average area of only 1.7 m^2, with the smallest garden being only 0.39 m^2 and the largest garden comprised 5.9 m^2. Across all gardens, plant coverage summed to a total of 432.95 m^2, being quadruple the amount of square meters compared to the total garden size sampled of 107.81 m^2. The top three plant species with highest coverage were *Rosa chinensis* (50.17 m, 12 %), *Rosa canina* (24.64 m, 6 %) and *Poaceae spp.* (22.80 m, 5 %). Of all plant species identified, 40 % were native (n = 94), 26 % were evergreen (n = 61), and 17 % were annual (n = 39). Plant species richness ranged from 1 – 28 with a mean of 8.9 species per façade garden.

Of all the 154 insect species, 55 % were identified as a flower-visitor (and potential pollinator, n = 85), and 25 % as a herbivore (n = 39). In parallel, 39 species (25 %) were neither solely flower-visitor nor herbivore, and were classified as carnivore or omnivore. The insect species richness observed in the gardens ranged from 0 — 19 with a mean of 8 species per garden. The three most abundant insect species were *Rhopalapion longiostre* (n = 963), *Lasius niger* (n = 553) and *Holotricapion pisi* (n = 321). The first and last species were frequently found on *Alcea rosea* which coverage summed to a total of 22.48 m^2 across all gardens (5 %), being the plant species with the fourth most coverage. In contrast, the most abundant orders of insects caught were *Diptera* (n = 79, 51 %), *Coleoptera* (n = 24, 16 %), *Hemiptera* (n = 22, 14 %) and *Hymenoptera* (n = 19, 12 %). Within the *Diptera* order both *Chironomidae* (n = 20, 25 %) and *Syrphidae* (n = 17, 22 %) were the most common families found. For the *Coleoptera* order, the *Coccinellidae* was the most frequently found family (n = 4, 17 %). For the *Hemiptera,* the most frequently found family was *Miridae* (n = 10, 45 %). Finally, for the *Hymenoptera* order, *Apidea* was the most commonly found family (n = 8, 42 %).

3.2. Response of all insects

The GAMs explained the data containing all the insects with a deviance of 57.8 % for species richness ($R^2 = 0.54$; Figs. 1A) and 40.0 %

Table 2

Results of Generalized Additive Models (GAMs) to explain species richness and Shannon diversity of all insects captured in façade gardens (n = 65). The intercept is shown with parametric coefficients, whereas covariates are represented with smooth terms. For details of predictor variables see Table 1. Significant *p*-values (*p* < 0.05) are indicated in bold. *edf – Estimated Degrees of Freedom.

All insects	**Species richness GAM**				**Shannon diversity GAM**			
Predictors	*Estimate*	*Std. error*	*t-value*	*p-value*	*Estimate*	*Std. error*	*t-value*	*p-value*
Intercept	8.01	0.39	20.55	**<0.001**	1.5	0.07	22.6	**<0.001**
Smooth terms		*edf**	*F-value*	*p-value*		*edf**	*F-value*	*p-value*
f (Cardinal direction)		0.41	0.16	0.31		<0.001	0	0.87
f (Date)		2.06	17.15	**<0.001**		1.00	10.83	**0.002**
f (Plant richness)		0.91	0.89	**0.006**		0.67	0.22	0.08
f (Vegetation coverage)		0.98	1.59	**<0.001**		0.95	1.15	**0.001**
f (Proportion of native vegetation)		0.65	0.21	0.10		<0.001	0	0.41
f (Number of flowers)		<0.001	0	0.78		<0.001	0	0.67
f (Number of flower colors)		<0.001	0	0.70		0.73	0.31	0.051
f (Garden size)		<0.001	0	0.99		<0.001	0	0.67
Adjusted R^2	0.54				0.37			
Explained deviance	57.8 %				40 %			
Observations (n)	65				65			

for Shannon diversity ($R^2 = 0.37$; Fig. 1B). In both models, sampling date and total plant coverage were significantly positive predictors ($p < 0.01$; Table 2). Plant richness was positively significant in the insect species richness model ($p < 0.01$). The number of flowers, the number of flower colours, the proportion coverage by native plants and garden size were not significant in either model ($p > 0.10$).

