

## Research Paper

# Local habitat factors and spatial connectivity jointly shape an urban insect community



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## HIGHLIGHTS

- Local and spatial factors jointly shape an urban insect community.
- The impact of urbanization varied among guilds and species.
- Leaf litter can maintain species richness on isolated trees.
- A dense network of local habitats is essential to preserve biodiversity.
- Litter accumulation can be a cost-effective urban management conservation strategy.

## ARTICLE INFO

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## ABSTRACT

As the world becomes more and more urbanized, it is increasingly important to understand the impacts of urban landscapes on biodiversity. Urbanization can change local habitat factors and decrease connectivity among local habitats, with major impacts on the structure of natural food webs. However, most studies have focused on single species, or compared rural to urban habitats, which do not inform us on how to design and manage cities to optimize biodiversity. To understand the local and spatial drivers of ecological communities within urban landscapes, we assessed the relative impact of local habitat factors (sunlight exposure and leaf litter) and spatial connectivity on an oak-associated herbivore community within an urban landscape. From the local habitat factors, leaf litter but not sunlight exposure was related to herbivore species richness, with leaf litter contributing to the maintenance of high species richness on isolated trees. Guilds and species differed strongly in their response to local habitat factors and connectivity, resulting in predictable variation in insect community composition among urban oaks. Taken together, our study shows an interactive effect of local and spatial factors on species richness and species composition within an urban context, with guild- and species-specific life histories determining the response of insects to urban landscapes. To maintain biodiversity in the urban landscape, preserving a dense network of local habitats is essential. Moreover, allowing leaf litter to accumulate can be a simple, cost-effective conservation management practice.

## 1. Introduction

The world is rapidly becoming more urbanized, with major consequences for species diversity, community composition, and food web structure. Studies focusing on the differences between rural and urban areas have generally shown a decrease in native species richness and evenness in urban areas, resulting from the disappearance of some species and an increase in abundance of a few other species able to exploit urban landscapes (McIntyre, 2000; McKinney, 2006; 2008;

McKinney & Lockwood, 1999, but see Baldock et al., 2015). However, urban landscapes are highly heterogeneous, and frequently contain parks, gardens, isolated trees, remnants of native vegetation, and transitional spaces. Urban landscapes are thus characterized by a mosaic of habitats with varying degrees of quality and connectivity (Breuste, Niemelä, & Snep, 2008), with consequences for species interactions and biodiversity (Thompson, 2005; Chamberlain, Bronstein, & Rudgers, 2014; Beninde, Veith, Hochkirch, & Haddad, 2015; Baldock et al., 2019).

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The local habitat can act as an environmental filter that shapes local community structure. For example, the microclimate in some local habitats can be particularly favorable to some species, but detrimental to others, which in turn is reflected in their distributions and abundances (McKinney & Lockwood, 1999; Smart et al., 2006). In an urban environment, buildings may alter light conditions by blocking sunlight, which may in turn affect temperature and moisture (Arnfield, 2003). Management practices often include the removal of leaf litter, where insects may overwinter (Denno & McClure, 1983; Aronson et al., 2017). Such variation in local habitat factors can have a major impact on the structure of plant-feeding insect communities (Maiorana, 1981; Denno & McClure, 1983; Crawley & Akhteruzzaman, 1988; Cregg & Dix, 2001; Moreira et al., 2019).

Spatial connectivity of local habitats, which is dependent on distance between plants and obstructions between them, can strongly affect movement between habitats and thereby local community structure. The number of species occupying a particular local habitat at any given time is influenced by rates of colonization and extinction (MacArthur, 1967; Leibold, Holyoak, Mouquet, Amarasekare, & Chase, 2004). A habitat with high connectivity will often have a higher colonization rate than a patch with a lower connectivity (Hanski, 1999). Increased dispersal rates can also influence the rescue effect, where local extinctions are counteracted by colonization, resulting in the maintenance of species richness (Brown & Kodric-Brown, 1977; Hanski, 1994). Connectivity, however, does not influence all species in a community in the same way. Limits on dispersal may differ depending on ecological guild, trophic level, and degree of specialization (Tscharntke & Brandl, 2004; Clober, Baguette, Benton, & Bullock, 2012). From the perspective of specialist plant-feeding insects, host plants can be thought of as habitat islands (MacArthur, 1967; Janzen, 1968; Opler, 1974) surrounded by a matrix of buildings and other non-habitat areas (McKinney, 2008; Werner & Zahner, 2010). Once surrounded by these more urbanized areas, recolonization of a remnant patch by an insect is less likely to occur, and differences in dispersal ability among species may result in a shift in species composition (Kozlov, 1996; Dyck, Matthysen, Dyck, & Matthysen, 1999).

With both the local habitat and connectivity influencing community structure, there is a need to assess their relative importance for, and interactive effects on, different types of organisms (Leibold et al., 2004; Logue, Mouquet, Peter, & Hillebrand, 2011). In general, specialist species have been especially hard hit by habitat destruction and fragmentation (Devictor, Julliard, & Jiguet, 2008; Pearse, 2019; Start, Barbour, Bonner, & Rodriguez-Cabal, 2020), and urban landscapes are generally highly fragmented from the perspective of any specialist herbivore. However, while we know that urban landscapes on average have a lower insect diversity than nearby rural areas, we lack insights in the relative importance of local habitat factors and connectivity on the distribution of specialist (or even generalist) insects within cities. As one example, species richness of specialized gall wasps on oaks was found to be positively impacted by patch connectivity, and local habitat factors influenced species diversity (Herrmann, Pearse, & Baty, 2012). Beyond independent effects, local habitat factors and spatial processes may also interact. While a previous study did not detect interactive effects of local and landscape factors on gall wasp diversity (Herrmann et al., 2012), one may still expect such interactive effects to occur in some cases. In particular, high levels of immigration may be important in safeguarding local biodiversity when the local habitat quality is poor (Opler, 1974; Pulliam, 1988).

