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Research article

Bottom–up and top–down drivers influence urbanization effects on insect herbivory in oaks

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Urban forests provide essential ecosystem services, including pest control, biodiversity conservation, and human health benefits. Herbivory is a widespread biotic interaction that shapes ecosystem functions, such as primary productivity and soil fertility, which underpin these services. Urbanization can disrupt plant–herbivore interactions by altering plant traits, such as nutrient content or phenolic compounds (bottom–up factors), or by changing the abundance of herbivore natural enemies (top–down control), potentially threatening pest regulation and the ecosystem services provided by urban forests. Disentangling these drivers of herbivory is crucial for designing and managing urban forests to enhance resilience. To address this, we examined insect leaf herbivory on *Quercus robur* trees in urban and rural forest stands across 13 European cities (n = 104 trees). To assess top–down effects on herbivory, we excluded vertebrate (e.g. birds, bats), invertebrate (e.g. ants), or both groups of predators from branches on each tree using different exclosure types. We then measured insect damage on both control and predator-excluded branches. To evaluate bottom–up drivers, we measured leaf traits, specifically nutrients and phenolic compounds, and tested for correlations with leaf damage. Additionally, we recorded temperature within stands, an abiotic factor that may modulate both top–down and bottom–up forcing on herbivory. Herbivory was 24% lower on urban trees compared to rural trees. In turn, excluding vertebrate (but not invertebrate) predators increased herbivory, on average, by 40%, but predator effects were stronger in urban stands. Urban trees also had higher leaf quality, with higher nutrient and lower phenolic concentrations; however, these traits did not correlate with herbivory. Temperature was positively associated with urbanization and correlated positively with predation, but did not correlate with herbivory and did not mediate the bottom–up or top–down effects of urbanization. Overall, we find that urbanization affects herbivory through both bottom–up and top–down processes, independent of temperature-related local conditions. Despite stronger predator effects and higher leaf quality, urban trees experienced lower herbivory, suggesting that unmeasured factors, such as changes in herbivore behaviour or community structure, may play an important role. Further studies are needed to deepen our understanding and inform urban forest management.

Keywords: herbivory, multi-trophic interactions, oak, plant-herbivore interactions, plant traits, temperature, urbanization, vertebrate and invertebrate predation

Introduction

Urban forests play a crucial role in providing ecosystem services by filtering fine particles and pollutants, serving as carbon sinks that help mitigate climate warming and heat islands, and acting as buffers against flooding and reduced soil compaction (Nowak et al. 2013, 2018, Endreny 2018, Nastran et al. 2019, Barwise and Kumar 2020). They also support biodiversity by offering food resources and habitat for animals, such as insects and birds, including migratory species (Atchison and Rodewald 2006, Leston and Rodewald 2006). Accordingly, there is growing interest in understanding the ecological mechanisms that enhance urban forest resilience and sustain these services, ultimately guiding the development of sustainable management practices for urban areas. This knowledge is particularly critical in light of accelerating urbanization and the expansion of cities at the expense of natural ecosystems (Toor et al. 2024).

Ecosystem services are mediated or influenced by species interactions in natural, managed and urban ecosystems (Theodorou 2022). Relative to rural or natural ecosystems, urban environments differ in biotic (e.g. species diversity, composition) and abiotic (e.g. temperature, light, nutrients) conditions which strongly affect these interactions (Johnson and Munshi-South 2017). As a major example of an interaction outcome, herbivory is ubiquitous and exerts strong control over ecosystem functions (e.g. primary productivity, nutrient cycling) and services (e.g. carbon sequestration, soil fertility; Schowalter 2012, Stam et al. 2014, Turcotte et al. 2014), and, like other interactions, is strongly shaped by urbanization (Just et al. 2019, Moreira et al. 2019, 2024). However, the linkages between urbanization, species biotic interactions, and ecosystem functions have been little studied (Moreira and Abdala-Roberts 2023). Previous research has already explored the impacts of urbanization on herbivory by comparing urban and rural forest stands or across rural-to-urban gradients, and by assessing the influence of various biotic and abiotic factors on herbivory within urban ecosystems (Moreira et al. 2019, van Dijk et al. 2022). Reported findings are mixed, with higher insect herbivory in urban areas relative to rural habitats in some cases (Cuevas-Reyes et al. 2013, Turrini et al. 2016, Miles et al. 2022), whereas in other cases the reverse has been found (Bode and Gilbert 2016, Kozlov et al. 2017, Moreira et al. 2019). Currently, the underlying drivers of these differences remain elusive and few studies have conducted mechanistic tests to uncover them.

Effects of urbanization on herbivory can be explained by shifts in bottom–up processes (Raupp et al. 2010, Moreira et al. 2019, van Dijk et al. 2022). Namely, variation in abiotic conditions, including microhabitat-level variables, can influence herbivore abundance or behaviour (Thompson et al. 2016, Moreira et al. 2024). High air temperature, characteristic of urban heat islands, can also influence insect physiology, behaviour, and life cycles, which may lead to lower insect population sizes or reduced feeding activity (Deutsch et al. 2008, Raupp et al. 2010, Schmitt and Burghardt 2021). At the same time, abiotic forces may also act on herbivory by driving changes in plant traits, such as physical and chemical defences and nutritional quality, which influence herbivore plant choice or feeding rate (Thompson et al. 2016, Kozlov et al. 2017, Moreira et al. 2019). For example, increased resource availability due to nutrient deposition (e.g. nitrogen) can lead to higher tree growth and, in turn, lowered defences (e.g. these functions trade off) in urban environments, ultimately leading to higher herbivory (Johnson et al. 2015, Miles et al. 2019). In contrast, a recent meta-analysis found no overall correlation of leaf traits and insect herbivory at large scale (Zvereva et al. 2024). In other cases, abiotic changes (e.g. increased water runoff, soil compaction) can result in physiological stress, leading to reduced tree growth and increased or decreased allocation to defences (Dale and Frank 2017, Meineke and Frank 2018). To date, studies explicitly testing and teasing apart these direct and indirect (trait-mediated) abiotic controls of urbanization on herbivory remain limited.