3.3. Response of flower visitors

The GAMs explained the data of only flower-visiting insects very well, with a deviance of 63.3 % for species richness ($R^2 = 0.59$) and 56.8 % for Shannon diversity ($R^2 = 0.52$). In both models, sampling date and plant coverage contributed significantly positive ($p < 0.01$; Table 3). For species richness as well as Shannon diversity, the number of flowers showed a significant curvilinear relationship ($p < 0.01$). Note, the curve in this relationship is dictated strongly by an outlier where the garden has a large exotic ornamental *Photinia sp.* shrub (8.25 m^2). Flower visiting species richness also correlated with plant species richness ($p < 0.01$). In contrast, neither model showed a significant contribution of the number of flower colors ($p = 0.64$), and the same was true for the proportion of coverage by native plants and garden size ($p > 0.10$).

3.4. Response of herbivorous insects

The GAMs explained the data of only herbivorous insects comparatively poorly, with a deviance of 20.0 % for species richness (R^2=0.14) and 19.5 % for Shannon diversity (R^2=0.14). This is reflected in the lack of any smooth being significantly linked to richness or diversity of herbivores. The model did not show any significant relationship with a vegetation indicator ($p > 0.05$; Table 4). In both models, plant coverage showed visually the strongest relationship and was nearly significant for Shannon diversity ($p = 0.07$) and less for the species richness ($p = 0.13$).

4. Discussion

4.1. Drivers of urban insect diversity

Our results show that even in small façade gardens (μ=1.7m^2) several design attributes are correlated with the diversity of insects they attract. We observed a large biodiversity comprising 235 plant and 154 insect species in an area of just 108 m^2 across a total of 65 gardens. Most importantly, we show that the strongest predictor for insect species richness and diversity is the total amount of plant coverage and richness of a garden. Moreover, the results suggest that flower-visiting insects are most strongly dependent on the amount of vegetation and to a lesser extent, but positively, on the availability of flowers. Important is also that correlations were much less evident for herbivorous insects. Our results on the relationship between plant cover and richness driving insect diversity are generally congruent with previous research and suggest that even in very small façade gardens, adding more plants and more plant species is quite likely to have a positive impact on the insect community (Pardee & Philpott, 2014; Beninde et al., 2015; Blaauw & Isaacs, 2014).

We found that flower-visiting and herbivorous insects responded quite differently to façade garden features. As expected, flower visitors

Table 3

Results of Generalized Additive Models (GAMs) to explain species richness and Shannon diversity of flower-visiting insects in façade gardens (n = 65). The intercept is shown with parametric coefficients, whereas covariates are represented with smooth terms. For details of predictor variables see Table 1. Significant *p*-values (*p* < 0.05) are indicated in bold. *edf – Estimated Degrees of Freedom.

Flower-visiting insects	**Species richness GAM**				**Shannon diversity GAM**			
Predictors	*Estimate*	*Std. error*	*t-value*	*p-value*	*Estimate*	*Std. error*	*t-value*	*p-value*
Intercept	2.98	0.19	15.32	**<0.001**	0.85	0.06	14.9	**<0.001**
Smooth terms		*edf**	*F-value*	*p-value*		*edf*	*F-value*	*p-value*
f (Cardinal direction)		<0.001	0	0.67		<0.001	0	0.45
f (Date)		1	9.66	**0.003**		1.00	10.11	**0.002**
f (Plant richness)		2.51	1.59	**0.001**		1.94	0.59	0.06
f (Vegetation coverage)		1.07	3.02	**<0.001**		1.03	2.28	**<0.001**
f (Proportion of native vegetation)		0.40	0.07	0.19		0.55	0.14	0.14
f (Number of flowers)		2.36	1.60	**0.001**		2.30	1.35	**0.003**
f (Number of flower colors)		<0.001	0	0.90		<0.001	0	0.94
f (Garden size)		<0.001	0	0.58		<0.001	0	0.84
Adjusted R^2	0.59				0.52			
Explained deviance	63.3 %				56.8 %			
Observations (n)	65				65			

