

RESEARCH ARTICLE

Published
2022-04-01

Cite as

Alex Stemmelen, Alain Paquette, Marie-Lise Benot, Yasmine Kadiri, Hervé Jactel and Bastien Castagneyrol (2022) *Insect herbivory on urban trees: Complementary effects of tree neighbours and predation*, Peer Community Journal, 2: e22.

Correspondence

alex.stemmelen@inrae.fr






Peer-review

Peer reviewed and recommended by PCI Ecology, <https://doi.org/10.24072/pci.ecology.100061>



This article is licensed under the Creative Commons Attribution 4.0 License.

Insect herbivory on urban trees: Complementary effects of tree neighbours and predation

Alex Stemmelen ¹, Alain Paquette ², Marie-Lise Benot ¹, Yasmine Kadiri¹, Hervé Jactel ¹, and Bastien Castagneyrol ¹

Volume 2 (2022), article e22

<https://doi.org/10.24072/pcjournal.106>

Abstract

Insect herbivory is an important component of forest ecosystems functioning and can affect tree growth and survival. Tree diversity is known to influence insect herbivory in natural forest, with most studies reporting a decrease in herbivory with increasing tree diversity. Urban ecosystems, on the other hand, differ in many ways from the forest ecosystem and the drivers of insect herbivory in cities are still debated. We monitored 48 urban trees from five species – three native and two exotic – in three parks of Montreal (Canada) for leaf insect herbivory and predator activity on artificial larvae, and linked herbivory with both predation and tree diversity in the vicinity of focal trees. Leaf insect herbivory decreased with increasing tree diversity and with increasing predator attack rate. Our findings indicate that tree diversity is a key determinant of multitrophic interactions between trees, herbivores and predators in urban environments and that managing tree diversity could contribute to pest control in cities.

¹BIOGECO, INRAE, Univ. Bordeaux – 33610 Cestas, France, ²Département des sciences biologiques, Centre d'étude de la forêt (CEF), Université du Québec à Montréal – Centre - Ville Station, P.O. Box 8888, Montréal, Qc H3C 3P8, Canada

Introduction

Insect herbivores have a major impact on tree growth and survival, hence on the functioning of forest ecosystems (Metcalf et al., 2014; Visakorpi et al., 2018; Zvereva et al., 2012). Tree diversity significantly influences insect herbivory in forest ecosystems (Castagneyrol et al., 2014; Jactel et al., 2017). Most studies report that herbivory declines as tree diversity increases (*i.e.*, associational resistance, Barbosa et al., 2009), although the opposite pattern has also been found (Haase et al., 2015; Schuldt et al., 2011). Recently, the interest in how tree diversity affects insect herbivory has expanded to include urban forests (Clem & Held, 2018; Dale & Frank, 2018; Frank, 2014), where pest damage can compromise the ecological and aesthetic values of urban trees (Nuckols & Connor, 1995; Tooker & Hanks, 2000; Tubby & Webber, 2010). Urban forests differ from natural forests in many ways. For example, most of the trees in cities are planted, found in lower density and/or mixed with native and exotic ornamental species that are rarely encountered in natural forests. Thus, given these specific characteristics of urban forests, it is still unclear how and why tree diversity might influence insect herbivory on urban trees.

The density and diversity of trees determine the amount and the quality of food and habitat resources available to herbivores and their enemies, and thus can have strong impact on the bottom-up and top-down forces acting upon insect herbivores (Haase et al., 2015; Muiruri et al., 2016; Setiawan et al., 2014). For example, some insect herbivores, in particular generalist species, could take advantage of tree diversity to acquire more abundant, complementary food resources or benefit from a more balanced food mix, thus causing more damage in mixed forests (Lefcheck et al., 2013). In contrast, insect herbivores generally find it easier to identify and orientate towards the signals emitted by their host trees when the latter are more concentrated (*the resource concentration hypothesis*, Hambäck & Englund, 2005; Root, 1973) while non-host trees can emit volatile compounds that interfere with the ability of herbivores to detect their preferred host (Jactel et al., 2011). Finally, the abundance and diversity of predatory birds and arthropods generally increases with plant density and diversity, which would result in a better top-down regulation of insect herbivores (*the enemies hypothesis*, Risch et al., 1983; Root, 1973). However, the evidence available to support the enemies hypothesis in forest is controversial (Muiruri et al., 2016; Riihimäki et al., 2005; Staab & Schuldt, 2020) and the contribution of natural enemies to the control of herbivores in urban area remains poorly explored.

Tree diversity and density vary widely between and within cities (Ortega-Álvarez et al., 2011; Sjöman et al., 2012). A consequence of this variability is that even within a common urban environment, herbivory may be reduced in some tree species and increased in others (Clem & Held, 2018; Frank, 2014), and the relative importance of bottom-up and top-down forces responsible for these effects may also differ. In addition, non-native trees have been widely planted in urban habitats (Cowett & Bassuk, 2014; Moro et al., 2014). While they often escape from herbivory by native insects (*'the enemy escape hypothesis'*, Adams et al., 2009; Keane & Crawley, 2002), cases of native herbivores spilling-over onto exotic trees have been recorded (e.g. Branco et al., 2015). Non-native tree species can also provide habitats to insectivorous birds or predatory arthropods (Gray & van Heezik, 2016). It is thus difficult to predict the effect of mixing native and exotic trees on insect herbivory in urban habitats (Clem & Held, 2018; Frank, 2014).

In this study, we investigated the effect of tree density, tree diversity, presence of conspecific trees, tree origin and predator activity on insect herbivory in urban trees of the city of Montreal (Quebec, Canada). We measured leaf area removed or otherwise damaged by insect herbivores on 48 trees of five species – three native and two exotic – in three urban parks. We concomitantly assessed predator activity by using artificial caterpillars exposed on tree branches. We tested the following hypotheses: (1) insect herbivory decreases with tree density, number of non-conspecific trees (host dilution) and diversity (associational resistance) around focal trees, (2) predator activity increases with increasing tree density and diversity and (3) predation and herbivory have different responses to tree diversity

on native and exotic trees. By doing so, our study builds toward a better understanding of the drivers of pest insect damage on urban trees.

Material and Method

Study site

The study was conducted in the city of Montreal (Canada, 45°50'N, -73°55'W), where the climate is temperate cold, with 6.8°C average temperature and 1000.3 mm annual rainfall during the 1981-2010 period (Pierre Elliott Trudeau airport weather station, www.canada.ca). The study took place in three parks of the southwest part of the city: Angrignon, Marguerite Bourgeoys and Ignace-Bourget (Table 1).

Tree selection

Every tree in Angrignon, Ignace-Bourget and Marguerite-Bourgeoys parks had been previously geolocalized and identified to the species level. This information was accessible through the city database for urban trees (<http://donnees.ville.montreal.qc.ca/dataset/arbres>). We selected a total of 48 trees of five deciduous species (Table 1). Three species are native to the study area (*Acer saccharinum* L., *Tilia americana* L., *Quercus rubra* L.) while two are exotics, from Europe (*Acer platanoides* L., *Tilia cordata* Mill.). These species are amongst the most abundant tree species in the city of Montreal where together they represent 37% of all the tree species of the public domain. In agreement with the city of Montreal administration, we only selected trees with a diameter at breast height (DBH) greater than 8 cm (mean \pm SD: 18.38 \pm 9.36) (to withstand the sampling of leaves required for the experiment) and with low branches that could be easily accessed using a stepladder (for safety).