The overarching aim of our study was to investigate the impact of local and spatial factors on the structure of an insect community within an urban landscape. For this, we focused on the impact of the local habitat factors sunlight exposure and leaf litter and spatial connectivity on the distribution of leaf miners, galling insects, and damage by free-feeding herbivores on urban oaks (*Quercus robur*) in Stockholm, Sweden. We addressed the following questions:

- 1) What is the relative importance and interactive effect of local habitat factors (sunlight and leaf litter) and spatial connectivity on insect community descriptors (species richness, species evenness and total abundance) and damage by free-feeding herbivores?
- 2) What is the relative importance and interactive effect of local habitat factors (sunlight and leaf litter) and spatial connectivity on community composition?
- 3) What is the relative importance and interactive effect of local habitat factors (sunlight and leaf litter) and spatial connectivity on the incidence and abundance of individual herbivore species?

We hypothesized that sunlight and leaf litter, by promoting local habitat suitability, will be positively related to insect community descriptors and the incidence and abundance of individual species. We hypothesized connectivity to be positively related to insect community descriptors and the incidence and abundance of individual species because of increased dispersal of insects among oaks. Leaf litter and connectivity were hypothesized to have interactive effects on insect communities, guilds and individual species, as leaf litter may promote insect overwintering and thus maintain diverse insect communities when immigration rates are low. We hypothesized to detect differences among guilds and species in the strength of the relationships with local habitat and connectivity, based on distinct life histories.

## 2. Material and methods

### 2.1. Study system

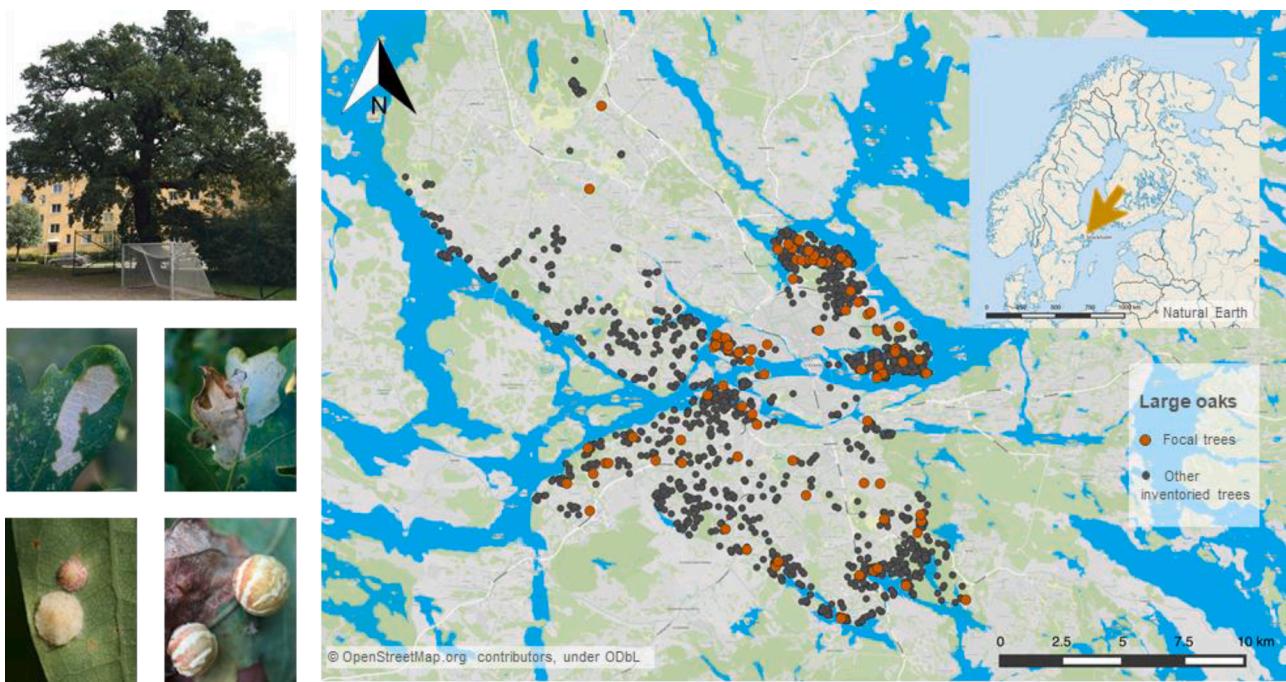
Oaks (Fagaceae: genus *Quercus*) provide habitat for a large diversity of species (Southwood, 1961). In Sweden, the pedunculate oak, *Quercus robur*, hosts nearly 1500 species, with more than half of them insects (Hultengren, Pleijel, & Holmer, 1997). Especially crucial for supporting this biodiversity are large, old oaks (Bovin, 2015; Bovin, Jaramillo, Bengtsson, Tuvendal, & Zeidlitz, 2016; Mörtberg, Zetterberg, & Gontier, 2007; Nilsson, 2007).