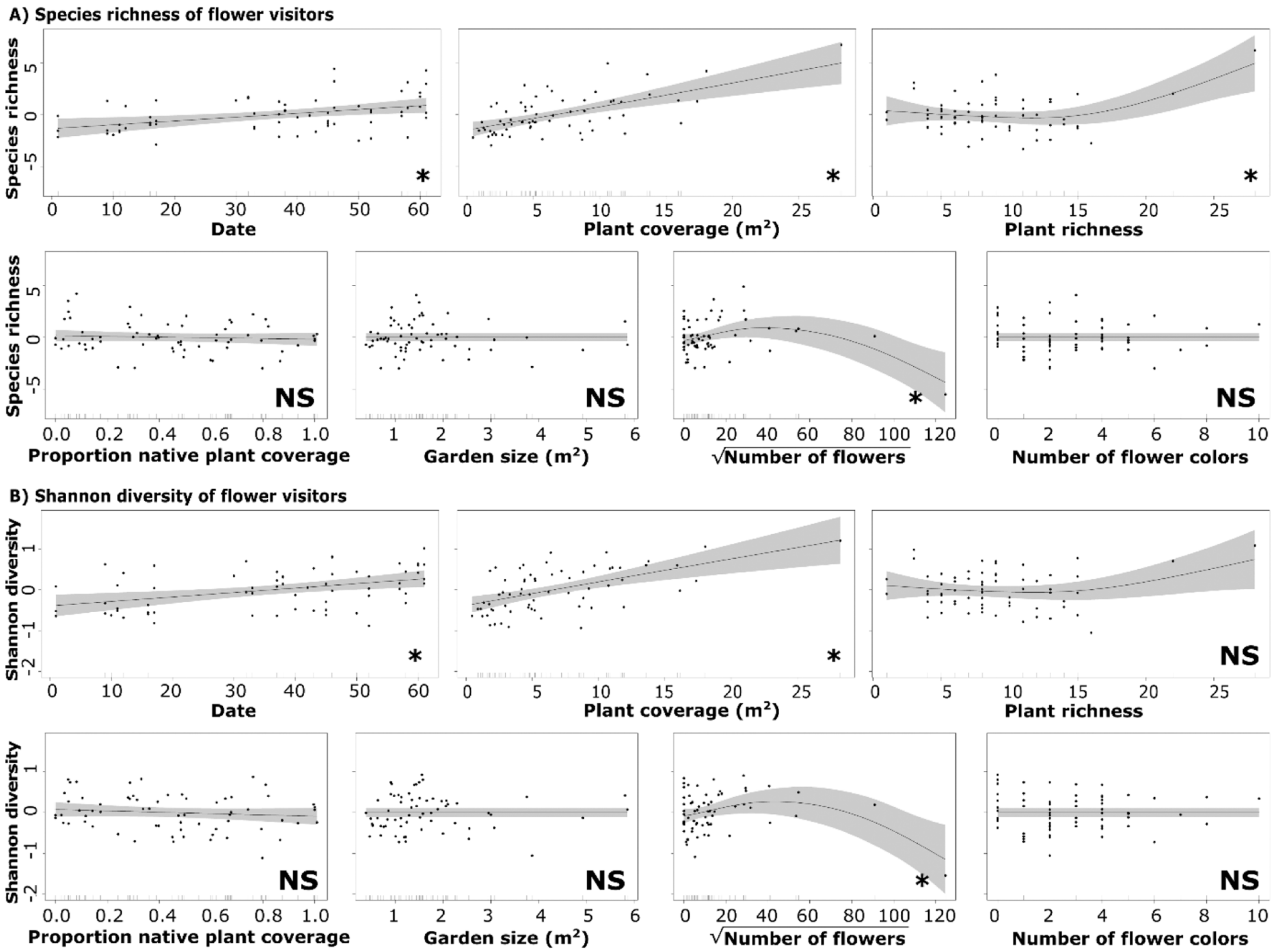


Fig. 2. Smooths of seven predictor variables in the Generalized Additive Models predicting A) Species richness and B) Shannon diversity of flower-visiting insects. Predictor panels are supplied with either a * indicating a p-value < 0.05, or NS indicating a non-significant relationship.

responded favourably to flower number as this variable reflects food availability, which is in line with previous studies (Quistberg et al., 2016). Overall, we found fewer species of herbivores than flower visitors in the façade gardens. Possibly, this is because flower-visiting insects are easier to detect than herbivorous insects which are generally hidden to avoid predation. Especially during the 15 minutes we spent capturing insects per site, flower-foraging insects are much more likely to fly from one garden to another to forage, making them more visible. Both the camouflage of herbivores and flying behaviour of flower-visiting insects would explain the result in a higher detection and thus capture rate of flower visitors than of herbivores.

In contrast to our expectations, flower-visiting insects showed a significantly positive relation with vegetation cover whereas herbivorous insects did not. We propose three different mechanisms, which each may play a part in explaining the different relationship with vegetation cover between herbivorous and flower-visiting insects. These mechanisms relate to differences in foraging strategies and partially to the use and effects of pesticides (Jones and Agrawal, 2017; Lowe et al., 2019). The first conceivable mechanism involves food availability, as herbivorous and flower-visiting insects have distinctly different food sources. Herbivores forage on leaves and stems, which form the bulk of plant aboveground biomass. Conversely, flower visitors forage on the much scarcer flowers, requiring