Another key factor driving the effect of urbanization on herbivory are shifts in the strength of top–down control by natural enemies (Crooks and Soulé 1999, Turrini et al. 2016, Kozlov et al. 2017). Several studies have found lower predator and parasitoid diversity and abundance in urban areas, which would be expected to favour weakened top–down control of herbivores (Burkman and Gardiner 2014, Beninde et al. 2015, Carmona et al. 2020, Korányi et al. 2022). However, these community-level patterns do not necessarily translate into reduced top–down forcing, as predation and parasitism responses appear to be highly variable and often difficult to explain (Faeth et al. 2005, Fischer et al. 2012, Philpott et al. 2020). Parasitoid responses to urbanization vary, showing higher (Sumoski et al. 2009), lower (Nelson and Forbes 2014, Kozlov et al. 2017), or no difference in parasitism rates (Fenoglio et al. 2020) between urban and rural sites. Likewise, predation by insectivorous birds has been shown to increase in urban areas relative to rural sites (Kozlov et al. 2017), whereas another study found that both bird predation and associated regulation of insect herbivory were highly variable within cities, partly due to the density and diversity of trees (Schillé et al. 2025). In addition, some studies have found increased predation by ants in urban sites (Kozlov et al. 2017), whereas another work found the reverse pattern (Youngsteadt et al. 2024). Strong inferences on causal mechanisms remain difficult to explain given the paucity of studies available and a lack of mechanistic understanding of variability in natural enemy responses, including behavioural changes (Estes and Mannan 2003, Faeth et al. 2005) or shifts in predator species abundance or composition (but see Youngsteadt et al. 2024). Mixed patterns could be explained by variable responses of different predator groups or guilds to urbanization (Faeth et al. 2005). Accordingly, studies jointly manipulating (e.g. using predator exclusions) different predator groups across urban versus rural or natural sites can shed light on the effect of urbanization on top–down forcing. Furthermore, addressing abiotic drivers such as temperature into this experimental context would enable testing for abiotically driven effects of urbanization on herbivory via changes in top–down predator pressure.

To address these gaps, we investigated candidate drivers of variation in insect leaf herbivory on *Quercus robur* trees across urban and rural forest stands in and around 13 European cities. We build on previous research with this oak species, examining urbanization effects on herbivory by looking at changes in leaf chemistry, abiotic factors, and forest cover (Moreira et al. 2019, 2024, Valdés-Correcher et al. 2022). Here, we take a step further by jointly assessing bottom–up and top–down drivers as well, adding novelty to our approach through experimental manipulations of vertebrate and invertebrate predation to disentangle their independent and combined (net) effects. To this end, we measured insect herbivory, levels of secondary metabolites (phenolic compounds) and nutritional traits (nitrogen and phosphorus), and conducted a field experiment excluding vertebrates (birds, bats), invertebrates (ants), or both groups of predators. In addition, to assess abiotic controls, we collected temperature data (a key abiotic driver in this system; Moreira et al. 2024), using data loggers in both urban and rural stands. We sought to answer the following questions: 1) does leaf herbivory differ between urban and rural sites? 2) do predator effects on herbivory differ between urban and rural sites, and are these effects contingent on the type of predator? 3) do oak leaf traits correlate with leaf damage and do they differ between urban and rural sites? 4) does temperature vary due to urbanization and is it directly or indirectly (via effects on predators or leaf traits) associated with herbivory? By jointly addressing bottom–up and top–down factors, as well as predator group-specific effects and abiotically mediated effects on herbivory, this study strengthens our understanding of the ecological mechanisms governingurbanization effects on plant–herbivore interactions, ultimately affecting urban forest resilience and ecosystem services provisioning.

Material and methods

Study species

Due to its extensive geographic range (from northern Portugal to southern Finland) and presence in urban areas (Petit et al. 2002), this study used pedunculate oak (*Q. robur*) to study the effect of urbanization on plant–herbivore interactions. In southern Europe, *Q. robur*'s leaf burst occurs in April, while in northern regions, it begins in May, with leaf senescence starting in October and September, respectively. This seasonality, coupled with its broad ecological distribution, enables comparisons across different abiotic conditions to understand urbanization influences on plant defences and insect herbivory (Moreira et al. 2019, van Dijk et al. 2022).

A rich insect community is associated with pedunculate oak, including leaf chewers, miners, and gall-forming herbivores (Southwood et al. 2005, Tack et al. 2010, Tack and Roslin 2011, Marković et al. 2021). As for other oaks, pedunculate oak produces chemical defences such as phenolic compounds that serve as toxic or deterrent agents against phytophagous insects (reviewed by Moreira and Abdala-Roberts 2020). Additionally, its leaves generally contain low levels of essential nutrients, such as nitrogen and phosphorus, which can limit herbivore growth and development by restricting the resources necessary for their metabolic processes (Forkner and Hunter 2000).