Predation rate assessment

We used artificial caterpillars made with modelling clay to estimate predation rate on sampled trees (Ferrante et al., 2014; Howe et al., 2009). We installed 15 artificial caterpillars per tree. We haphazardly selected three low (2.5-3.5 m from ground) branches facing different directions and installed five artificial caterpillars per branch (total: 720 caterpillars). Caterpillars were 3 cm long, and modelled to match the approximate form and size of real caterpillars. They were modelled using a 1-cm ball of non-toxic and odourless green modelling clay (*Sculpey III String Bean colour*) and secured on thin branches using a 12-cm long, 0.5 mm diameter, non-shiny metallic wire.

Table 1. Mean (\pm SD) diameter at breast height (in cm) and number of trees initially selected for each park and species.

Species	Angrignon (AN) (45°26'N, -73°36'W)	Marguerite-Bourgeoys (MB) (45°47'N, -73°36'W)	Ignace-Bourget (IB) (45°45'N, -73°60'W)
<i>Acer saccharinum</i>	37.55 (n = 5)	37.55 (n = 2)	15.1 (n = 2)
<i>Acer platanoides</i>	21.60 (n = 1)	23.68 \pm 1.97 (n = 6)	26.25 (n = 2)
<i>Tilia cordata</i>	22.40 (n = 1)	30.60 \pm 3.37 (n = 5)	9.67 \pm 0.51 (n = 4)
<i>Tilia americana</i>	10.52 \pm 0.55 (n = 4)	22.06 \pm 1.87 (n = 3)	27.60 \pm 1.20 (n = 3)
<i>Quercus rubra</i>	8.96 \pm 0.37 (n = 5)	NA	12.30 1.45 (n = 5)

We exposed artificial caterpillars for 11 days in late spring (from May 29th to June 9th, 2018) and for 6 days in early summer (from July 18th to July 24th, 2018). These seasons were chosen to cover the main activity period of both predators and herbivores. Artificial caterpillars were left untouched for the full duration of each survey. We estimated total predator attack rate as the number of artificial larvae

with any predation mark, divided by the total length of the observation period in days. There were uncertainties regarding predator identity responsible for predation marks. Most of the marks were attributable to birds or arthropods, while very few were attributable to small mammals, therefore, we chose to combine predation marks primarily attributed to birds or arthropods into a single category, which we refer to as total predation.

Branches of three trees were accidentally pruned by city workers in late spring so that the predation rate could not be estimated on these trees for the first survey. Three new trees of the same species were selected for the second survey, in early summer.

Leaf insect herbivory

We estimated insect herbivory on leaves (Kozlov et al., 2017) as the percentage of leaf area removed or impacted by insect herbivores (including chewing, skeletonizing and mining damage, collectively referred to as ‘herbivory’). At the end of the second predation survey, we collected 10 leaves per branch on the same branches on which we had exposed artificial caterpillars, starting with the most apical, fully-developed, leaf to the 10th leaf down to branch basis (Total: 30 leaves per tree). We estimated total herbivory (i.e., total leaf area consumed or impacted by herbivores, regardless of their identity) as well as damage made by chewing, mining and sap-feeding herbivores at the level of individual leaves by using an ordinal scale of eight percentage classes of defoliation: 0%; 0-1%, 1-5%; 6-10%; 11-25%; 26-50%; 51-75% and 76-100%. We counted the number of galls per leaf. Most damage was made by leaf chewers, while other damage had a skewed distribution, preventing detailed analyses for each type of damage separately. We therefore analysed total herbivory by averaging herbivory at the level of individual trees and using the median of each class of defoliation. Herbivory was scored by a single observer (BC), who was blind to tree identity.

Tree neighbourhood

We used three variables to describe tree neighbourhood in a 20-m radius around each focal tree: tree density (defined as the number of neighbouring trees in that radius), tree species diversity (Shannon diversity index) and the number of conspecific trees around each focal tree. Those variables were obtained using QGIS Geographic Information System software (QGIS Development Team, 2018). Excluding focal tree species, the most common tree species in the vicinity of focal trees were the smooth serviceberry (*Amelanchier leavis* Wiegand), the white spruce (*Picea glauca* Voss), the green ash (*Fraxinus pennsylvanica* Marshall) and the eastern cottonwood (*Populus deltoides* Marshall), all of them native to the region. We should note that, as focal trees were not necessarily 20m or more apart, we could not avoid that some “neighbour” trees were used in more than one neighbourhood, and some focal trees were also within the neighbourhood of another focal tree.

Statistical analyses

We used the information theory framework to identify the best model fitting our data and applied model averaging whenever necessary to estimate model coefficient parameters (Grueber et al., 2011). We first built a full model including tree density (*Density*), tree diversity (*Diversity*), number of conspecifics (*Conspecific*), origin of the focal tree (*Origin*, native of exotic), park (*Park*), and predation rate (*Predation*) as fixed factors and tree species identity (*Species*) as a random factor:

$$(1) \quad Y_{ij} \sim \beta_0 + \beta_1 \times \text{Density}_{ij} + \beta_2 \times \text{Diversity}_{ij} + \beta_3 \times \text{Conspecific}_{ij} + \beta_4 \times \text{Origin}_{\text{exotic}, ij} + \beta_5 \times \text{Park}_{\text{IB}, ij} + \beta_6 \times \text{Park}_{\text{MB}, ij} + \beta_6 \times \text{Predation}_{ij} + \gamma_j + \epsilon_{ij}$$

Where Y_{ij} is the herbivory on tree individual i in tree species j , β are model coefficient parameters for fixed effects, γ_j is the random effect of tree species identity and ϵ the residuals.

To ease the interpretation of parameter estimates after model averaging, we standardized the input variables using Gelman’s approach (Gelman, 2008). We then applied a procedure of model selection based on the Akaike’s criterion corrected for small sample size (AICc) by running every model nested within the full model. As tree density and tree diversity were correlated (Pearson’s correlation: $r =$

0.71), we excluded all sub-models that included these predictors together. We ranked all models based on difference in AICc between each model and the top ranked model with the lowest AICc (ΔAICc). Models with a $\Delta\text{AICc} < 2$ are generally considered equally supported by the data or not differentiable from the top ranked model. Finally, we estimated model fit by calculating marginal ($R^2\text{m}$) and conditional ($R^2\text{c}$) R^2 values, corresponding to variance explained by fixed effects only ($R^2\text{m}$) and by fixed and random effects ($R^2\text{c}$) (Nakagawa & Schielzeth, 2013). When multiple models had a $\Delta\text{AICc} < 2$, we used a model averaging approach to build a consensus model including all variables found in the set of best models. We considered that a given predictor had a significant effect if its 95% confidence interval did not overlap zero. When only one model had a $\Delta\text{AICc} < 2$, we used it as the best model. We used a square-root transformation of insect herbivory to satisfy model assumptions of normality and homogeneity of residuals.