them to forage in larger areas covering multiple gardens. The second mechanism could be simply that more vegetation coverage does not necessarily equate to more food availability for herbivorous insects. For example, Fontaine et al. (2009) demonstrated that herbivores have a more specialized food network than flower visitors, which may translate into a narrower selection of plants the herbivores feed on. Consequently, flower-visiting insects that forage on nectar and/or pollen would be attracted by any community of flowering plants and cover gardens more equally (Underwood et al., 2020). This pattern can also partly be found in our results. For example, the plant *Alcea rosea* was visited by multiple flower visiting insects, yet we noticed very few herbivorous insect species tended to feed on it, likely because *Alcea rosea* is mostly eaten by the exotic and monophagous *Rhopalapion longiostre* which has a known specialistic relationship with *Malvaceae* plant family (Kuijper-Nannenga, 1995). A third mechanism may be that pesticides impact herbivores much more severely than flower visitors. Urban gardens are often designed with the intent to be either aesthetic, native or biodiverse, through rigorous design and management of the constituting (ornamental) plants (Noe et al., 2021). Gardens with high plant coverage may indicate that the owners intended to facilitate other species as well. Unfortunately, many owners regard herbivorous insects as pests and use pesticides to protect their garden, potentially resulting in a lower diversity of herbivorous insects. In addition, many ornamental plants are treated with pesticides before they are sold (Lentola et al. 2017). There is evidence that most pesticides used would also harm pollinators through different pathways than intended (Cecala and Wilson Ranking, 2021; Chagnon et al., 2015; Sánchez-Bayo, 2021).