Experimental design

We selected one rural and one urban forest stand in each of 13 European cities across eight countries (Fig. 1), for a total of 26 stands. Each stand had a minimum area of 2500 m², with *Q. robur* as the dominant species, accounting for over 50% of the stand density. Urban locations included stands located as close to the city center as possible (< 2 km), while rural locations were represented by stands of natural or semi-natural forests situated 10–20 km from the city limits. At the beginning of the growing season (March to June 2023, depending on the study site), we selected four adult trees (n = 104; 6–10 m in height) per stand and randomly assigned four low-hanging branches (2 m above ground level) on each tree to one of the following treatments: 1) control (no manipulation), 2) vertebrate predator exclusion (mainly birds and bats), 3) invertebrate predator exclusion (mainly ants), and 4) joint vertebrate and invertebrate predator exclusion. Vertebrate predator exclusions consisted of 1.5 × 1.5 m wide agricultural mesh netting (1.9 cm mesh diameter,

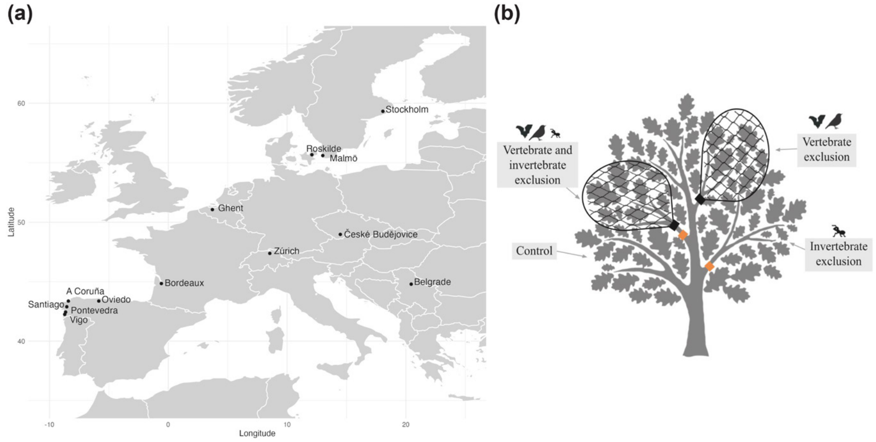

Figure 1. (a) Map showing the thirteen European cities where we selected urban and surrounding rural forest stands. (b) Schematic representation of an adult *Quercus robur* tree with the four experimental exclusion treatments.

Feitore) installed on each branch (Nell and Mooney 2019). To exclude invertebrates, we placed bands of sticky paste (Tanglefoot, Tanglefoot Company) around the base of the selected branches (Moreira et al. 2012a) (Fig. 1). By following this experimental design, we were able to test for differences in the strength of top–down effects by each group as well as their combined effects. In addition, information on non-additive dynamics due to interactions between predator groups (e.g. complementarity versus interference or intraguild predation; Polis and Holt 1992, Rakowski et al. 2021) can also be drawn from observed patterns, e.g. if the exclusion of each group separately in both cases led to a significant increase in herbivory and their joint exclusion produced the same (or lower, e.g. non-significant difference relative to controls) magnitude of increase (suggestive of antagonistic interactions, e.g. intraguild predation or interference; Finke and Denno 2004), or, if joint exclusion led to disproportionate increase versus controls relative to increases from separate exclusions (i.e. a greater than additive increase considering both individual exclusion treatments; suggestive of synergy between predator groups, e.g. complementarity via prey partitioning; Snyder et al. 2006).

Leaf sampling and herbivory measurements

At the end of the growing season (August–September 2023, depending on the study site), for each tree we randomly collected ten fully expanded leaves per selected branch (i.e. 40 leaves in total per tree). For branches with vertebrate predator exclusions, we ensured that leaves in contact with the net, where predators might have access, were avoided. Collected leaves were dried at 40°C for 48 h and shipped to the Misión Biológica de Galicia (Pontevedra, Spain). Most leaf damage (> 95%) was caused by chewing insects, hereafter referred to as 'herbivory'. All leaves were photographed and we estimated chewing herbivory by calculating the percentage of leaf area removed from each leaf by using the BioLeaf – Foliar AnalysisTM mobile app (Brandoli Machado et al. 2016).

Quantification of leaf phenolic compounds

For each tree, we selected four leaves (out of the ten originally sampled) from control branches showing little or no herbivore damage, oven-dried them at 40°C for 48 h, and ground them together using liquid nitrogen to obtain a single pooled sample for phenolic and nutrient analyses. We used undamaged leaves to partially control for variation associated with induced defences, specifically local induction. We extracted phenolic compounds from 20 mg of dry pulverized leaf tissue with 1 ml of 70% methanol in an ultrasonic bath for 15 min, followed by centrifugation (Moreira et al. 2014). We then transferred the extracts to chromatographic vials. For phenolic quantification, we used ultra-high-performance liquid chromatography system (UHPLC; ACQUITY UPLC H-Class PLUS; Waters) equipped with a UV/VIS photodiode array detector. The compound separation was carried out as detailed in Vázquez-González et al. (2025). We identified four groups of phenolic compounds: 1) flavonoids; 2) ellagitannins and gallic acid derivatives ('hydrolysable tannins' hereafter); 3) proanthocyanidins ('condensed tannins' hereafter); and 4) phenolic acids. Classification was based on a combination of molecular ion masses, fragmentation patterns, UV absorbance spectra, and chromatographic retention times, which were compared with commercial standards and published references. These groups are widely recognized for their involvement in plant defence against herbivores (Mithöfer and Boland 2012). Quantification of each group was performed using external calibration curves with six standard concentrations (0.16, 0.8, 4, 20, 100 and 500 μg ml^{-1}). Results were expressed in mg of compound per g of dry tissue, using rutin for flavonoids, gallic acid for hydrolysable tannins, catechin for condensed tannins, and ferulic acid for phenolic acids as the respective standard equivalents (Moreira et al. 2018, Vázquez-González et al. 2025).

Quantification of leaf nutrients

To quantify phosphorus and nitrogen concentration in undamaged leaves from control branches, we used colorimetric methods (Moreira et al. 2012b). Nitrogen was quantified using the indophenol blue method, and phosphorus using the molybdenum blue method, with absorbance measured at 650 nm and 700 nm, respectively, using a Biorad 650 microplate reader (Walinga et al. 1995). Both concentrations were expressed in mg g^{-1} dry tissue.