We used the same approach to test the effect of tree neighbourhood on predation rate, log-transforming predation rate to satisfy model assumptions. Model equation (2) included the fixed effect of sampling season (*Season*) and the random effect of tree identity (τ_k), nested within tree species identity as an additional random factor accounting for repeated measurements of the same individuals:

$$(2) \quad Y_{ijk} \sim \beta_0 + \beta_1 \times \text{Density}_{ijk} + \beta_2 \times \text{Diversity}_{ijk} + \beta_3 \times \text{Conspecific}_{ijk} + \beta_4 \times \text{Origin}_{\text{exotic},ijk} + \beta_5 \times \text{Park}_{\text{IB},ijk} \\ + \beta_6 \times \text{Park}_{\text{MB},ijk} + \beta_7 \times \text{Season}_{\text{summer},ijk} + \gamma_j + \tau_{k|j} + \epsilon_{ijk} \\ \gamma \sim N(0; \sigma_{\text{species}}^2) \quad \tau \sim N(0; \sigma_{\text{individual}}^2) \quad \epsilon \sim N(0; \sigma_{\epsilon}^2)$$

Statistical analyses were performed using the R software version 3.4.4 (R Core Team 2019) with packages *lme4* (Bates et al., 2015) and *MuMIn* (Barton 2019).

Results

Insect herbivory

Herbivory was on average (\pm SE) 7.19 ± 0.70 % ($n = 48$). Leaf damage was lower in *Acer platanoides* (3.53 ± 0.54) and *A. saccharinum* (3.86 ± 0.47) than in *Quercus rubra* (8.77 ± 1.65), *Tilia americana* (10.3 ± 1.37) and *T. cordata* (8.75 ± 1.75) (Fig. 1A).

There were six models competing with the top ranked model in a range of 2 units of ΔAICc (Table 2). These models included tree Shannon diversity, predation rate and tree origin as predictors. Insect herbivory decreased significantly with increasing tree diversity (average model coefficient parameter estimate \pm CI: $-0.482 \pm [-0.91; -0.05]$, Fig. 2A, Table 3) and with increasing predation rate ($-0.473 \pm [-0.91; -0.003]$) (Fig. 2B, Table 3). Among the set of best models, fixed effects explained between 7 and 12% of variability in insect herbivory. Fixed and random effects together explained between 47 and 65% of variability in insect herbivory.

Predation

Of the 1,315 artificial caterpillars that we installed, 198 displayed marks unambiguously attributable to predators (*i.e.*, 15%). Predation rate varied between 0 and 0.87 per caterpillar-day (Fig. 1B).

Only one model had a $\Delta\text{AICc} < 2$ and was thus selected as the best model. This best model included only Season, with predation rate two times higher in late spring (mean \pm CI: $0.44 \pm [0.31, 0.58]$ caterpillars-day⁻¹) than in early summer ($0.20 \pm [0.16, 0.24]$ caterpillars-day⁻¹). Season explained 56 % of variability in predation rate and, collectively, fixed and random effects explained 59 % of variability in predation rate.

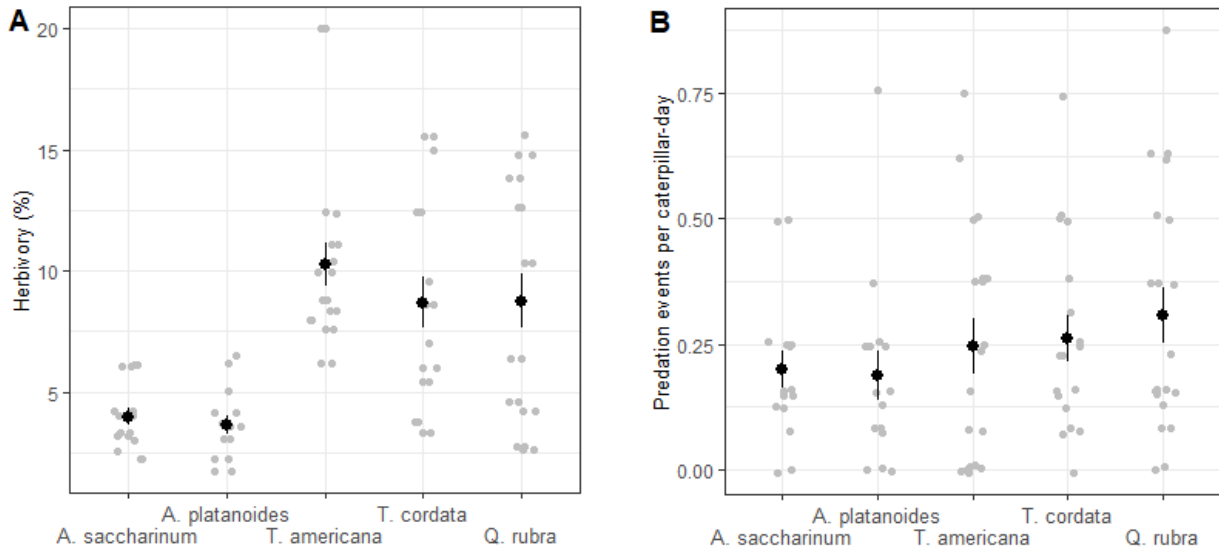


Figure 1. Effect of tree species identity on insect herbivory (A) and predation rate (B). Black dots and solid lines represents mean \pm SE calculated on raw data. Herbivory is the percentage of leaf area removed or impacted by herbivores in early summer. Predation events per caterpillar-day is the number of caterpillars attacked per day in late spring

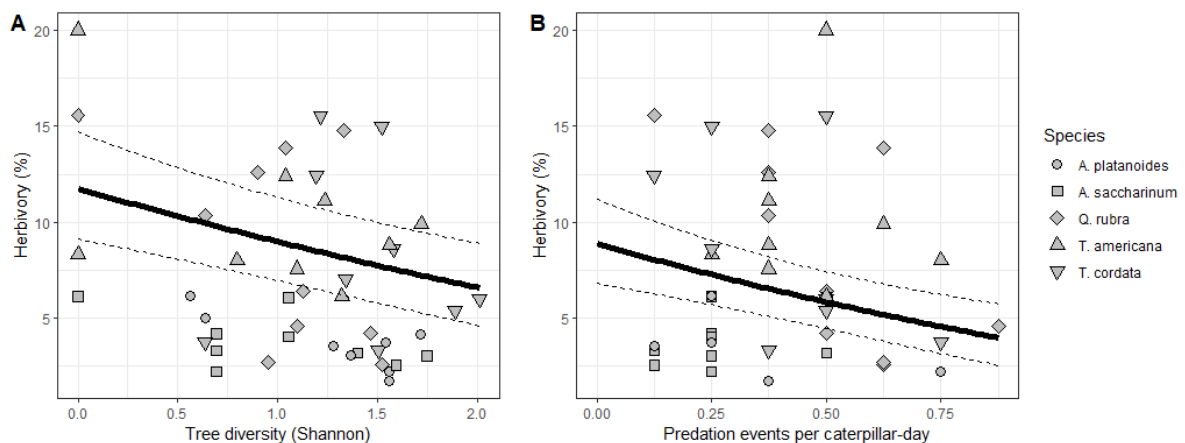


Figure 2. Effects of tree diversity (A) and predation rate (B) on insect herbivory. Solid and dashed lines represent prediction and adjusted standard error of the average model respectively (Table 3). Herbivory is the percentage of leaf area removed or impacted by herbivores in early summer. Tree diversity is represented by Shannon's diversity index. Predation events per caterpillar-day is the number of caterpillars attacked per day in late spring.