Oaks are attacked by several insect guilds. Among these, leaf-mining and gall-building insects are two species-rich guilds with often highly host-specific larvae that feed on and live inside plant tissue for most, if not all, of their larval stage. The larvae produce identifiable and countable structures, which lend themselves to studies on abundance and community structure (Tack, Ovaskainen, Pulkkinen, & Roslin, 2010). Leaf miner larvae form distinctive tunnels or blotches as they feed in between leaf layers (Fig. 1) (Connor & Taverner, 1997). Gallers induce host plant tissue to form spheres and other distinctly shaped structures that provide nutrients for the development of larvae within them (Fig. 1) (Stone, Schönrogge, Atkinson, Bellido, & Pujade-Villar, 2002). Most oak gall wasps have complex lifecycles, alternating between a sexual generation in spring and an asexual generation in summer or autumn (Stone et al., 2002). Their specialized relationship with oaks provides a useful model to study how habitat characteristics and distribution can shape variation in community structure (Cornell, 1985). Oaks also harbor a large diversity of generalist and specialist free-feeding herbivorous insects (Moreira et al., 2018; Richard Southwood, Wint, Kennedy, & Greenwood, 2004).

A large majority of these insect species overwinter in the leaf litter (Hering, 1951; Gustafsson, 2017), with a minority overwintering in the bark, tree hollows, soil, vegetation, or nearby buildings. Hence, the habitat below and surrounding the tree may have a major impact on the diversity and structure of the oak-associated insect community during the growing season (Herrmann et al., 2012).

### 3. Study location and tree selection

We conducted this study in Stockholm municipality, Sweden (Fig. 1). Stockholm municipality is c. 187 km<sup>2</sup>, and 40% of the land area is covered by parks and other green spaces (Stockholm Stad Utredningar,



**Fig. 1.** Examples of study organisms and a distribution map of large oak trees within Stockholm. Photos show a pedunculate oak, *Quercus robur* (top), an oak leaf with signs of free-feeding herbivory (middle left), a leaf mine of the moth *Acrocercops brongniardella* (middle right), and asexual generation galls of the wasps *Neuroterus quercusbaccarum* (bottom left) and *Cynips longiventris* (bottom right). The map shows the distribution of focal (large orange circles) and non-focal (small green circles) large oak trees within Stockholm. Large oak trees within Stockholm were mapped by Stockholm Municipality ([Stockholm Stad Ek databasen, 2006](#)). In the map inset, the arrow shows the location of Stockholm within Sweden, Europe. Photo credits: Anna E. Barr (top), Laura J. A. van Dijk (middle left and right), and Ayco J. M. Tack (bottom left and right). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2017). These green spaces include what is considered the world's first national urban park, Royal National City Park (*Kungliga nationalstadsparken*), and seven nature reserves ([Stockholm Stad Friluftsliv, 2016](#)). Pedunculate oaks are patchily distributed throughout these green areas as well as interspersed in more heavily urbanized areas (Fig. 1).

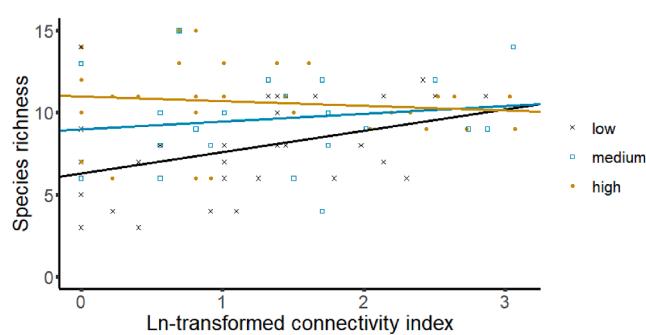
To study the impact of habitat and connectivity on the oak food web, we selected a subset of oaks from the Stockholm Oak Database (*Ekdatabasen*) ([Stockholm Stad Ek databasen, 2006](#)). This database was built during a management and restoration study ([Nilsson, 2007](#)) and includes all 2704 of the region's large oak trees (Fig. 1). The inventory includes all Stockholm oaks of at least 100 cm in trunk diameter, with the addition of some 80 cm diameter trees with a particularly high conservation value. An initial pool of study trees was selected from the database based on the following factors: i) low-hanging branches, ii) health (>75% canopy alive), and iii) location access (i.e., not growing on private property). This decreased the pool to 485 possibly usable

trees. Using a stratified design, we randomly selected ([Haahr, 1998](#)) subsets of trees to represent the different location types (e.g., park environment and deciduous forest) and connectivity levels within distinct parts of the city. We surveyed 84 of these trees in the study (Fig. 1).

#### 4. Measurement of local habitat, connectivity, and oak-associated insects

Local habitat characteristics (sunlight exposure and leaf litter) were measured from 29 July to 28 August 2017. From each focal tree, we recorded canopy sunlight exposure, using a categorical scale: i) completely freestanding, unshaded with at least 5 m from the edge of the crown to the nearest tree or other structure; ii) almost open, <25% shaded; iii) half open, with 25%-75% shaded ([Nilsson, 2007](#)). We further estimated the percentage of ground area covered by oak leaf litter within a 5 m radius around the tree trunk ([Terry, Chillingar, & Hancock, 1955](#); [Ministry of Forests, 1997](#)). Leaf litter percentage was assumed to be related to litter removal, e.g. due to management practices or by wind, and not reflective of canopy size or shape (which were rather similar between the trees).