Microhabitat abiotic data (air temperature)

At the beginning of the growing season, we installed an Elitech RC-5 data logger (Elitech) 1.5 m above the ground on a tree in each stand to quantify air temperature. Loggers were positioned on shaded branches to avoid direct sunlight and recorded ambient temperatures hourly throughout the duration of the experiment. For statistical analyses, we used the mean temperature, standard deviation, and maximum and minimum temperatures for each device based on data recorded hourly throughout the sampling period. Mean temperature differed significantly between rural and urban stands ($F_{1,8} = 5.53$, $p = 0.04$) being higher in urban stands (18.11 ± 0.3°C) compared to rural ones (17.59 ± 0.4°C).

Data analysis

First, we ran a linear mixed model (LMM) to test the effects of urbanization (two levels; urban and rural), predator exclusion (four levels; vertebrate-excluded, invertebrate-excluded, vertebrate and invertebrate-excluded, and control branches), and their interaction (all fixed factors) on herbivory (mean percent leaf area removed per branch). We also included city (13 levels), stand nested within city (26 levels), and tree nested within stand (101 levels, as we lost data from three trees during the experiment) as random factors, with the latter accounting for non-independence among branches sampled from each tree. Herbivory was square root-transformed to achieve normality of residuals. We ran follow-up post hoc mean contrast analyses to test for differences between groups within each factor (urbanization and predator exclusion). The significance of random factors was assessed with likelihood ratio tests (LRT). Second, we ran LMMs to test the effects of urbanization (a fixed factor with two levels: urban versus rural) on leaf traits using data from control branches only, focusing on total phenolics (overall and by phenolic group), as well as nitrogen and phosphorus concentrations. Thesemodels also included city (13 levels) and stand nested within city (26 levels) as random factors. To achieve normality of residuals, we squared root transformed flavonoids, and log-transformed condensed tannins, hydrolysable tannins, and phosphorous content to achieve normality of residuals. We also performed LRT to assess the significance of random effects.

In addition, we ran two piecewise structural equation model (PSEM) (Lefcheck 2016) to elucidate the mechanistic pathways linking urbanization and herbivory. First, we conducted a 'bottom–up model' using data from control branches testing of relationships between urbanization, microhabitat temperature, leaf traits and herbivory. Second, we ran a 'top–down model' testing the associations between urbanization, microhabitat temperature, and predator exclusion effects on herbivory. Before running the PSEMs, we summarized variation in temperature-related variables using the first axis of a PCA which explained 52% of the variation and was strongly positively related to mean temperature, maximum temperature, and temperature standard deviation, and negatively related to minimum temperature. We used the PC z-score for the PSEMs. We used phenolic acids, hydrolysable tannins, and phosphorus as they were found to be significantly modulated by urbanization in the LMMs. We computed predation effects on herbivory as Hedges' *g* effect size for predator exclusion, the standardized mean difference between control and branches subjected to predator exclusion, where more negative values indicate lower herbivory on control branches relative to predator-excluded branches (stronger reduction of herbivory by predation). We computed effect sizes only for the vertebrate exclusion treatment level, as this was the only one that significantly influenced herbivory in the LMMs. In the bottom–up PSEM, we assessed the following direct effects: 1) urbanization (encoded as a binary variable: rural = 0, urban = 1) on temperature PC, leaf traits, and herbivory; 2) temperature on leaf traits (phenolic acids, hydrolysable tannins and phosphorus) and herbivory, and 3) leaf traits on herbivory. In addition, we tested the indirect effects of 4) urbanization on leaf traits via temperature, and 5) urbanization on herbivory via leaf traits or temperature. For the top–down model, we tested for the direct effects of: 1) urbanization on temperature PC and predation effects (Hedges' *g*), and 2) of temperature on predation effects, as well as 3) the indirect effect of urbanization on predation via temperature. In both models, standardized path coefficients were used to estimate direct relationships, whereas indirect effects were computed as bootstrapped coefficients representing the product of intervening direct effects along the specified causal pathways. Both models included city as a random factor and herbivory data were square root transformed to achieve normality.

All statistical procedures were carried out in R ver. 4.2.1 (www.r-project.org). To fit linear mixed-effects models, we used the *lmer* function included in the 'lmerTest' package (Kuznetsova et al. 2017), adopting type III sum of squares and estimating degrees of freedom using the Satterthwaite method via the *anova* function. Variance components for random effects were obtained with *summary*, and their significance was assessed through likelihood ratio tests using *ranova*. Post hoc comparisons were conducted using the *emmeans* function from the 'emmeans' package (Lenth et al. 2023), applying the Sidak correction and estimating degrees of freedom based on the Kenward–Roger approximation. For structural equation modelling, we used the *psem* function from the 'piecewiseSEM' package (Lefcheck 2016) to estimate standardized path coefficients (direct effects), and the *semEff* function from the 'semEff' (Lefcheck 2016) package to derive bootstrapped estimates of indirect effects and their standard errors. Principal component analysis (PCA) was performed with the *PCA* function from the 'FactoMineR' package (Lê et al. 2008). We computed Hedges' g as a measure of effect size for predation, to be included as an endogenous variable in the PSEM, using the *cohen.d* function with correction from the 'effsize' package (Torchiano 2020).

Results

Effects of urbanization and predator exclusion on leaf herbivory

The LMM revealed a significant effect of urbanization (urban vs. rural stands) on leaf herbivory (Table 1), with urban trees exhibiting a 24% lower mean herbivory than rural trees (urban: 5.77 ± 0.42%; rural: 7.62 ± 0.41 %; Fig. 2). Predator exclusion also had a significant effect on leaf herbivory (Table 1), with vertebrate-excluded branches exhibiting approximately 40% higher mean herbivory than control branches; invertebrate exclusion and joint predator type exclusion, on the other hand, had no significant effect on herbivory (control: 5.44 ± 0.46%; vertebrate-excluded: 7.84 ± 0.67%; invertebrate-excluded: 5.95 ± 0.54%; vertebrate and invertebrate-excluded: 7.74 ± 0.68%) (Fig. 2). There was no significant interaction between urbanization and predator exclusion (Table 1, Fig. 2).

