INSECT HERBIVORY ON URBAN TREES: COMPLEMENTARY EFFECTS OF TREE NEIGHBOURS AND PREDATION

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Abstract

1. 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.

2. 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, evaluated the relationships between herbivory, predation, and tree diversity in the vicinity of focal trees.

3. Insect herbivory on leaves decreased with increasing tree diversity and with increasing predator attack rate.

4. 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.

Keywords : Artificial prey, Insect herbivory, Tree diversity, Top-down control, Urban biodiversity

Introduction

Insect herbivores have a major impact on tree growth and survival, hence on the functioning of forest ecosystems (Metcalfe et al., 2014; Visakorpi et al., 2018; Zvereva, Zverev, & Kozlov, 2012). Tree diversity significantly influences insect herbivory in forest ecosystems (Castagneyrol, Jactel, Vacher, Brockerhoff, & Koricheva, 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, Rainio, & Koricheva, 2016; Setiawan, Vanhellemont, Baeten, Dillen, & Verheyen, 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, Whalen, Davenport, Stone, & Duffy, 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, Birgersson, Andersson, & Schlyter, 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, Andow, & Altieri, 1983; Root, 1973). However, the evidence available to support the enemies hypothesis in forest is controversial (Muiruri et al., 2016; Riihimäki, Kaitaniemi, Koricheva, & Vehviläinen, 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, Rodríguez-Correa, & MacGregor-Fors, 2011; Sjöman, Östberg, & Bühler, 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, Westerkamp, & de Araújo, 2014). While they often escape from herbivory by native

78   insects ('*the enemy escape hypothesis*', Adams et al., 2009; Keane & Crawley, 2002), cases of
79   native herbivores spilling-over onto exotic trees have been recorded (e.g. Branco, Brockerhoff,
80   Castagneyrol, Orazio, & Jactel, 2015). Non-native tree species can also provide habitats to
81   insectivorous birds or predatory arthropods (Gray & van Heezik, 2016). It is thus difficult to
82   predict the effect of mixing native and exotic trees on insect herbivory in urban habitats (Clem
83   & Held, 2018; Frank, 2014).

84   In this study, we investigated the effect of tree density, tree diversity, presence of conspecific
85   trees, tree origin and predator activity on insect herbivory in urban trees of the city of Montreal
86   (Quebec, Canada). We measured leaf area removed or otherwise damaged by insect herbivores
87   on 48 trees of five species – three native and two exotic – in three urban parks. We
88   concomitantly assessed predator activity by using artificial caterpillars exposed on tree
89   branches. We tested the following hypotheses: (1) insect herbivory decreases with tree density,
90   number of non-conspecific trees (host dilution) and diversity (associational resistance) around
91   focal trees, (2) predator activity increases with increasing tree density and diversity and (3)
92   predation and herbivory have different responses to tree diversity on native and exotic trees.
93   By doing so, our study builds toward a better understanding of the drivers of pest insect damage
94   on urban trees.

Materials and methods

Study site

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

Tree selection

103   Every tree in Angrignon, Ignace-Bourget and Marguerite-Bourgeoys parks had been
104   previously geolocalized and identified to the species level. This information was accessible
105   through the city database for urban trees (http://donnees.ville.montreal.qc.ca/dataset/arbres).
106   We selected a total of 48 trees of five deciduous species (Table 1). Three species are native to
107   the study area (*Acer saccharinum* L.*, Tilia americana* L.*, Quercus rubra* L.) while two are
108   exotics, from Europe (*Acer platanoides* L.*, Tilia cordata* Mill.). These species are amongst the
109   most abundant tree species in the city of Montreal where together they represent 37% of all the
110   tree species of the public domain. In agreement with the city of Montreal administration, we
111   only selected trees with a diameter at breast height (DBH) greater than 8 cm (mean ± SD: 18.38
112   ± 9.36) (to withstand the sampling of leaves required for the experiment) and with low
113   branches that could be easily accessed using a stepladder (for safety).