We used the Oak Database to calculate a connectivity index to the other database oaks within a 200 m radius. We chose this distance based on previous estimates of leaf miner and galler dispersal on the pedunculate oak in northern Europe, with the large majority of dispersal events within a couple of hundred meters ([Gripenberg, Ovaskainen, Morrién, & Roslin, 2008](#), [Supplementary file S2](#); [Zheng, Ovaskainen, Roslin, & Tack, 2015](#), Fig. 2) and many individuals remaining within tens of meters ([Kozlov, 1996](#); [Gripenberg et al., 2008](#)). Based on this, we counted the number of database trees within three buffer zones surrounding the focal trees: i) 0–49 m, ii) 50–99 m, and iii) 100–199 m. To account for the lower contribution of more distant trees to the number of immigrating insects ([Hanski, 1999](#)), and as based on empirical estimates of leaf miner and galler dispersal ([Gripenberg et al., 2008](#); [Zheng et al.,](#)



**Fig. 2.** The interactive effect of leaf litter and connectivity on species richness of insects on the pedunculate oak, *Quercus robur*. The relationship is shown separately for oak trees with low (0–15%; n = 30 trees), medium (16–50%; n = 23 trees) and high levels (51–100%; n = 31 trees) of leaf litter within a 5 m radius around the tree trunk.

2015), we calculated the connectivity index as follows:

$$\begin{aligned} \text{Connectivity index} = \\ 1 \times (\text{number of } 0-49 \text{ m trees}) + \\ 0.5 \times (\text{number of } 50-99 \text{ m trees}) + \\ 0.25 \times (\text{number of } 100-199 \text{ m trees}) \end{aligned}$$

We also estimated a visual connectivity index that included all oak trees taller than 5 m that were visible within a 100 m radius from the focal tree. Trees smaller than 5 m were not included, as these trees were expected to have minor impacts on connectivity due to relatively little foliage. We counted the number of visible trees within 0–49 m and within 50–100 m from the focal tree, whereby any trees visually blocked by obstructions were not included, and calculated the visual connectivity index as follows:

$$\begin{aligned} \text{Visual connectivity index} = \\ 1 \times (\text{number of } 0-49 \text{ m trees}) + \\ 0.5 \times (\text{number of } 50-99 \text{ m trees}) \end{aligned}$$

As the results for both connectivity indices generally showed similar patterns, we only mention the results on visual connectivity when discrepancies were detected. All results on visual spatial connectivity are provided in the supplementary material (Table S3).

The insect community survey was conducted well before leaf drop, from 13 September to 3 October 2017. Species were identified by their galls and leaf mines, using knowledge from previous studies (e.g. Tack et al., 2010; Blanchet et al., 2018), specialized literature (Redfern, Shirley, & Bloxham, 2002; The British Plant Gall Society, 2011) and online guides (e.g., <https://www.plantmicrobeinsect.com/artguiden>). Some taxa (i.e., Coleophora spp., Phyllonorycter spp., and Stigmella spp.) were only identifiable to genus level, and species within these taxa have relatively similar feeding ecologies (Hering 1951).

For each tree, we first recorded the percentage of herbivory by free-feeding herbivores on 25 randomly selected leaves from reachable (i.e. low-hanging) branches. Before analyses, we calculated the average percentage of herbivory for each tree. While scoring free-feeding herbivory, we recorded the presence of any galls or leaf mines. For each species detected, we then conducted 2 min dedicated counts on reachable branches (cf. Herrmann et al., 2012). During these counts, any newly observed species were added to the list and subsequently tallied in separate 2 min dedicated counts. Once all counts were completed in this manner, we reviewed the list of possible species and spent 5 min searching for those species that had not yet been observed (Herrmann et al., 2012). If any were observed, we tallied these separately in 2 min counts. In a few instances, a species observed during the survey was not tallied during the dedicated 2 min counts, in which case we assigned the species an abundance of 1. Counting times were always limiting the amount of leaves that could be inspected, thus preventing any biases related to the numbers of leaves inspected. From the counts, we calculated multiple descriptors of the community: species richness, total abundance and Pielou's evenness index (Pielou, 1966).

## 5. Statistical analyses

To investigate the relative impacts of local habitat factors and spatial connectivity, we modeled the insect community descriptors (species richness, total abundance, Pielou's evenness), free-feeding herbivory, species-specific incidence and species-specific abundance as functions of sunlight exposure, leaf-litter coverage, and ln-transformed connectivity (Table S1). As the importance of leaf litter may depend on the spatial context of the trees, we included the interaction between leaf litter and connectivity. To allow comparison of effect sizes, we scaled the factors leaf litter and connectivity to mean zero and unit variance. Models of community descriptors were run for the total insect community and separately for the leaf-mining and galling guilds. For species richness and abundance, we used a Poisson distribution with a log link; for evenness and ln-transformed percentage of free-feeding herbivory, we

used a normal distribution with identity link; and for species incidence we used a binomial distribution with logit link. Models with a Poisson distribution were refitted using a quasi-Poisson distribution if the data were overdispersed (i.e., if the residual deviance value was greater than twice the residual degrees of freedom). Statistical outputs of the species-specific models were not corrected for multiple testing, as the high number of species-specific models would have led to strong corrections, possibly obscuring any real effects. Consequently, these results should be interpreted with care, without making strong inferences based on the significant relationship of a single species. Analyses were performed in R version 3.6.3 (R Core Team, 2020) and assessed for significance ( $p < 0.05$ ) using the *Anova* function with Type III sum of squares in the *car* package (Fox & Weisberg, 2011). We checked model assumptions with the DHARMA (Hartig, 2020) and sjPlot packages (Lüdecke, 2020). Multicollinearity of the predictor variables was low ( $VIF < 2$ , James, Witten, Hastie, & Tibshirani, 2013), and semi-variograms showed that there was no spatial autocorrelation in the model residuals (Pebesma, 2004; Gräler, Pebesma, & Heuvelink, 2016).