Surprisingly, there was no relationship between the proportion of coverage by native plants in the garden and insect diversity or richness. Generally, native plants are assumed to be better for biodiversity

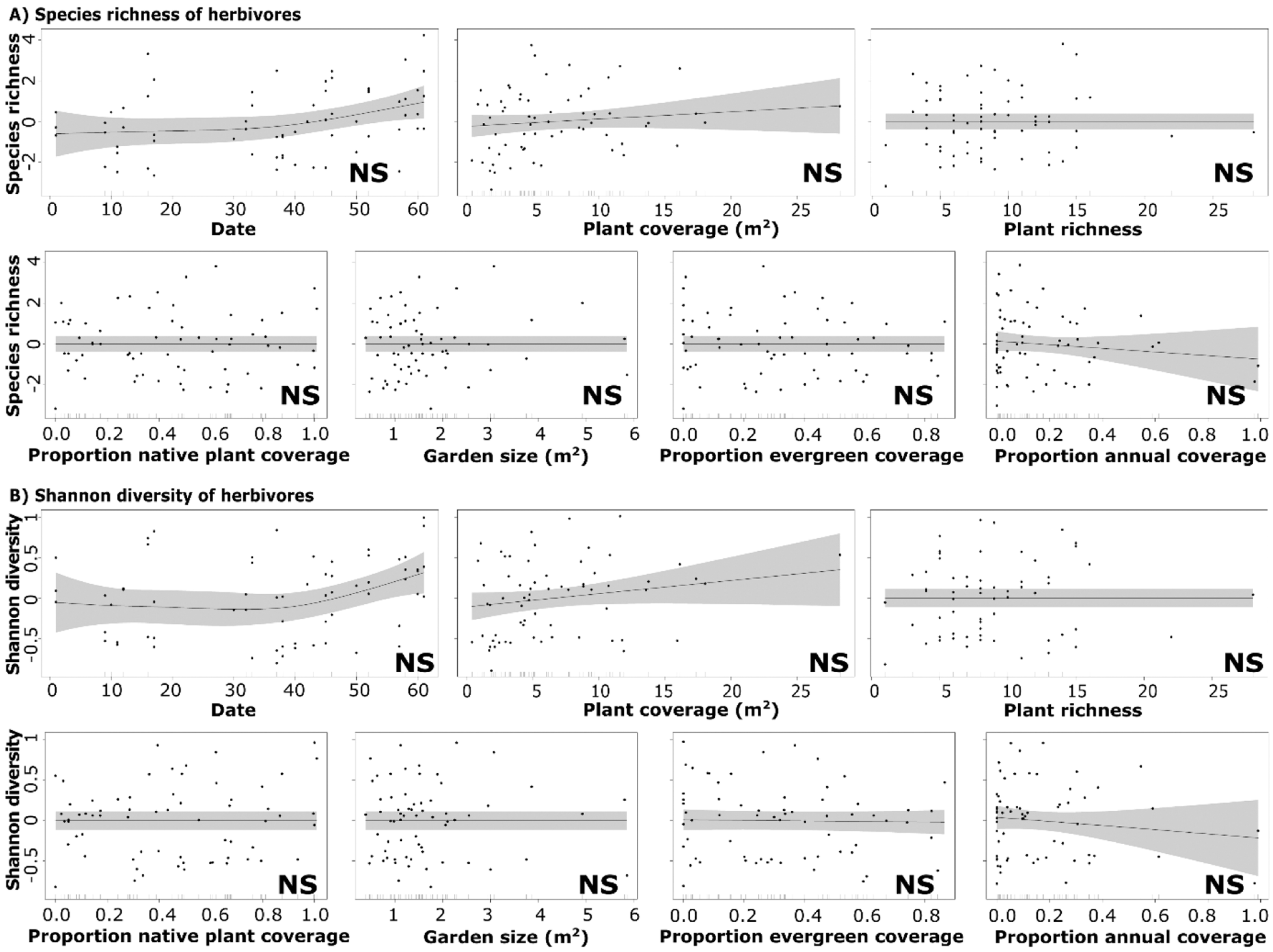


Fig. 3. Smooths of seven predictor variables in the Generalized Additive Models predicting A) Species richness and B) Shannon diversity of herbivorous insects only. Predictor panels are supplied with either a * indicating a p-value < 0.05, or NS indicating a non-significant relationship.