Effects of urbanization on leaf traits

Urbanization had a marginally significant effect on total leaf phenolics (Table 2), with rural oak trees exhibiting a 14% higher mean concentration than urban trees (rural: 13.9 ± 0.80 mg g^{-1} DW; urban: 12.2 ± 0.84 mg g^{-1} DW). Analyses for each group of phenolic compounds similarly indicated a marginally significant effect of urbanization on phenolic acids and a significant effect on hydrolysable tannins (Table 2, Fig. 3d), with higher mean values for rural, compared to urban stands in both cases (phenolic acids: 2.05 ± 0.12 mg g^{-1} DW in rural stands, 1.72 ± 0.11 mg g^{-1} DW in urban stands; hydrolysable tannins: 0.48 ± 0.07 mg g^{-1} DW in rural stands, 0.55 ± 0.08 mg g^{-1} DW in urban stands; Fig. 3d). There was no significant effect on flavonoids or condensed tannins (Table 2, Fig. 3c). For leaf nutrients, urbanization had a marginally significant effect on phosphorus concentration, with rural oak trees showing a lower mean value than urban trees (rural: 0.99 ± 0.29 mg g^{-1} DW; urban: 1.1 ± 0.04 mg g^{-1} DW; Fig. 3), but had no effect on nitrogen (Table 2, Fig. 3).

Table 1. Summary of the linear mixed model evaluating the influence of herbivory (urban and rural), predation (vertebrate-excluded, invertebrate-excluded, vertebrate and invertebrate-excluded and control branches), and their interaction on the percentage of leaf herbivory on *Quercus robur* trees. The table reports F-statistics, degrees of freedom (numerator, denominator), and associated p-values for each fixed effect as obtained from the anova analysis. It also includes the variance (σ^2) explained by the random factors and significance based on a likelihood ratio test (LRT). Statistically significant or marginal p-values are indicated in bold.

	DF (num, den)	F-value	p
Fixed effects			
Urbanization	1, 86	5.17	**0.04**
Predation	3, 277	6.74	**< 0.001**
Urbanization × Predation	3, 277	0.80	0.50
Random effects	σ^2	LRT	p
Tree	0.09	5.93	**0.02**
Stand	0.20	14.22	**<0.001**
City	0.33	4.47	**0.03**
Residual	0.61	-	

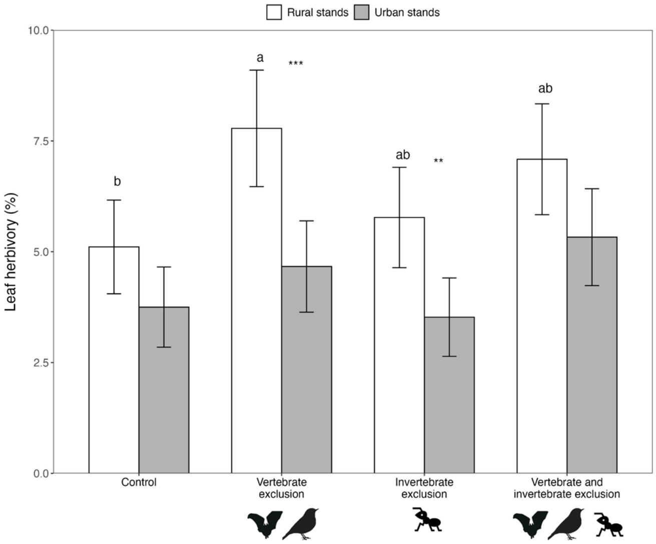

Figure 2. Effect of urbanization (two levels; urban and rural stands) and the top–down effect of predation by vertebrates and invertebrates (four levels; vertebrate-excluded, invertebrate-excluded, vertebrate and invertebrate-excluded and control branches) on the percentage leaf herbivory on oak trees. Bars represent emmeans (± SE) as predicted by the corresponding linear mixed model (n = 380). Different letters indicate significant differences between predation treatments for rural stands (there were no differences between groups for urban stands). Asterisks highlight pairwise contrasts where the urban–rural difference was significantly different from zero within each predator exclusion group (** = p < 0.01, *** = p < 0.001).

Mechanisms for urbanization effects on herbivory

Bottom–up PSEM

We found a significant positive association between urbanization and temperature, with urban stands being warmer than rural stands (Supporting information, Fig. 4a). Additionally, urbanization had a marginally significant negative effect on phenolic acid content and a significant positive effect on hydrolysable tannins and phosphorus content (Supporting information, Fig. 4a). Temperature did not have a significant effect on leaf traits or herbivory, nor did leaf traits have a significant direct effect on herbivory (Supporting information, Fig. 4a). Consequently, we did not find significant indirect effects of urbanization on leaf traits via temperature, nor of urbanization on herbivory via leaf traits or temperature (Supporting information).

Top–down PSEM

Urbanization significantly positively correlated with vertebrate predator exclusion indicating that the exclusion effect on herbivory was less negative, (i.e. weaker) on urban than on rural trees (Supporting information, Fig. 4b). Again, as in the bottom-up model, there was a significant positive association between urbanization and temperature, and in this case also

Table 2. Results from the linear mixed model testing the effect of urbanization (urban and rural), on individual leaf traits in control branches (without predator exclusions). The table reports F-statistics, degrees of freedom (numerator, denominator), and associated p-values for each fixed effect of the corresponding model. It also includes the variance (σ^2) explained by random factors and significance based on a likelihood ratio test (LRT) are shown. Significant or marginal p-values are indicated in bold. The degree of significance is indicated with: ● = $p < 0.1$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