To examine the impact of local habitat and spatial connectivity on the insect community composition, we used generalized linear models for multivariate incidence and abundance data with the function *manyglm* in the *mvabund* package (Wang, Naumann, Wright, & Warton, 2012; Wang, Naumann, Eddelbuettel, Wilshire, & Warton, 2021). In contrast to distance-based approaches, this method accounts for the mean-variance relationship of multivariate incidence and abundance data. We modelled species incidence and abundance matrices with a binomial and negative binomial model respectively, with sunlight, leaf litter coverage, connectivity and leaf litter coverage  $\times$  connectivity as predictor variables. Significance of predictor variables was assessed with the *anova.manyglm* function. To visualize the species' relations to the gradients of the predictor variables, we plotted species scores from a NMDS ordination, and fitted vectors of the significant predictors using the *envfit* function. NMDS is an indirect ordination method preferable for community composition data (McCune & Grace, 2002). We ran a three dimensional ordination to reduce the stress and used default settings, which include the Bray-Curtis distance measure.

## 6. Results

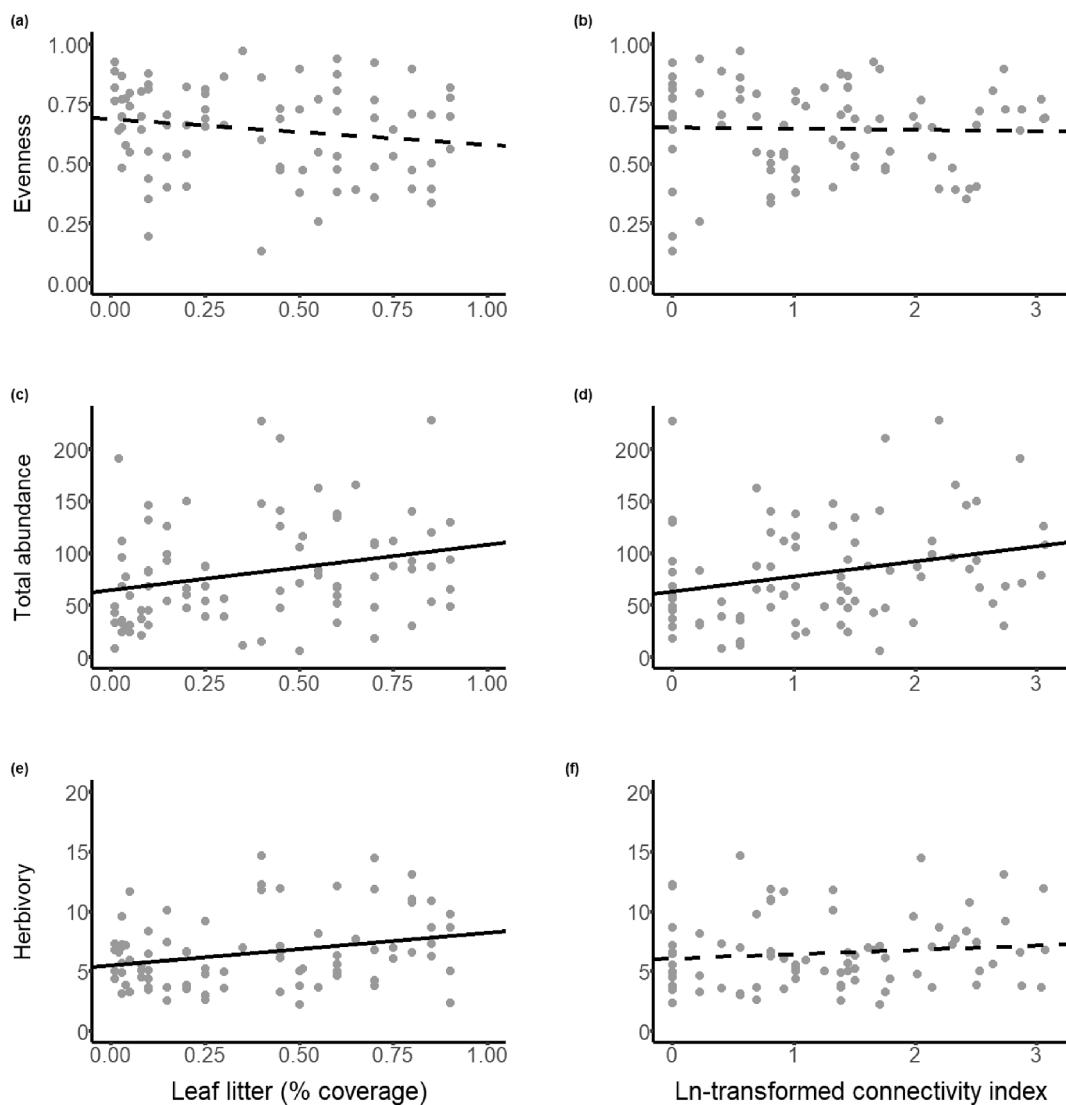
There was an interactive effect of leaf litter and connectivity on species richness, which indicated that communities were species-poor on isolated trees when leaf litter was low, but not when leaf litter was high (Fig. 2, Table 1). Leaf litter was independently and positively related to total abundance and free-feeding herbivory, but not evenness (left panels in Fig. 3, Table 1). In contrast, sunlight exposure was not related to any of the community descriptors (Table 1). Spatial connectivity was independently and positively related to total abundance, but not to evenness or free-feeding herbivory (right panels in Fig. 3, Table 1). Visual connectivity was positively related to species richness, but there was no interactive effect of the visual connectivity and leaf litter on species richness (Table S3). Total abundance, however, was affected by the interaction between visual connectivity and leaf litter, with low insect abundances for isolated trees with low leaf litter, but not for isolated trees with medium or high leaf litter (Table S3, Fig. S2).