Table 4

Results of Generalized Additive Models (GAMs) to explain species richness and Shannon diversity of herbivorous insects in façade gardens (n = 65). The intercept is shown with parametric coefficients, whereas covariates are represented with smooth terms. For details of predictor variables see Table 1. Significant p-values (p < 0.05) are indicated in bold. *edf – Estimated Degrees of Freedom.

Herbivorous insects	Species richness GAM				Shannon diversity GAM			
Predictors	*Estimate*	*Std. error*	*t-value*	*p-value*	*Estimate*	*Std. error*	*t-value*	*p-value*
Intercept	2.47	0.24	10.27	**<0.001**	0.63	0.06	10.96	**<0.001**
Smooth terms		*edf**	*F-value*	*p-value*		*edf*	*F-value*	*p-value*
ƒ (Cardinal direction)		0.95	0.52	0.19		<0.001	0	0.49
ƒ (Date)		1.86	3.63	0.11		2.30	3.11	0.08
ƒ (Plant richness)		<0.001	0	0.80		<0.001	0	0.91
ƒ (Vegetation coverage)		0.59	0.16	0.13		0.74	0.30	0.07
ƒ (Proportion of native vegetation)		<0.001	0	0.93		<0.001	0	0.88
ƒ (Proportion of evergreens)		<0.001	0	0.59		0.13	0.02	0.72
ƒ (Proportion of annuals)		1.00	0.92	0.34		1.02	0.86	0.37
ƒ (Garden Size)		<0.001	0	0.62		<0.001	0	0.92
Adjusted R^2	0.14				0.14			
Explained deviance	20 %				19.5 %			
Observations (n)	65				65			

(Fleishman et al., 2011; Berthon et al., 2021). This is mostly because insects and plants originating from the same region are thought to have co-evolved and are therefore assumed to have innate interactions, so that non-native resources are less accessible to native insect species. More recently there seems to be a paradigm shift away from nativeness and towards species' functions and traits to explain biodiversity patterns (Davis et al., 2011). For example, some evidence suggests that canopy coverage is the most important driver for soil-surface and plant-associated invertebrate diversity (Salisbury et al., 2020). Moreover, the effect of nativeness of plant species seems to be dependent on the invertebrate taxa studied and the functional traits of the plant species (Davis et al., 2011; Salisbury et al., 2020).

We propose four mechanisms that jointly could explain the lack of a significant relationship between insect diversity and the proportion of native plants in gardens. First, exotic plants have traits or functions similar to the local native counterparts, allowing insect specialists to feed on exotic plants (Leffler et al., 2014). Second, insect species in the urban environment have adapted and broadened their diet, and therefore do not exhibit specialistic relationships with floral traits. Indeed, some evidence shows that dense urban environments are associated with diets to cover plant species more equally in small pollinators such as the *Syrphidae* and solitary bees species (Geslin et al., 2013). Therefore, an increase of exotic plant species, with different traits, may not limit overall insect plant interactions. Third, specialistic insect species that require certain native plants may be hindered by other factors than the presence of such species, such as the barrier that the 'grey' urban matrix may pose for migration (Catzim et al., 2022). A final, but more unlikely, explanation could be that a some of the found insect species may be exotic of origin, just like the plants they forage on, and are therefore adapted to the exotic plant community. In our case, an example is the relationship between the plant *Alcea rosea* and heabirvours insect *Rhopalapion longiostre*, where both the plant and the insect originate from Asia (Kuijper-Nannenga, 1995). A combination of these mechanisms likely explains why there is no apparent relationship between insect diversity and the proportion of native plant coverage in urban façade gardens. Unfortunately, our data lacks some species-level identification to establish these characteristics of the insects and plants observed. Therefore, we encourage future research to include data where possible on the origin of both the insect and plant species, and a metric on specialism for insect species. These data will allow for delineation of the above mention mechanism.