	Fixed effect	Random effects		
	F-value $_{(NumDF,\ DenDF)}$	σ^2 $_{(LRT)}$		
	Urbanization	Stand	City	Residual
Total phenolics (mg g^{-1})	**3.93** $_{\mathbf{(1,86)}}$ ●	0.00 $_{(0.00)}$	**12.06** $_{\mathbf{(11.57)}}$ ***	0.46
Flavonoids (mg g^{-1})	1.26 $_{(1,86)}$	**0.00** $_{\mathbf{(0.00)}}$ ***	**0.19** $_{\mathbf{(10.75)}}$ **	0.35
Phenolic acids (mg g^{-1})	**3.97** $_{\mathbf{(1,12)}}$ ●	0.07 $_{(1.13)}$	0.07 $_{(0.84)}$	0.51
Condensed tannins (mg g^{-1})	0.42 $_{(1,13)}$	0.03 $_{(1.45)}$	**0.13** $_{\mathbf{(6.81)}}$ **	0.16
Hydrolysable tannins (mg g^{-1})	**10.57** $_{\mathbf{(1,86)}}$ **	0.00 $_{(0.00)}$	**1.07** $_{\mathbf{(4.15)}}$ *	3.99
Phosphorus content (mg g^{-1})	**3.48** $_{\mathbf{(1,12)}}$ ●	**0.02** $_{\mathbf{(18.69)}}$ ***	0.01 $_{(0.73)}$	0.02
Nitrogen content (mg g^{-1})	0.17 $_{(1,12)}$	2.71 $_{(2.64)}$	**11.38** $_{\mathbf{(7.29)}}$ **	11.03

a marginally significant effect of temperature on vertebrate predator exclusion (Fig. 4b). However, there was no significant indirect effect of urbanization on predation via temperature (Supporting information).

Discussion

Urbanization effects on leaf herbivory

–We provide robust evidence for urbanization effects on herbivory based on a broad sampling scheme encompassing marked variation in urban and natural forest features across western Europe. Herbivory was consistently lower on *Q. robur* trees in urban locations compared to rural ones, in line with previous studies on this oak species (Moreira et al. 2019, 2024). Similarly, Kozlov et al. (2017) reported reduced leaf area loss to insect herbivores on 11 tree species, including *Q. robur*, in urban (vs. rural) sites across 16 European cities. These patterns are consistent with the plant vigor hypothesis (Price 1991), which predicts that herbivores preferentially feed on larger, faster-growing, or otherwise higher-quality plants – traits that may be less pronounced in urban trees due to environmental constraints or altered resource availability. However, not all studies support the pattern of lower herbivory in urban settings. Earlier work summarized by Raupp et al. (2010) reported higher herbivory on urban trees, and studies on herbaceous plants similarly found elevated herbivory in urban sites (Cuevas-Reyes et al. 2013,

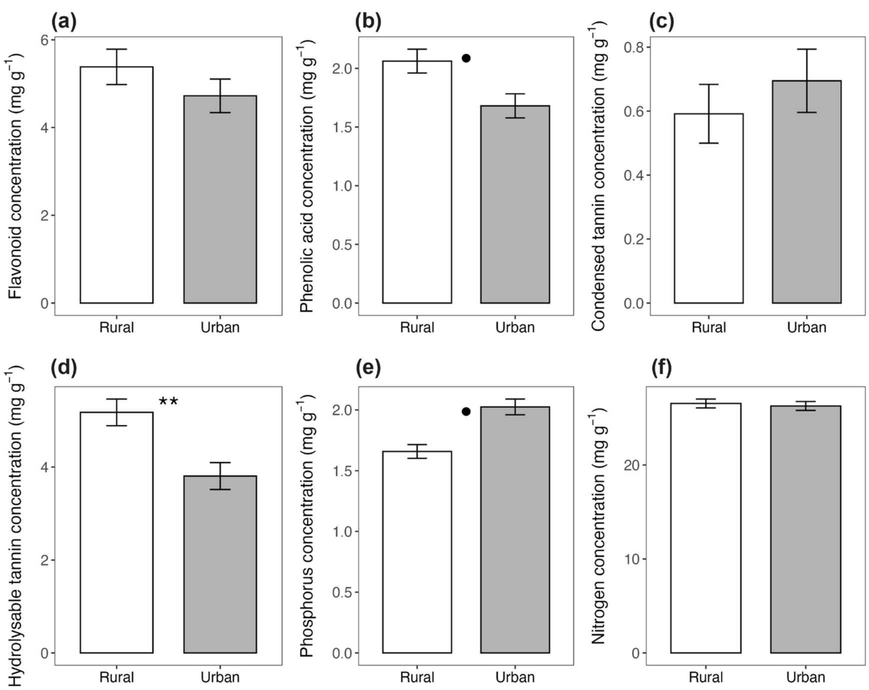

Figure 3. Effect of urbanization (rural versus urban stands) on the concentration of (a) flavonoids, (b) phenolic acids, (c) condensed tannins, (d) hydrolysable tannins, (e) phosphorus content, and (f) nitrogen content. Bars represent emmeans (± SE) as predicted by the corresponding linear mixed model. Statistical differences between urban and rural stands are indicated with asterisks (* = $p < 0.05$, ** = $p < 0.01$).