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Table 1. Mean (± 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')	Marguerite-Bourgeoys (MB) (45°47'N, -73°36'W)	Ignace-Bourguet (IB) (45°45'N, -73°60'W)
Acer saccharinum	37.55 (n = 5)	37.55 (n = 2)	15.1 (n = 2)
Acer platanoides	21.60 (n = 1)	23.68 ± 1.97 (n = 6)	26.25 (n = 2)
Tilia cordata	22.40 (n = 1)	30.60 ± 3.37 (n = 5)	9.67 ± 0.51 (n = 4)
Tilia americana	10.52 ± 0.55 (n = 4)	22.06 ± 1.87 (n = 3)	27.60 ± 1.20 (n = 3)
Quercus rubra	8.96 ± 0.37 (n = 5)	NA	12.30 ± 1.45 (n = 5)

Predation rate assessment

We used artificial caterpillars made with modelling clay to estimate predation rate on sampled trees (Ferrante, Lo Cacciato, & Lovei, 2014; Howe, Lövei, & Nachman, 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.

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.

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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, Nakagawa, Laws, & Jamieson, 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:

$$Y_{ij} \sim \beta_0 + \beta_1 \times Density_{ij} + \beta_2 \times Diversity_{ij} +$$
$$\beta_3 \times Conspecific_{ij} + \beta_4 \times Origin_{exotic, ij} + \beta_5 \times Park_{IB, ij} +$$
$$\beta_6 \times Park_{MB, ij} + \beta_6 \times Predation_{ij} +$$
$$\gamma_j + \varepsilon_{ij} \tag{1}$$

5

173 $$\gamma \sim N(0; \sigma_{species}^2) \qquad \varepsilon \sim N(0; \sigma_e^2)$$

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

176 To ease the interpretation of parameter estimates after model averaging, we standardized the
177 input variables using Gelman's approach (Gelman, 2008). We then applied a procedure of
178 model selection based on the Akaike's criterion corrected for small sample size (AICc) by
179 running every model nested within the full model. As tree density and tree diversity were
180 correlated (Pearson's correlation: $r = 0.71$), we excluded all sub-models that included these
181 predictors together. We ranked all models based on difference in AICc between each model
182 and the top ranked model with the lowest AICc (ΔAICc). Models with a ΔAICc < 2 are
183 generally considered equally supported by the data or not differentiable from the top ranked
184 model. Finally, we estimated model fit by calculating marginal (R^2m) and conditional (R^2c) R^2
185 values, corresponding to variance explained by fixed effects only (R^2m) and by fixed and
186 random effects (R^2c) (Nakagawa & Schielzeth, 2013). When multiple models had a ΔAICc $<$
187 2, we used a model averaging approach to build a consensus model including all variables
188 found in the set of best models. We considered that a given predictor had a significant effect if
189 its 95% confidence interval did not overlap zero. When only one model had a ΔAICc < 2, we
190 used it as the best model. We used a square-root transformation of insect herbivory to satisfy
191 model assumptions of normality and homogeneity of residuals.

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

197 $Y_{ijk} \sim \beta_0 + \beta_1 \times Density_{ijk} + \beta_2 \times Diversity_{ijk} +$
198 $\qquad \beta_3 \times Conspecific_{ijk} + \beta_4 \times Origin_{exotic,\ ijk} + \beta_5 \times Park_{IB,\ ijk} +$
199 $\qquad \beta_6 \times Park_{MB,\ ijk} + \beta_6 \times Season_{summer,\ ijk} +$
200 $\qquad \gamma_j + \tau_{k|j} + \varepsilon_{ijk}$ (2)
201 $\qquad \gamma \sim N(0; \sigma_{species}^2) \qquad \tau \sim N(0; \sigma_{individual}^2) \qquad \varepsilon \sim N(0; \sigma_e^2)$
202

203 Statistical analyses were performed using the R software version 3.4.4 (R Core Team 2019)
204 with packages *lme4* (Bates, Mächler, Bolker, & Walker, 2015) and *MuMIn* (Barton 2019).