Table 2. Summary results of model selection of tree neighbourhood effect on herbivory rate: set of models with $\Delta AICc < 2$. Only predictors that were present at least once in the set of best models are represented. R^2m and R^2c represent fixed and fixed *plus* random factor, respectively.

Model	Model covariates				Model selection			
	Intercept	Predation	Origin	Diversity	K	Log L	$\Delta AICc$	R^2m (R^2c)
1	2.53			-0.52	1	-46.44	0.00	0.09 (0.46)
2	2.52	-0.52		-0.44	2	-45.18	0.04	0.12 (0.58)
3	2.51	-0.51			1	-46.79	0.70	0.07 (0.56)
4	2.53	-0.44	0.171	-0.43	3	-44.64	1.67	0.12 (0.65)
5	2.53		0.078	-0.52	2	-46.07	1.82	0.08 (0.53)
6	2.53	-0.53	0.357		2	-46.12	1.92	0.08 (0.62)

Table 3. Summary results after model averaging: effects of each parameter presents on the set of best models on herbivory rate. Bold parameter are significant. Relative importance is a measure of the prevalence of each parameter in each model used in model averaging.

Parameter	Estimate	Adjusted SE	Confidence interval	Relative importance
(Intercept)	2.53	0.31	(1.91, 3.14)	
Diversity	-0.48	0.21	(-0.91, -0.05)	0.72
Predation	-0.47	0.22	(-0.91, -0.003)	0.64
Origin	0.19	0.71	(-1.20, 1.60)	0.31

Discussion

We confirmed that tree diversity can influence insect herbivory on urban trees. Specifically, we found that insect herbivory decreased with increasing tree diversity providing support for the associational resistance hypothesis (Castagneyrol et al., 2017). We also found a negative correlation between predator attack rate and insect herbivory. Although further analyses are needed to confirm this relationship, our findings provide support for the view that increasing tree diversity can enhance regulation of insect herbivores by natural enemies in urban forests.

Our results are in line with several studies having reported reduced herbivory in trees surrounded by heterospecific neighbours (reviewed by Castagneyrol et al., 2014; Jactel et al., 2017). It also adds to the growing number of studies documenting diversity-resistance relationships in urban environments (Clem & Held 2018; Doherty et al., Frank 2014). However, it conflicts with other results suggesting an increase in herbivore abundance with increasing plant diversity in urban environments (Mata et al., 2017), although the relationship between herbivore abundance and actual herbivory is not always positively correlated (Barbosa et al., 2009; Schueller et al., 2019). Tree diversity may have influenced the probability of focal trees being found and colonized by herbivores. Theory predicts that specialist herbivores have greater difficulties finding their host trees when they are surrounded by heterospecific neighbours (Castagneyrol et al., 2014; Jactel et al., 2009). It is possible that non-host neighbours disrupted the physical and chemical cues used by insect herbivores to locate their hosts (Damien et al., 2016; Jactel et al., 2011; Zhang & Schlyter, 2004). However, and contrary to our expectations, we did not find any significant effect of conspecific tree density on insect herbivory, thus ruling out the resource concentration hypothesis in this particular case. However, because our study was observational, we could not separate the effect of conspecific neighbour density from heterospecific neighbour density. In the absence of data on the identity of herbivores responsible for herbivory, further speculation would be hazardous.

Insect herbivory varied across tree species but did not differ between native and non-native species, thus not providing support for predictions of the enemy release hypothesis (Cincotta et al., 2009; Meijer et al., 2016). One possible explanation for this result could be that native herbivores spilled over exotic tree species from neighbouring native tree species, as it was recorded in previous studies (Branco et al., 2015). This would have been facilitated by the fact that exotic tree species (from Europe) had congeneric species in Canada. Although we only surveyed a handful of native and exotic species, making any generalization hazardous, we can speculate on the lack of difference between native and non-native species. It is also important to note that a large part of the variability in leaf insect damage was attributable to the species on which leaf samples were collected. In particular, both *Acer platanoides* and *A. saccharinum* were far less damaged than *Tilia cordata*, *T. americana* and *Quercus rubra*. In a recent study in Michigan, Schueller et al., (2019) also reported greater insect herbivory (and herbivore diversity) on *Quercus* species as compared to *Acer* species, which is consistent with the view that plant species identity can drive arthropods community and abundance on forest host trees (Burghardt et al., 2009; Pearse & Hipp, 2009).

We found a significant negative correlation between predator attack rate and insect herbivory measured later in the season. This finding suggests a potential relationship between herbivory and predation in urban environments (Faeth et al., 2005; Kozlov et al., 2017 but see Long & Frank, 2020). However, we refrain from concluding that predation was the main driver of insect herbivory for several reasons. First, the effect size of the herbivory-predation relationship was small, as was model R^2 (Table 3). Second, concerns remain about how well predation on artificial prey represents of actual predation (Lövei & Ferrante, 2017; Rößler et al., 2018). In particular, artificial caterpillars used to assess predation rate modelled lepidopteran-like leaf chewing caterpillars and thus, caution is needed when it comes to extrapolate predator attack rates to other herbivore feeding guilds. Third, we had no information on actual natural prey density in focal and neighbouring trees. Yet, prey availability may have influenced the functional response of bird insectivores (e.g. optimal foraging) such that we cannot exclude that herbivory actually drove predation rate instead of the other way around. Finally,

the putative effect of predation on herbivory may be weak in respect to other factors acting directly upon herbivores in urban environments such as drought (Huberty & Denno, 2004; Mattson, 1980; Meineke & Frank, 2018), extreme heat (Dale & Frank, 2014; Meineke et al., 2013) and pollution leading to altered foliage quality (Kozlov et al., 2017; Mattson, 1980; Moreira et al., 2019).

Contrary to the important effect of tree species identity on insect herbivory, tree species had no clear influence on predation rate on dummy caterpillars, which contradicts the view that tree species identity can modulate attack rates of caterpillars by birds (Mooney & Singer, 2012; Nell et al., 2018). Variation in predator density between plants is often related to an indirect effect of the plant on the density (Bailey et al. 2006) or quality (Brower et al. 1967, Clancy & Price, 1987) of their preys (herbivores). However, such effect of plant identity is not relevant when using dummy caterpillars, as neither their abundance nor their quality can be affected by plant species identity, which could explain the contradiction between past results and our study.

Predation was greater during the first survey, in late spring, than during the second survey, in early summer. This result could be explained either by a lower foliage density in trees in spring, making it easier for predators to detect artificial caterpillars, or by greater predator activity matching the phenology of wild caterpillars and feeding period of chicks (Coley, 1980; Raupp & Denno, 1983). We cannot either exclude that birds learned to avoid artificial caterpillars, thus resulting in much lower predation pressure during the second survey. However, unless bird ability to avoid artificial caterpillar varied between tree species and neighbourhood, we do not see this possibility as a major threat to our inferences.

Conclusion

Our study suggests several ecological factors drive leaf insect herbivory in the urban trees of the Montreal city. In particular, we found that insect herbivory decreased with both increasing tree diversity and predator activity. While biological invasions and global warming are increasing risks to urban trees, more and more cities choose to ban or reduce the use of pesticides in urban parks and green areas (Sustainable Use of Pesticides Directive 2009), such as in Montreal. In this context, diversifying urban tree cover in urban parks might help to reduce insect damage, which could result in a better provision of services provided by trees in cities (Beyer et al., 2014; Bowler et al., 2010; Nowak et al., 2014).