Of the 6793 insects we observed in total, 3881 individuals were leaf miners (mean  $\pm$  sd =  $46.2 \pm 41.2$  per tree) and 2912 individuals were gallers (mean  $\pm$  sd =  $34.7 \pm 32.9$  per tree). When analyzing these guilds separately, species richness of gallers, but not leaf miners, was positively related to leaf litter and spatial connectivity (Fig. 4ab, Table 1). Evenness of gallers increased with leaf litter, whereas total abundance of gallers was not related to leaf litter (Fig. 4ce, Table 1). In contrast, evenness of leaf miners decreased, and total abundance increased, with leaf litter (Fig. 4ce, Table 1). Total abundance of gallers increased with spatial connectivity, whereas evenness and the total abundance of leaf miners were unrelated to spatial connectivity (Fig. 4df, Table 1). As for the overall community, neither gallers nor leaf miners were related to

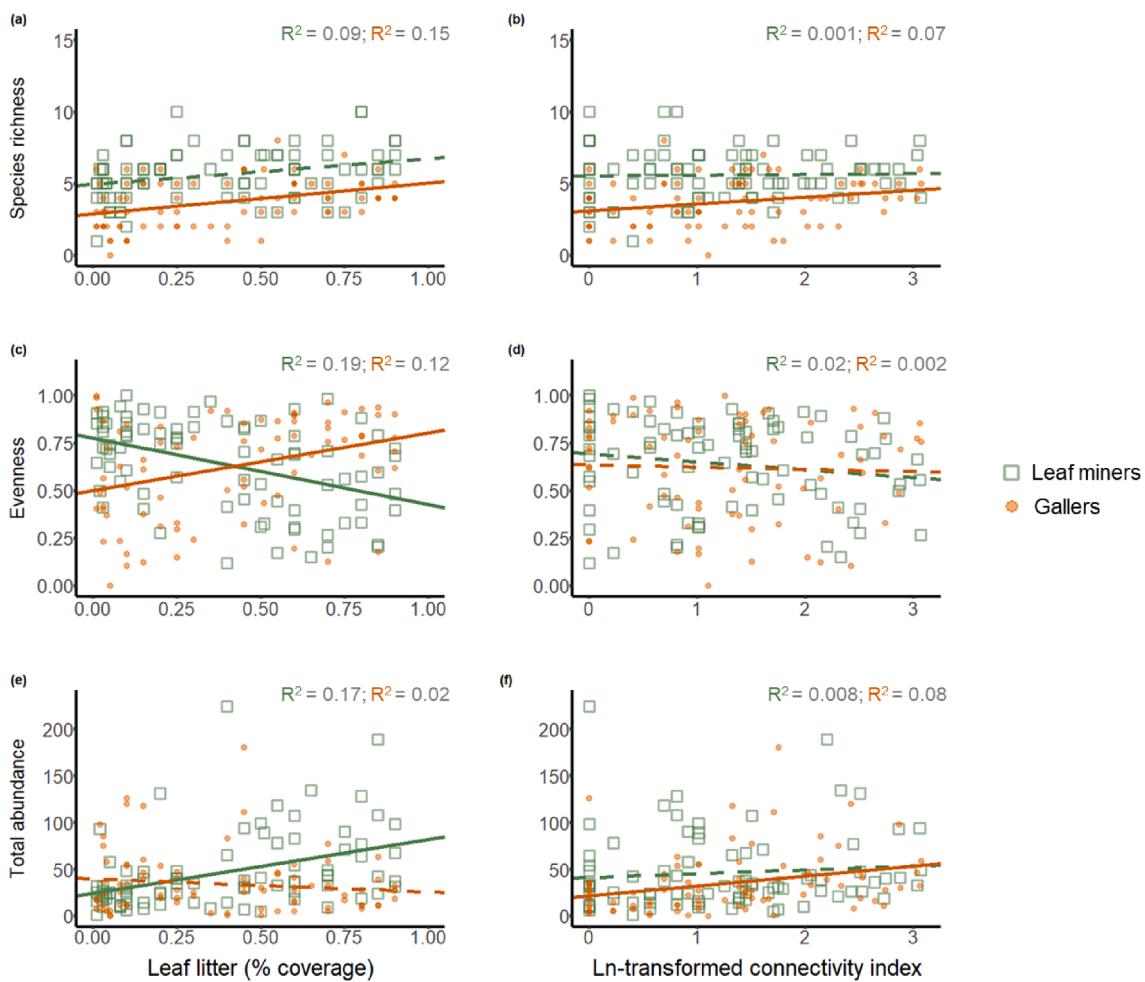
**Table 1**

The relationship between local habitat factors and spatial connectivity, and the structure of the overall insect community, leaf miners, gallers, and free-feeding herbivory on 84 trees. Shown are *P*-values from generalized linear (mixed effects) models, with significant *P*-values in bold. The direction of the response is shown in parentheses. For a summary of all fitted models, see Table S1, and for slope estimates and test statistics, see Table S2. Degrees of freedom for each predictor are given in parentheses in the column headers.

Descriptor	Sunlight exposure (df = 2)	Leaf litter (df = 1)	Connectivity(df = 1)	Leaf litter × Connectivity (df = 1)
<i>Species richness</i>				
Full community	0.861	<b>0.004 (+)</b>	0.074	<b>0.036</b>
Leaf miners	0.930	0.110	0.634	0.069
Gallers	0.920	<b>0.008 (+)</b>	<b>0.026 (+)</b>	0.235
<i>Evenness index</i>				
Full community	0.291	0.228	0.737	0.333
Leaf miners	0.351	<0.001 (-)	0.135	0.534
Gallers	0.510	<b>0.002 (+)</b>	0.553	0.384
<i>Total abundance</i>				
Full community	0.978	<b>0.021 (+)</b>	<b>0.007 (+)</b>	0.136
Leaf miners	0.353	<0.001 (+)	0.342	0.662
Gallers	0.347	0.132	<b>0.003 (+)</b>	0.183
<i>Free-feeding herbivory</i>	0.820	<b>0.025 (+)</b>	0.254	0.907



**Fig. 3.** The relationship between leaf litter and spatial connectivity, and the insect community of the pedunculate oak, *Quercus robur*. Shown are a–b) evenness, c–d) total abundance and e–f) free-feeding herbivory on 84 trees. Trendlines were predicted from simple linear regressions, with significant relationships shown as a solid line, and non-significant relationships as a dashed line.