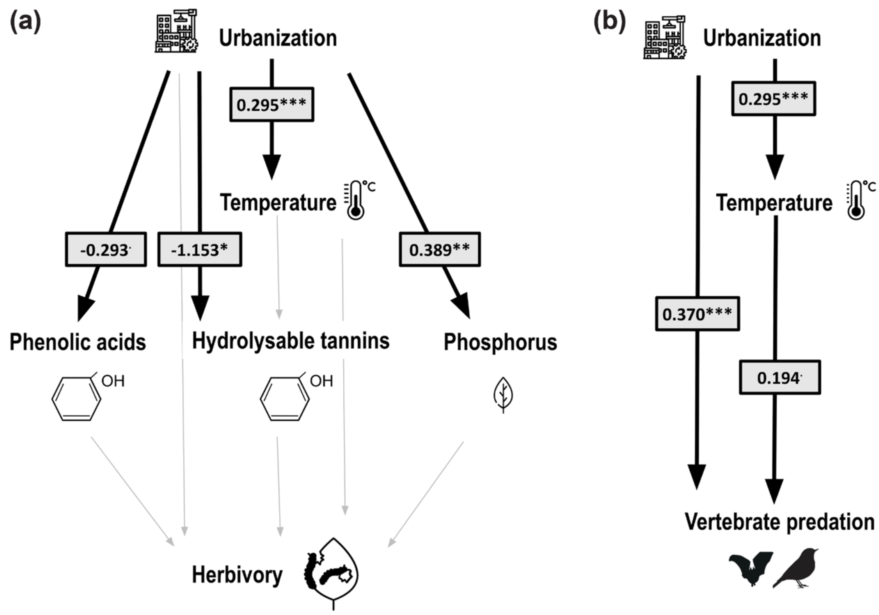

Figure 4. Diagram showing results from piecewise structural equation model (PSEM) testing for direct and indirect associations between (a) urbanization, temperature (axis 1 of a principal components analysis of the abiotic factors), leaf traits (phenolic compounds, hydrolysable tannins, and phosphorus), and herbivory; and (b) urbanization, temperature (axis 1 of the PCA of the abiotic factors), and predator exclusion (vertebrate, invertebrate or vertebrate and invertebrate exclusions calculated as Hedges' g effect sizes) on oaks across the 13 cities in Europe. Significant or marginally significant (● = $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and non-significant path coefficients (arrows) are in black and grey, respectively. Indirect associations were not significant and are therefore not shown for ease of visualization. (a) Fisher's C = 73.41, p = 0.000 (model AICc =1479.686). (b) Fisher's C = 18.47, p = 0.005 (model AICc = 597.592).

Turrini et al. 2016). Insect responses are often species-specific, as observed in *Populus* (Dobrosavljević et al. 2023), and some of this variation may be linked to traits associated with feeding guilds (Valdés-Correcher et al. 2022). Focusing on traits such as herbivore diet breadth and mobility could help clarify the mechanisms behind differing herbivory responses to urbanization. More broadly, comprehensive data on herbivore community composition are needed to determine how urban environmental filters shape insect community structure and, in turn, influence the amount and type of herbivory in urban versus rural forest stands.

Urbanization effects on predation

We found a significant effect of predator exclusion on herbivory, but this was only observed in the case of vertebrate predators. Branches where vertebrates were excluded showed higher leaf damage, as expected, indicating that vertebrates (mainly birds, bats) exert top–down control over herbivory by leaf-chewing insects. In contrast, excluding invertebrates or applying dualexclusion did not result in any detectable changes in herbivory. Together, these findings align with previous studies highlighting net negative effects of vertebrate predators on herbivory, often stronger than predation pressure exerted by invertebrate predators (Mooney et al. 2010, Romero and Koricheva 2011, Roslin et al. 2017, Nell and Mooney 2019). It is also possible that vertebrate predation compensated for invertebrate predator exclusion, preventing an increase in herbivory. However, we found no evidence suggestive of non-additive effects between predator groups, i.e. dualexclusion tended to produce the same effect than vertebrate-only exclusion. This condition was possibly precluded by the lack of invertebrate predator effects (i.e. invertebrate predator exclusion) on insect herbivory, and is consistent with the idea that this predator group did not exert biologically meaningful top–down control. That said, further work on predator species composition, prey composition, and direct observations of predator behaviour (e.g. abundances and behaviours of invertebrates and birds when together and when the other group is excluded) is needed before discarding invertebrate predator effects and interactions between predator groups influencing top–down control.

Although the LMM showed no detectable interaction between urbanization and predator exclusion, the PSEM indicated that the effect of vertebrate predator exclusion on herbivory was weaker in urban than in rural stands. Contrary to this, Kozlov et al. (2017) reported that leaf miner mortality caused by ants and birds, as well as attack rates by birds on dummy larvae, were higher in cities compared to rural habitats. More recently, Schillé et al. (2025), also using dummy caterpillars, instead found no difference in bird attack rates in urban areas, despite observing a reduction in bird diversity and a shift toward generalist bird species in more urbanized areas. Besides changes in predator composition or abundance (favouring lower predation), other reasons for decreased bird predation on *Q. robur* at urban sites could be changes in bird foraging behaviour, such as increased movement between and shorter residence times within patches leading to lower consumption rates on individual trees (e.g. weakening of density-dependent responses) as a result of habitat fragmentation and reduced connectivity (Van Bael et al. 2008, Muiruri et al. 2016). Additionally, lower diversity or abundance of both trees (Stemmelen et al. 2022, Schillé et al. 2025) and prey (Korányi et al. 2021) could explain weaker top–down control in urban environments. On the other hand, the lack of an effect of invertebrate predator exclusion was consistent across environment types and did not correlate with urbanization, suggesting that invertebrate predator effects on *Q. robur* leaf-chewer herbivory were overall negligible and unaffected by urbanization. Interestingly, a recent study by Youngsteadt et al. (2024) found higherpredation by ants in rural compared to urban sites, presumably due to lower ant species richness at urban sites. More work with dominant oaks and other temperatre tree species is needed to examine changes in both vertebrate and invertebrate predator community structure and behaviour, in addition to exploring how other types of insect herbivory which might respond to invertebrate predators.

The fact that damage was overall lower in cities despite weaker predator effects suggests that top–down forcing was not the primary factor responsible for reduced leaf damage at urban sites. Other factors acting in the opposite direction could be at play, reducing herbivore abundance or diversity, and thus leading to weaker herbivore pressure in urban environments. These factors include habitat fragmentation or differences in microclimatic conditions contributing to behavioural changes (Burkman and Gardiner 2014, Schmitt and Burghardt 2021, van Dijk et al. 2022, Youngsteadt et al. 2024), similar to those discussed above for predators. For example, Youngsteadt et al. (2024) found that the effects of predatory ants were stronger in rural compared to urban sites, but that overall herbivory rates did not differ between these sites. They suggest that lower insect herbivore density or diversity due to other conditions prevent an increase in herbivory in urban areas despite reduced top–down control. Further studies conducting predator exclusions across multiple seasons, along with data on changes in predator behaviour, abundance, and composition, are needed for a better understanding of how urbanization shapes top–down forcing on herbivory. Measuring herbivory at different time points in the season (e.g. early spring or mid-summer) would also provide more detailed information on changes in predator–herbivore interactions, particularly during specific periods of high insect abundance, including short-lived outbreaks.