Acknowledgements

We thank Charles Desroches, Elyssa Cameron, Christian Messier, summer interns at UQAM, and the city of Montréal, Arrondissement du Sud-Ouest for their help with field work. We also thank Frédéric Barraquand and Benjamin Brachi for their constructive comments on the preliminary version of the paper. We thank Luc Barbaro and Steve Frank for their friendly reviews of early drafts of this paper. Finally, we are grateful to Ian Pearse and Freerk Molleman for their reviews of prior manuscript versions. A preprint version of this article has been reviewed and recommended by Peer Community In Ecology ([10.24072/pci.ecology.100061](https://doi.org/10.24072/pci.ecology.100061)).

Funding

This study has been carried out with financial support from (i) the French National Research Agency (ANR) in the frame of the Investments for the future Programme to BC, within the Cluster of Excellence COTE (ANR-10-LABX-45), (ii) the Conseil Franco-Québécois de Coopération Universitaire (FRQNT – Samuel-de-Champlain fund) to BC and AP, and (iii) a Discovery grant to AP from the Natural Sciences and Engineering Research Council of Canada.

Conflict of interest disclosure

The authors of this article declare that they have no financial conflict of interest with the content of this article. Bastien Castagneyrol is one of the PCI Ecology recommenders.

Data, script and code availability

Data, script, codes and supplementary material are available online from the Data INRAE repository: <https://doi.org/10.15454/R4NESA>

References

- Adams, J. M., Fang, W., Callaway, R. M., Cipollini, D., Newell, E., & Transatlantic Acer platanoides Invasion Network (TRAIN). (2009). A cross-continental test of the Enemy Release Hypothesis: Leaf herbivory on *Acer platanoides* (L.) is three times lower in North America than in its native Europe. *Biological Invasions*, 11(4), 1005-1016. <https://doi.org/10.1007/s10530-008-9312-4>
- Akaike, H. (1998). Information Theory and an Extension of the Maximum Likelihood Principle. In E. Parzen, K. Tanabe, & G. Kitagawa (Eds.), *Selected Papers of Hirotugu Akaike* (pp. 199–213). Springer. https://doi.org/10.1007/978-1-4612-1694-0_15
- Andow, D. A. (1991). Vegetational Diversity and Arthropod Population Response. *Annual Review of Entomology*, 36(1), 561-586. <https://doi.org/10.1146/annurev.en.36.010191.003021>
- Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 1-20. <https://doi.org/10.1146/annurev.ecolsys.110308.120242>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1). <https://doi.org/10.18637/jss.v067.i01>
- Bernays, E. A., Bright, K. L., Gonzalez, N., & Angel, J. (1994). Dietary Mixing in a Generalist Herbivore: Tests of Two Hypotheses. *Ecology*, 75(7), 1997-2006. <https://doi.org/10.2307/1941604>
- Beyer, K. M. M., Kaltenbach, A., Szabo, A., Bogar, S., Nieto, F. J., & Malecki, K. M. (2014). Exposure to neighborhood green space and mental health: Evidence from the survey of the health of Wisconsin. *International Journal of Environmental Research and Public Health*, 11(3), 3453-3472. <https://doi.org/10.3390/ijerph110303453>
- Blood, A., Starr, G., Escobedo, F., Chappelka, A., & Staudhammer, C. (2016). How Do Urban Forests Compare? Tree Diversity in Urban and Periurban Forests of the Southeastern US. *Forests*, 7(6), 120. <https://doi.org/10.3390/f7060120>
- Bowler, D. E., Buyung-Ali, L. M., Knight, T. M., & Pullin, A. S. (2010). A systematic review of evidence for the added benefits to health of exposure to natural environments. *BMC Public Health*, 10(1), 456. <https://doi.org/10.1186/1471-2458-10-456>
- Branco, M., Bockerhoff, E. G., Castagneyrol, B., Orazio, C., & Jactel, H. (2015). Host range expansion of native insects to exotic trees increases with area of introduction and the presence of congeneric native trees. *Journal of Applied Ecology*, 52(1), 69-77. <https://doi.org/10.1111/1365-2664.12362>
- Burghardt, K. T., Tallamy, D. W., & Gregory Shriver, W. (2009). Impact of native plants on bird and butterfly biodiversity in suburban landscapes. *Conservation Biology: The Journal of the Society for Conservation Biology*, 23(1), 219-224. <https://doi.org/10.1111/j.1523-1739.2008.01076.x>
- Burkman, C. E., & Gardiner, M. M. (2014). Urban greenspace composition and landscape context influence natural enemy community composition and function. *Biological Control*, 75, 58-67. <https://doi.org/10.1016/j.biocontrol.2014.02.015>
- Castagneyrol, B., Bonal, D., Damien, M., Jactel, H., Meredieu, C., Muiruri, E. W., & Barbaro, L. (2017). Bottom-up and top-down effects of tree species diversity on leaf insect herbivory. *Ecology and Evolution*, 7(10), 3520-3531. <https://doi.org/10.1002/ece3.2950>

- Castagneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E. G., & Koricheva, J. (2014). Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *Journal of Applied Ecology*, 51(1), 134-141. <https://doi.org/10.1111/1365-2664.12175>
- Christie, F. J., & Hochuli, D. F. (2005). Elevated Levels of Herbivory in Urban Landscapes: Are Declines in Tree Health More Than an Edge Effect? *Ecology and Society*, 10(1). <https://doi.org/10.5751/ES-00704-100110>
- Cincotta, C. L., Adams, J. M., & Holzapfel, C. (2009). Testing the enemy release hypothesis: A comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). *Biological Invasions*, 11(2), 379-388. <https://doi.org/10.1007/s10530-008-9255-9>
- Clark, J., & Kjelgren, R. (1990). Water as a Limiting Factor in the Development of Urban Trees. *Journal of Arboriculture*, 16(8), 203-208.
- Clem, C. S., & Held, D. W. (2018). Associational Interactions Between Urban Trees: Are Native Neighbors Better Than Non-Natives? *Environmental Entomology*, 47(4), 881-889. <https://doi.org/10.1093/ee/nvy071>
- Coley, P. D. (1980). Effects of leaf age and plant life history patterns on herbivory. *Nature*, 284(5756), 545-546. <https://doi.org/10.1038/284545a0>
- Cocos, D., Cerretti, P., Caruso, V., Mei, M., Falco, M., & Marini, L. (2019). Impact of urbanization on predator and parasitoid insects at multiple spatial scales. *PLOS ONE*, 14(4), e0214068. <https://doi.org/10.1371/journal.pone.0214068>
- Cowett, F. D., & Bassuk, N. L. (2014). Statewide assessment of street trees in New York State, USA. *Urban Forestry & Urban Greening*, 13(2), 213-220. <https://doi.org/10.1016/j.ufug.2014.02.001>
- Cuevas-Reyes, Pablo; Gilberti, Livia; González-Rodríguez, Antonio; Fernandes, G. Wilson (2013). Patterns of herbivory and fluctuating asymmetry in *Solanum lycocarpum* St. Hill (Solanaceae) along an urban gradient in Brazil. *Ecological Indicators*, 24, 557-561. <https://doi.org/10.1016/j.ecolind.2012.08.011>
- Cupitra-Rodríguez, J., Cruz-Bernate, L., & Montoya-Lerma, J. (2018). Degree of urbanization and predation pressure on artificial lepidopteran caterpillars in Cali, Colombia. *BioRxiv*, 493924. <https://doi.org/10.1101/493924>
- Dale, A. G., & Frank, S. D. (2014). Urban warming trumps natural enemy regulation of herbivorous pests. *Ecological Applications*, 24(7), 1596-1607. <https://doi.org/10.1890/13-1961.1>
- Dale, A. G., & Frank, S. D. (2018). Urban plants and climate drive unique arthropod interactions with unpredictable consequences. *Current Opinion in Insect Science*, 29, 27-33. <https://doi.org/10.1016/j.cois.2018.06.001>
- Damien, M., Jactel, H., Meredieu, C., Régolini, M., van Halder, I., & Castagneyrol, B. (2016). Pest damage in mixed forests: Disentangling the effects of neighbor identity, host density and host apparency at different spatial scales. *Forest Ecology and Management*, 378, 103-110. <https://doi.org/10.1016/j.foreco.2016.07.025>
- Dix, M. E., Johnson, R. J., Harrell, M. O., Case, R. M., Wright, R. J., Hodges, L., Brandle, J. R., Schoeneberger, M. M., Sunderman, N. J., Fitzmaurice, R. L., Young, L. J., & Hubbard, K. G. (1995). Influences of trees on abundance of natural enemies of insect pests: A review. *Agroforestry Systems*, 29(3), 303-311. <https://doi.org/10.1007/BF00704876>
- Doherty, E. M., Meagher, R. L., & Dale, A. G. (2019). Turfgrass Cultivar Diversity Provides Associational Resistance in the Absence of Pest Resistant Cultivars. *Environmental Entomology*, 48(3), 623-632. <https://doi.org/10.1093/ee/nvz026>
- Faeth, S. H., Warren, P. S., Shochat, E., & Marussich, W. A. (2005). Trophic Dynamics in Urban Communities. *BioScience*, 55(5), 399-407. [https://doi.org/10.1641/0006-3568\(2005\)055\[0399:TDIUC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0399:TDIUC]2.0.CO;2)
- Ferrante, M., Lo Cacciato, A., & Lovei, G. L. (2014). Quantifying predation pressure along an urbanisation gradient in Denmark using artificial caterpillars. *European Journal of Entomology*, 111(5), 649-654. <https://doi.org/10.14411/eje.2014.082>

- Frank, S. D., & Shrewsbury, P. M. (2004). Effect of Conservation Strips on the Abundance and Distribution of Natural Enemies and Predation of *Agrotis ipsilon* (Lepidoptera: Noctuidae) on Golf Course Fairways. *Environmental Entomology*, 33(6), 1662-1672. <https://doi.org/10.1603/0046-225X-33.6.1662>
- Frank, S. D. (2014). Bad neighbors: Urban habitats increase cankerworm damage to non-host understory plants. *Urban Ecosystems*, 17(4), 1135-1145. <https://doi.org/10.1007/s11252-014-0368-x>
- Frey, D., Vega, K., Zellweger, F., Ghazoul, J., Hansen, D., & Moretti, M. (2018). Predation risk shaped by habitat and landscape complexity in urban environments. *Journal of Applied Ecology*, 55(5), 2343-2353. <https://doi.org/10.1111/1365-2664.13189>
- Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, 27(15), 2865-2873. <https://doi.org/10.1002/sim.3107>
- Graham, M. H. (2003). Confronting Multicollinearity in Ecological Multiple Regression. *Ecology*, 84(11), 2809-2815. <https://doi.org/10.1890/02-3114>
- Gray, E. R., & van Heezik, Y. (2016). Exotic trees can sustain native birds in urban woodlands. *Urban Ecosystems*, 19(1), 315-329. <https://doi.org/10.1007/s11252-015-0493-1>
- Grossiord, C. (2019) Having the right neighbors: How tree species diversity modulates drought impacts on forests. *New Phytologist*, 228, 42-49. <https://doi.org/10.1111/nph.15667>
- Grossman, J. J., Vanhellefont, M., Barsoum, N., Bauhus, J., Bruelheide, H., Castagneyrol, B., Cavender-Bares, J., Eisenhauer, N., Ferlian, O., Gravel, D., Hector, A., Jactel, H., Kreft, H., Mereu, S., Messier, C., Muys, B., Nock, C., Paquette, A., Parker, J., Verheyen, K. (2018). Synthesis and future research directions linking tree diversity to growth, survival, and damage in a global network of tree diversity experiments. *Environmental and Experimental Botany*, 152, 68-89. <https://doi.org/10.1016/j.envexpbot.2017.12.015>
- Grueter, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology*, 24(4), 699-711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>
- Gutbrodt, B., Dorn, S., Unsicker, S. B., & Mody, K. (2012). Species-specific responses of herbivores to within-plant and environmentally mediated between-plant variability in plant chemistry. *Chemoecology*, 22(2), 101-111. <https://doi.org/10.1007/s00049-012-0102-1>
- Haase, J., Castagneyrol, B., Cornelissen, J. H. C., Ghazoul, J., Kattge, J., Koricheva, J., Scherer-Lorenzen, M., Morath, S., & Jactel, H. (2015). Contrasting effects of tree diversity on young tree growth and resistance to insect herbivores across three biodiversity experiments. *Oikos*, 124(12), 1674-1685. <https://doi.org/10.1111/oik.02090>
- Hambäck, P. A., & Englund, G. (2005). Patch area, population density and the scaling of migration rates: The resource concentration hypothesis revisited. *Ecology Letters*, 8(10), 1057-1065. <https://doi.org/10.1111/j.1461-0248.2005.00811.x>
- Hanks, L. M., & Denno, R. F. (1993). Natural Enemies and Plant Water Relations Influence the Distribution of an Armored Scale Insect. *Ecology*, 74(4), 1081-1091. <https://doi.org/10.2307/1940478>
- Howe, A., Lövei, G. L., & Nachman, G. (2009). Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. *Entomologia Experimentalis et Applicata*, 131(3), 325-329. <https://doi.org/10.1111/j.1570-7458.2009.00860.x>
- Huberty, A. F., & Denno, R. F. (2004). Plant Water Stress and Its Consequences for Herbivorous Insects: A New Synthesis. *Ecology*, 85(5), 1383-1398. <https://doi.org/10.1890/03-0352>
- Jactel, H., Birgersson, G., Andersson, S., & Schlyter, F. (2011). Non-host volatiles mediate associational resistance to the pine processionary moth. *Oecologia*, 166(3), 703-711. <https://doi.org/10.1007/s00442-011-1918-z>