4.2. Implications for management and research

This is one of the first studies focussing specifically on urban façade gardens, a very small type of UGS. Our results show that, although small, façade gardens can support insect communities. This is regardless of cardinal direction, indicating that also garden facing north may benefit insects. The results also suggest that to support and promote biodiversity in UGS, it may be more effective to focus on increasing overall plant coverage and richness rather than specifically promoting native plant species. We suggest to increase the plant coverage by both increasing the plants present in a garden and decreasing management activities that reduce plant biomass. For example, garden-owners can be incentivized to have plants that grow vertically across the walls, increasing the habitat for insects while taking minimal soil space. In parallel, garden-owners should be encouraged to reduce management activities by not weeding unknown plants or by reducing the amount of pruning.

City managers and urban gardeners could consider incorporating non-native plants strategically, such as using them to fill gaps in plant coverage where native species may not have the required traits to survive in the harsh urban environment. Extreme care must of course be taken, to avoid use of potentially invasive species, or species that disrupt balances is delicate urban ecosystems. Many non-native plants, such as *Buddleja* or *Rhododendron*, are very attractive to (generalist) insect flower-visitors, and may increase their resources, provide food over a longer time period and consequently boost insect population sizes (Salisbury et al. 2015). Specific non-native plants could hence provide ample benefits to biodiversity in contrast to the other dominant options that the urban environment provides, namely paved surfaces. Nevertheless, while native plants were not correlated with insect biodiversity in the small façade gardens, they still play a valuable role in supporting ecosystems and provide meaningful services. Native plant species, as host plants, are known to be essential to maintain populations of their insect partner in native mutualistic relationships (Mitchell et al., 2009). For humans, native plants have also been shown to provide substantial cultural benefits at sacred sites (Gopal et al., 2018). In addition, native interactions between plants and insects also have higher educational value, and may increase the connectedness between garden owners and nature (van Heezik et al., 2012).

Future scientific endeavours should focus on a more detailed understanding of the links between plant and insect communities along the urban gradient. One of the more pressing questions is whether the relationship we observed between summed vegetation coverage and insects is moderated by the network of UGS, their configuration and connectivity in the urban matrix (Beninde et al., 2015). And at what level of urbanisation does habitat become a limiting factor to insects? Additionally, we must further acknowledge a lack of understanding of which type of species are impacted more by a shortage of suitable habitat. For example, specialist species may be more vulnerable to a species-poor plant community than generalist species. The challenge of finding the appropriate food could also be amplified by a species' capacity to forage over longer distances. Finally, our results and observed patterns solely exhibit the relationships between vegetation and insects in 65 façade gardens in two cities in the Netherlands. Care must be taken when translating these findings to other parts of the world as there may be different geographical, cultural and ecological contexts that may play an important part in explaining urban insect biodiversity. Therefore, we highly encourage researchers to replicate this study to increase robustness and omit geographic confounding factors as most garden biodiversity studies are either in Europe or North America (Delahay et al., 2023).

5. Conclusions

Protecting biodiversity across urban areas is crucial to meeting targets set by global conservation frameworks (e.g., Sustainable Development Goals, Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services and the Global Biodiversity Framework). Our results show that in Dutch cities, small urban green spaces such as façade gardens and their design are important for sustaining insect biodiversity. Together, the investigated gardens showed a large variety in plant ($n = 235$) and insect species ($n = 154$). Our analysis shows that the design of very small gardens ($\mu = 1.7 m^2$) matters, and that increasing vegetation density and plant richness led to higher insect diversity. Based on our results, an extensive network of small gardens with high vegetation density is likely a valuable addition to existing (public) urban green spaces for enhancing insect communities. We recommend policymakers and practitioners to focus on promoting non-destructive gardening and management practices, aiming to increase the density and richness of vegetation in urban gardens, in order to support and strengthen insect communities. Future research should focus on delineating a potential moderating effect of urbanisation on different types of species.

CRediT authorship contribution statement

Joeri Morpurgo: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **J. Gerard B. Oostermeijer:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization. **Margot A. Huurdeman:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Roy P. Remme:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2024.128531.

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