**Fig. 4.** The relationship between leaf litter and spatial connectivity, and gallers and leaf miners on the pedunculate oak, *Quercus robur*. Shown are a–b) species richness, c–d) evenness, and e–f) total abundance of gallers and leaf miners on 84 trees. Trendlines were predicted from simple linear regressions, with significant relationships shown as a solid line, and non-significant relationships as a dashed line. Dots (orange) and squares (green) represent raw data points for gallers and leaf miners respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sunlight exposure (Table 1).

Species composition was related to an interactive effect of leaf litter and connectivity, both in terms of species incidences and abundances ( $LRT_{1,78} = 40.56$ ,  $p = 0.019$  and  $LRT_{1,78} = 39.05$ ,  $p = 0.044$  respectively; Fig. S1). The relationships between local habitat factors and connectivity and the incidence and abundance of individual species were highly variable. From a total of 22 species, five species were significantly related to local habitat factors, whereas four species were related to connectivity (Tables S4 and S5). Leaf litter was positively related to the incidence and total abundance of the leaf miner *Acrocercops brongniardella* and the incidence of the gallers *Cynips longiventris*, *Neuroterus albipes*, and *N. quercusbaccarum* (Tables S4 and S5). Sunlight exposure was only related to the galler *Biorhiza pallida*, which had the highest abundance on trees with intermediate levels of sunlight exposure (Table S5). Connectivity was positively related to the incidence of the leaf miner *Orchestes quercus* and abundance of the gallers *N. albipes* and *N. quercusbaccarum*, whereas the abundance of the leaf miner *Profenusa pygmaea* was negatively related to connectivity (Tables S4 and S5). Four species were related to the interactive effect between leaf litter and connectivity (Tables S4 and S5).

## 7. Discussion

In line with our hypotheses, both leaf litter and connectivity were positively related to insect abundance, whereas sunlight was not related

to any of the insect community descriptors. Leaf litter and connectivity interactively affected species richness, suggesting that local habitat factors are important in maintaining high species richness when immigration rates are low. Beyond these general patterns, guilds and species differed strongly in their response to local habitat factors and connectivity. Taken together, our findings suggest that local habitat factors and connectivity jointly structure insect communities on oaks within an urban setting, with major implications for management.

Identifying the local habitat factors that matter for different urban biodiversity components is of key importance for developing conservation management strategies. Here, we found that leaf litter, but not sunlight exposure, was positively related to species richness of gallers, total abundance of leaf miners, and herbivory. Matching our findings on gallers, Herrmann et al. (2012) found a strong positive impact of leaf litter on gall species richness in urban environments. Our study shows that these patterns extend to free-feeding herbivores and leaf miners, suggesting a general positive effect of leaf litter on a wide diversity of herbivores. On the other hand, we found no relationship between leaf litter and species richness of leaf miners. This finding was surprising, as we expected overwintering leaf miners to rely on leaf litter to maintain a humid environment and prevent desiccation (Price et al., 1998; Fernandes, Castro, Faria, Marques, & Greco, 2004; Yarnes & Boecklen, 2005). One reason for the absence of a relationship may be that some leaf miner species are less affected by local conditions due to high immigration rates (Connor, Faeth, & Simberloff, 1983), even though

previous studies found no differences in the dispersal ability of gallers and leaf miners on oak (Tack & Roslin, 2010; Zheng et al., 2015). Total abundance of leaf miners increased, and evenness decreased, with leaf litter, suggesting that some leaf miner species may benefit from the presence of leaf litter. Such decrease in leaf miner evenness in locations with more leaf litter, that are frequently less managed, contrasts with the general observation of higher evenness in rural than urban environments (Raupp, Shrewsbury, & Herms, 2010; Meineke, Dunn, Sexton, Frank, & Bond-Lamberty, 2013). While a previous study suggested a positive impact of sunlight on gallers, their findings differed among galler species and host trees (Kampichler & Teschner, 2002). Our study did not detect a relation between sunlight exposure and any of the insect community descriptors on oak.

While there seemed to be a generally positive relationship between leaf litter and insects at the community and guild-level, we also detected strong variation among galler and leaf miner species in their relation to leaf litter, which may be due to differences in morphology and life history. Species that are large in size or remain attached to or survive within the leaf during winter may be removed along with the litter, whereas species that stay behind are no longer protected by the leaf litter's insulative layer, which may increase the risk of desiccation, overheating and subzero temperatures. The three gallers whose incidence was positively related to leaf litter (*Cynips longiventris*, *Neuroterus albipes*, and *N. quercusbaccarum*) indeed induce relatively large galls (5–10 mm), and *C. longiventris* remains attached to leaves after leaf drop (Redfern et al., 2002). In contrast, *Neuroterus anthracinus* produces small galls (1–3 mm) that dehisce from the leaf, and this galler was unrelated to leaf litter coverage. Notably, local habitat factors may have a different impact on the distribution and abundance of the sexual and asexual galls, which can be found in the early and late season, respectively (Sinclair et al., 2015). Indeed, the abundance of a spring gall that was included in our study (*B. pallida*) was affected by sunlight, and not leaf litter. It would be interesting for future studies to explore the impacts of management and local habitat on the different generations of gall wasps. Contrary to expectation, leaf miners that are known to overwinter as pupae or larvae inside leaves (e.g., *Tischeria ekebladella* and *Tischeria dodonaea*) were not significantly related to leaf litter, whereas *Acrocercops brongniardella*, which overwinters as an adult, was positively related to leaf litter.