- Jactel, H., Brockerhoff, E., & Duelli, P. (2009). A test of the biodiversity-stability theory: Meta-analysis of tree species diversity effects on pest infestations, and re-examination of responsible factors. *Ecological Studies*, 176, 235-362. https://doi.org/10.1007/3-540-26599-6_12
- Jactel, H., Gritti, E. S., Drössler, L., Forrester, D. I., Mason, W. L., Morin, X., Pretzsch, H., & Castagneyrol, B. (2018). Positive biodiversity-productivity relationships in forests: Climate matters. *Biology Letters*, 14(4). <https://doi.org/10.1098/rsbl.2017.0747>
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J. R., Koricheva, J., Meurisse, N., & Brockerhoff, E. G. (2017). Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Current Forestry Reports*, 3(3), 223-243. <https://doi.org/10.1007/s40725-017-0064-1>
- Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A., & Koricheva, J. (2012). Drought effects on damage by forest insects and pathogens: A meta-analysis. *Global Change Biology*, 18(1), 267-276. <https://doi.org/10.1111/j.1365-2486.2011.02512.x>
- Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, 17(4), 164-170. [https://doi.org/10.1016/S0169-5347\(02\)02499-0](https://doi.org/10.1016/S0169-5347(02)02499-0)
- Kozlov, M. V., Zverev, V., & Zvereva, E. L. (2017). Combined effects of environmental disturbance and climate warming on insect herbivory in mountain birch in subarctic forests: Results of 26-year monitoring. *Science of The Total Environment*, 601-602, 802-811. <https://doi.org/10.1016/j.scitotenv.2017.05.230>
- Kozlov, M. V., Lanta, V., Zverev, V., Rainio, K., Kunavin, M. A., & Zvereva, E. L. (2017). Decreased losses of woody plant foliage to insects in large urban areas are explained by bird predation. *Global Change Biology*, 23(10), 4354-4364. <https://doi.org/10.1111/gcb.13692>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, 82(1), 1-26. <https://doi.org/10.18637/jss.v082.i13>
- Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia*, 139(1), 1-10. <https://doi.org/10.1007/s00442-004-1497-3>
- Lefcheck, J. S., Whalen, M. A., Davenport, T. M., Stone, J. P., & Duffy, J. E. (2013). Physiological effects of diet mixing on consumer fitness: A meta-analysis. *Ecology*, 94(3), 565-572. <https://doi.org/10.1890/12-0192.1>
- Leius, K. (1963). Effects of Pollens on Fecundity and Longevity of Adult *Scambus buolianae* (Htg.) (Hymenoptera: Ichneumonidae). *The Canadian Entomologist*, 95(2), 202-207. <https://doi.org/10.4039/Ent95202-2>
- Letourneau, D. K. (1987). The Enemies Hypothesis: Tritrophic Interactions and Vegetational Diversity in Tropical Agroecosystems. *Ecology*, 68(6), 1616-1622. <https://doi.org/10.2307/1939853>
- Lohr, V., Kendal, D., & Dobbs, C. (2016). Urban trees worldwide have low species and genetic diversity, posing high risks of tree loss as stresses from climate change increase. *Acta Horticulturae*, 1108, 263-270. <https://doi.org/10.17660/ActaHortic.2016.1108.34>
- Long, L. C., & Frank, S. D. (2020). Risk of bird predation and defoliating insect abundance are greater in urban forest fragments than street trees. *Urban Ecosystems*. <https://doi.org/10.1007/s11252-020-00939-x>
- Lövei, G. L., & Ferrante, M. (2017). A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. *Insect Science*, 24(4), 528-542. <https://doi.org/10.1111/1744-7917.12405>
- Marando, F., Salvatori, E., Sebastiani, A., Fusaro, L., & Manes, F. (2019). Regulating Ecosystem Services and Green Infrastructure: Assessment of Urban Heat Island effect mitigation in the municipality of Rome, Italy. *Ecological Modelling*, 392, 92-102. <https://doi.org/10.1016/j.ecolmodel.2018.11.011>
- Mata, L., Threlfall, C. G., Williams, N. S. G., Hahs, A. K., Malipatil, M., Stork, N. E., & Livesley, S. J. (2017). Conserving herbivorous and predatory insects in urban green spaces. *Scientific Reports*, 7(1), 1-12. <https://doi.org/10.1038/srep40970>

- Mattson, W. J. (1980). Herbivory in Relation to Plant Nitrogen Content. *Annual Review of Ecology and Systematics*, 11(1), 119-161. <https://doi.org/10.1146/annurev.es.11.110180.001003>
- Mattson, W. J., & Haack, R. A. (1987). The Role of Drought in Outbreaks of Plant-Eating Insects. *BioScience*, 37(2), 10. <https://doi.org/10.2307/1310365>
- Meijer, K., Schilthuizen, M., Beukeboom, L., & Smit, C. (2016). A review and meta-analysis of the enemy release hypothesis in plant-herbivorous insect systems. *PeerJ*, 4. <https://doi.org/10.7717/peerj.2778>
- Meineke, E. K., Dunn, R. R., Sexton, J. O., & Frank, S. D. (2013). Urban Warming Drives Insect Pest Abundance on Street Trees. *PLOS ONE*, 8(3). <https://doi.org/10.1371/journal.pone.0059687>
- Meineke, E. K., & Frank, S. D. (2018). Water availability drives urban tree growth responses to herbivory and warming. *Journal of Applied Ecology*, 55(4), 1701-1713. <https://doi.org/10.1111/1365-2664.13130>
- Metcalfe, D. B., Asner, G. P., Martin, R. E., Espejo, J. E. S., Huasco, W. H., Amézquita, F. F. F., Carranza-Jimenez, L., Cabrera, D. F. G., Baca, L. D., Sinca, F., Quispe, L. P. H., Taype, I. A., Mora, L. E., Dávila, A. R., Solórzano, M. M., Vilca, B. L. P., Román, J. M. L., Bustios, P. C. G., Revilla, N. S., ... Malhi, Y. (2014). Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters*, 17(3), 324-332. <https://doi.org/10.1111/ele.12233>
- Moreira, X., Abdala-Roberts, L., Teran, J. C. B. M. y, Covelo, F., Mata, R. de la, Francisco, M., Hardwick, B., Pires, R. M., Roslin, T., Schigel, D. S., Hoopen, J. P. J. G. ten, Timmermans, B. G. H., Dijk, L. J. A. van, Castagneyrol, B., & Tack, A. J. M. (2019). Impacts of urbanization on insect herbivory and plant defences in oak trees. *Oikos*, 128(1), 113-123. <https://doi.org/10.1111/oik.05497>
- Moro, M. F., Westerkamp, C., & de Araújo, F. S. (2014). How much importance is given to native plants in cities' treescape? A case study in Fortaleza, Brazil. *Urban Forestry & Urban Greening*, 13(2), 365-374. <https://doi.org/10.1016/j.ufug.2014.01.005>
- Muiruri, E. W., Rainio, K., & Koricheva, J. (2016). Do birds see the forest for the trees? Scale-dependent effects of tree diversity on avian predation of artificial larvae. *Oecologia*, 180(3), 619-630. <https://doi.org/10.1007/s00442-015-3391-6>
- Mundim, F. M., & Pringle, E. G. (2018). Whole-Plant Metabolic Allocation Under Water Stress. *Frontiers in Plant Science*, 9. <https://doi.org/10.3389/fpls.2018.00852>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133-142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Nowak, D. J., Pasek, J. E., Sequeira, R. A., Crane, D. E., & Mastro, V. C. (2001). Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. *Journal of Economic Entomology*, 94(1), 116-122. <https://doi.org/10.1603/0022-0493-94.1.116>
- Nowak, D. J., Hirabayashi, S., Bodine, A., & Greenfield, E. (2014). Tree and forest effects on air quality and human health in the United States. *Environmental Pollution*, 193, 119-129. <https://doi.org/10.1016/j.envpol.2014.05.028>
- Nuckols, M. S., & Connor, E. F. (1995). Do trees in urban or ornamental plantings receive more damage by insects than trees in natural forests? *Ecological Entomology*, 20(3), 253-260. <https://doi.org/10.1111/j.1365-2311.1995.tb00455.x>
- Oke, T. R. (1982). The energetic basis of the urban heat island. *Quarterly Journal of the Royal Meteorological Society*, 108(455), 1-24. <https://doi.org/10.1002/qj.49710845502>
- Ortega-Álvarez, R., Rodríguez-Correa, H. A., & MacGregor-Fors, I. (2011). Trees and the City: Diversity and Composition along a Neotropical Gradient of Urbanization. *International Journal of Ecology*, 2011, 1-8. <https://doi.org/10.1155/2011/704084>
- Pearse, I. S., & Hipp, A. L. (2009). Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks. *Proceedings of the National Academy of Sciences*, 106(43), 18097-18102. <https://doi.org/10.1073/pnas.0904867106>