Urbanization effects on leaf traits

Urbanization was associated with lower levels of leaf phenolic compounds and higher nutrient content, particularly phosphorus. These findings suggest higher leaf quality for herbivores in urban areas, supporting previous research with *Q. robur* (Moreira et al. 2019). That said, higher leaf quality would, in principle, favour higher herbivory at urban sites but this was not the case. Accordingly, SEM results indicated that none of the leaf traits measured correlated with herbivory, and, correspondingly, there was no indirect effect of urbanization on herbivory via plant traits. In a previous study on *Q. robur*, a significant correlation between herbivory and leaf phosphorus was found, but this trait did not mediate the urbanization effect on herbivory (Moreira et al. 2019). Similarly, work with *Fraxinus excelsior* (Moreira et al. 2024) and other temperate trees (Kozlov et al. 2017) found changes in tree leaf chemistry between urban and rural sites, but these did not explain differences in herbivory. As a whole, work conducted to date with *Q. robur* and other temperate tree species suggest that plant trait-mediated bottom–up effects of urbanization on herbivory are of limited importance. Further mechanistic work assessing the relative importance and interactions between urbanization, plant traits, and herbivory is needed, including the measurement of additional leaf traits in situ at different time points, such as early in the season, as well as measurements on offspring of maternal plants to control for environmental effects and test for population divergence in defensive traits. These data can in turn be linked with in situ changes in herbivore and predator pressure.

Temperature as a driver of urbanization effects

Urbanization was associated with higher values for PC1 temperature, i.e. higher mean annual temperatures and temperature variability (seasonality) within forest stands. However, temperature did not correlate with herbivory, consistent with a recent study on *Q. robur* which also recorded microhabitat temperature variation (Moreira et al. 2024). Furthermore, in agreement with previous work, there was no indirect link between temperature and herbivory via leaf traits, presumably precluded by the lack of correlation between leaf traits and leaf damage. Therefore, we find no support for temperature-associated effects of urbanization on herbivory, at least during this study and based on the leaf traits measured. Recent work by Santangelo et al. (2022) with white clover *Trifolium repens* showed that lower herbivory and higher temperatures in cities have selected for reductions in plant chemical defences in urban relative to rural sites. Although this study was not designed or aimed at assessing direct and indirect links between abiotic factors, plant traits and herbivory, it importantly highlights urbanization effects on plant defences and plant–herbivore interactions acting through changes in the joint action of biotic and abiotic pressures. Further research measuring multiple microclimatic variables in more detail, including light availability, is needed for increased resolution on urbanization-related abiotic changes affecting herbivory and plant traits at local scales. At the same time, assessing the effects of macroclimatic variation (along elevational or latitudinal gradients) as an exogenous force shaping local-scale abiotic effects of urbanization on herbivory and plant traits is also relevant in itself and to test for abiotic linkages across scales (De Frenne et al. 2013).

In contrast with herbivory, top–down effects of predators, particularly vertebrates, were positively correlated with tree stand temperature. Previous studies have shown that temperature and other abiotic factors can influence predation rates, with urban environments often exhibiting altered predator activity (Preisser and Strong 2004, Van Bael et al. 2008). Changes in temperature, resulting from habitat fragmentation or the urban heat island effect, can lead to shifts in predator abundance and behaviour, such as increased or decreased activity (Theodorou 2022). Additionally, light pollution has been shown to affect predator behaviour, potentially disrupting feeding patterns, reproductive cycles, and predator–prey interactions (Theodorou 2022). Nonetheless, and despite that urbanization was positively associated with temperature, there was no detectable indirect influence of urbanization on predator top–down control via increased temperature. It would be valuable to further investigate the relationships between other abiotic factors and predation, including abiotic changes associated with stand-level features such as canopy openness, tree species composition, and abundance known to influence predator behaviour and community structure (Nell and Mooney 2019, Butz et al. 2023) and may play an important role in determining the strength and direction of urbanization effects on predator top–down control.

Limitations of the study and future directions

Despite providing insights into the effects of urbanization on herbivory in *Q. robur*, our study has several limitations. First, focusing on a single tree species and a relatively short experimental timeframe limits the generalizability of the results. Second, the use of a categorical approach to characterize urbanization (urban versus rural) restricts the ability to detect more nuanced patterns along continuous urban gradients, which are increasingly recommended in urban ecology research (McDonnell and Hahs 2008, Verheyen et al. 2019). Third, while vertebrate predators were shown to influence herbivory, the exclusion of invertebrate predators may have inadvertently removed some herbivores, potentially biasing results, and flying predators were not excluded, yet their contribution to herbivory control was not considered. Finally, we did not measure herbivore abundance, behaviour, or community composition, nor did we capture detailed microclimatic or leaf-trait variation, which could mediate urbanization effects on herbivory. Future research should address these limitations by incorporating multiple tree species across extended temporal scales, applying continuous urbanization gradients, and measuring detailed biotic and abiotic factors – including herbivore and predator communities, microclimatic conditions and leaf traits. Experimental designs that account for both invertebrate and flying predators, along with observations of herbivore communities, their behaviour and interactions with plant traits, would help clarify the mechanisms driving herbivory patterns. Such approaches would provide a more comprehensive understanding of how urbanization shapes plant–herbivore–predator interactions and inform urban forest management and conservation strategies.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.s7h44j1mr (Quiroga et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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