Connectivity was positively related to the total abundance and species richness of gallers, while leaf miners were not related to connectivity. While we only detected a relationship between connectivity and galler richness, previous studies in natural landscapes found that species richness of both gallers and leaf miners were higher on oaks in dense oak patches than on isolated oak trees (Tack et al., 2010; Kaartinen, 2011; Zheng et al., 2015). Matching our finding of higher species richness of gallers with increasing connectivity, Herrmann et al. (2012) found that the species richness of gallers increased with the number of neighboring oaks across ten Californian cities. In contrast, another study has found gall abundance and species richness to increase in isolated trees (Maldonado-López, Cuevas-Reyes, Stone, Nieves-Aldrey, & Oyama, 2015).

Although connectivity was significantly related to guild-level effects in this study—showing the strongest relationship to gall abundance and gall species richness—there was also much variation in its effects on species within guilds. Connectivity was the most important factor in determining the abundance of the asexual generations of the gall wasps *Neuroterus albipes* and *N. quercusbaccarum* and the leaf miner *Orchestes quercus*. While the dispersal abilities of *N. albipes* and *O. quercus* are unknown, *N. quercusbaccarum* has one of the community's shortest (c. 100 m) dispersal abilities (Zheng et al., 2015), possibly explaining the positive relationship between connectivity and this species. *Profenusa pygmaea* was the only leaf miner for which we detected a negative relationship between connectivity and abundance, which may be related to increased dispersal of its natural enemies. As the hymenopteran *P. pygmaea* is phylogenetically distinct from all other leaf miners in this study (which are lepidopterans), it may have a distinct parasitoid

community. Hence, while a decrease in connectivity from habitat fragmentation has been shown to more strongly affect parasitoids than their host species (Kruess & Tscharntke, 1994; Gibb & Hochuli, 2002), the parasitoids of *Profenusa pygmaea* may be less sensitive to dispersal limitation. As there is robust evidence that parasitoids can control populations of leaf miners and gallers (Morris, Lewis, & Godfray, 2004; Prior & Hellmann, 2013), one promising avenue for future research is to explore the effects of urbanization on higher trophic levels, like parasitoids and predators, and its consequences for top-down control of herbivore populations (Start et al., 2020).

The interactive effect of leaf litter and connectivity on species richness suggests that leaf litter facilitates the maintenance of species richness when connectivity is low, and therefore becomes more important in more urbanized parts of the city. Most likely, some of the species that overwinter in the leaf litter can repopulate the tree's foliage on a yearly basis when there is plenty of litter beneath them, and therefore species persistence on these trees is less dependent on immigration. In contrast, when there is little or no suitable habitat for overwintering, local populations are more prone to extinction, and immigration becomes increasingly important. In contrast to our finding, the only comparable study to date did not find an interactive effect of leaf litter and connectivity on oak gallers within an urban environment (Herrmann et al., 2012). When looking at visual connectivity, the detected patterns diverged: Species richness was affected by leaf litter and visual connectivity but not their interaction, while total abundance was affected by the interaction between leaf litter and visual connectivity, with fewer insect abundances on isolated trees with low leaf litter cover. While both connectivity measures emphasize the importance of the interplay between local habitat factors and connectivity in shaping insect communities, these results also show that different connectivity metrics may reveal different patterns. Thus, it is important for future studies to study multiple connectivity metrics, and to investigate the mechanisms that drive differences between them.

While our study identifies potential local and spatial factors within the urban landscape that can influence insect communities, we do note that the patterns observed in our study are correlational. Though we consider it very likely that our results reflect causal and biologically meaningful patterns, we cannot exclude potential underlying effects of unmeasured variables. For example, tree vigour might have caused the relationship between leaf litter and richness of insect communities; vigorous trees may have more leaves, and thus produce more litter, and may also harbour richer insect communities due to their high resource quality (Price, 1991). Thus, we need follow-up studies with an experimental approach to prove causalities. As one example, artificial removal of leaf litter could reveal the importance of litter in maintaining insect diversity on isolated versus connected trees. A main challenge in urban research is to identify the relevant variables that affect natural communities. It is thus important that future studies focus on a multitude of local habitat factors related to urbanization, such as carbon emissions, microclimate and heat islands, as well as plant traits, such as genotype and genetic diversity (Egan & Ott, 2007; Tack & Roslin, 2010; Evans, Clark, Whipple, & Whitham, 2012; Pearse, 2019). Furthermore, to uncover whether our findings are generalizable among urban landscapes and study systems, we need similar studies conducted in different cities and across a broad range of plant taxa.

While comparisons between rural and urban environments have highlighted that biodiversity is generally lower in urban environments, we lack insights into the patterns and drivers of biodiversity within urban environments. Our results indicate a joint impact of local habitat factors and spatial connectivity on a plant-feeding insect community associated with a common tree in an urban setting. Beyond supporting the importance of preserving dense tree networks, this study suggests that allowing leaf litter to accumulate in already fragmented habitats can be a simple and cost-effective way to help preserve diversity.

## 8. Data accessibility

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.63xsj3v2m>.

## 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.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2021.104177>.

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