- Philpott, S. M., & Bichier, P. (2017). Local and landscape drivers of predation services in urban gardens. *Ecological Applications: A Publication of the Ecological Society of America*, 27(3), 966-976. <https://doi.org/10.1002/eap.1500>
- Raupp, M., & Denno, R. (1983). Leaf age as a predictor of herbivore distribution and abundance [Herbivorous insects including the willow leaf beetle]. <https://doi.org/10.1016/B978-0-12-209160-5.50010-6>
- Rider, D. A. (1996). The True Bugs of the World (Hemiptera: Heteroptera). Classification and Natural History. *Annals of the Entomological Society of America*, 89(4), 609-610. <https://doi.org/10.1093/aesa/89.4.609>
- Riihimäki, J., Kaitaniemi, P., Koricheva, J., & Vehviläinen, H. (2005). Testing the enemies hypothesis in forest stands: The important role of tree species composition. *Oecologia*, 142(1), 90-97. <https://doi.org/10.1007/s00442-004-1696-y>
- Risch, S. J., Andow, D., & Altieri, M. A. (1983). Agroecosystem Diversity and Pest Control: Data, Tentative Conclusions, and New Research Directions. *Environmental Entomology*, 12(3), 625. <https://doi.org/10.1093/ee/12.3.625>
- Root, R. B. (1973). Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (*Brassica Oleracea*). *Ecological Monographs*, 43(1), 95-124. <https://doi.org/10.2307/1942161>
- Rößler, D. C., Pröhl, H., & Lötters, S. (2018). The future of clay model studies. *BMC Zoology*, 3(1), 6. <https://doi.org/10.1186/s40850-018-0033-6>
- Russell, E. P. (1989). Enemies Hypothesis: A Review of the Effect of Vegetational Diversity on Predatory Insects and Parasitoids. *Environmental Entomology*, 18(4), 590-599. <https://doi.org/10.1093/ee/18.4.590>
- Schueller, S. K., Paul, S., Payer, N., Schultze, R., & Vikas, M. (2019). Urbanization decreases the extent and variety of leaf herbivory for native canopy tree species *Quercus rubra*, *Quercus alba*, and *Acer saccharum*. *Urban Ecosystems*, 22(5), 907-916. <https://doi.org/10.1007/s11252-019-00866-6>
- Schuldt, A., Both, S., Bruelheide, H., Härdtle, W., Schmid, B., Zhou, H., & Assmann, T. (2011). Predator Diversity and Abundance Provide Little Support for the Enemies Hypothesis in Forests of High Tree Diversity. *PLOS ONE*, 6(7), e22905. <https://doi.org/10.1371/journal.pone.0022905>
- Setiawan, N. N., Vanhellemont, M., Baeten, L., Dillen, M., & Verheyen, K. (2014). The effects of local neighbourhood diversity on pest and disease damage of trees in a young experimental forest. *Forest Ecology and Management*, 334, 1-9. <https://doi.org/10.1016/j.foreco.2014.08.032>
- Shrewsbury, P. M., Lashomb, J. H., Hamilton, G. C., Zhang, J., Patts, J. M., & Casagrande, R. A. (2004). The influence of flowering plants on herbivore and natural enemy abundance in ornamental landscapes. *International Journal of Ecology and Environmental Sciences*, 30(1), 23-33.
- Sjöman, H., Östberg, J., & Bühler, O. (2012). Diversity and distribution of the urban tree population in ten major Nordic cities. *Urban Forestry & Urban Greening*, 11(1), 31-39. <https://doi.org/10.1016/j.ufug.2011.09.004>
- Spencer, H. J., & Port, G. R. (1988). Effects of Roadside Conditions on Plants and Insects. II. Soil Conditions. *Journal of Applied Ecology*, 25(2), 709-714. <https://doi.org/10.2307/2403856>
- Staab, M., & Schuldt, A. (2020). The Influence of Tree Diversity on Natural Enemies-A Review of the "Enemies" Hypothesis in Forests. *Current Forestry Reports*. <https://doi.org/10.1007/s40725-020-00123-6>
- Sustainable use of pesticides. Retrieved April 7, 2020, from Food Safety - European Commission website: https://ec.europa.eu/food/plant/pesticides/sustainable_use_pesticides_en
- Tooker, J. F., & Hanks, L. M. (2000). Influence of plant community structure on natural enemies of pine needle scale (Homoptera: Diaspididae) in urban landscapes. *Environmental Entomology*, 29(6), 1305-1311. <https://doi.org/10.1603/0046-225X-29.6.1305>
- Tubby, K. V., & Webber, J. F. (2010). Pests and diseases threatening urban trees under a changing climate. *Forestry: An International Journal of Forest Research*, 83(4), 451-459. <https://doi.org/10.1093/forestry/cpq027>

- Turrini, T., Sanders, D., & Knop, E. (2016). Effects of urbanization on direct and indirect interactions in a tri-trophic system. *Ecological Applications: A Publication of the Ecological Society of America*, 26(3), 664-675. <https://doi.org/10.1890/14-1787>
- Unsicker, S. B., Oswald, A., Köhler, G., & Weisser, W. W. (2008). Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia*, 156(2), 313-324. <https://doi.org/10.1007/s00442-008-0973-6>
- Visakorpi, K., Gripenberg, S., Malhi, Y., Bolas, C., Oliveras, I., Harris, N., Rifai, S., & Riutta, T. (2018). Small-scale indirect plant responses to insect herbivory could have major impacts on canopy photosynthesis and isoprene emission. *The New Phytologist*, 220(3), 799-810. <https://doi.org/10.1111/nph.15338>
- Whelan, C. J., & Maina, G. G. (2005). Effects of Season, Understorey Vegetation Density, Habitat Edge and Tree Diameter on Patch-Use by Bark-Foraging Birds. *Functional Ecology*, 19(3), 529-536. <https://doi.org/10.1111/j.1365-2435.2005.00996.x>
- Zhang, Q.-H., & Schlyter, F. (2004). Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agricultural and Forest Entomology*, 6(1), 1-20. <https://doi.org/10.1111/j.1461-9555.2004.00202.x>
- Zvereva, E. L., Zverev, V., & Kozlov, M. V. (2012). Little strokes fell great oaks: Minor but chronic herbivory substantially reduces birch growth. *Oikos*, 121(12), 2036-2043. <https://doi.org/10.1111/j.1600-0706.2012.20688.x>