205 Results

206 ***Insect herbivory*** – Herbivory was on average ($\pm$ SE) 7.19 ± 0.70 % ($n = 48$). Leaf damage was
207 lower in *Acer platanoides* (3.53 ± 0.54) and *A. saccharinum* (3.86 ± 0.47) than in *Quercus*
208 *rubra* (8.77 ± 1.65), *Tilia americana* (10.3 ± 1.37) and *T. cordata* (8.75 ± 1.75) (Fig. 1A).
209

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

Figure 1. Effect of tree species identity on insect herbivory (A) and predation rate (B). Black dots and solid lines represents mean ± 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
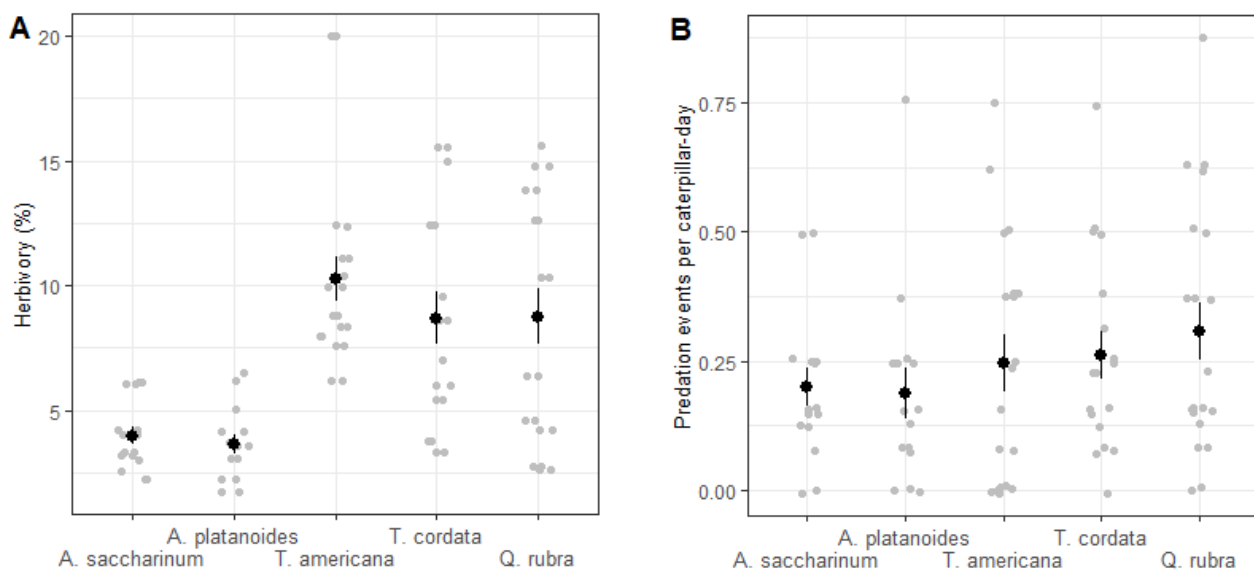
217   *Predation* – Of the 1,315 artificial caterpillars that we installed, 198 displayed marks
218   unambiguously attributable to predators (*i.e.*, 15%). Predation rate varied between 0 and 0.87
219   per caterpillar-day (Fig. 1B).
220   Only one model had a ΔAICc < 2 and was thus selected as the best model. This best model
221   included only Season, with predation rate two times higher in late spring (mean ± CI: 0.44 ±
222   [0.31, 0.58] caterpillars·day^{-1}) than in early summer (0.20 ± [0.16, 0.24] caterpillars·day^{-1}).
223   Season explained 56 % of variability in predation rate and, collectively, fixed and random
224   effects explained 59 % of variability in predation rate.

Table 2. Summary results of model selection of tree neighbourhood effect on herbivory rate: set of models with ΔAICc < 2. Only predictors that were present at least once in the set of best models are represented. R²m and R²c represent fixed and fixed *plus* random factor, respectively.

	Model covariates				Model selection			
Model	Intercept	Predation	Origin	Diversity	K	Log L	Δ*AIC*c	R²m (R²c)
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.

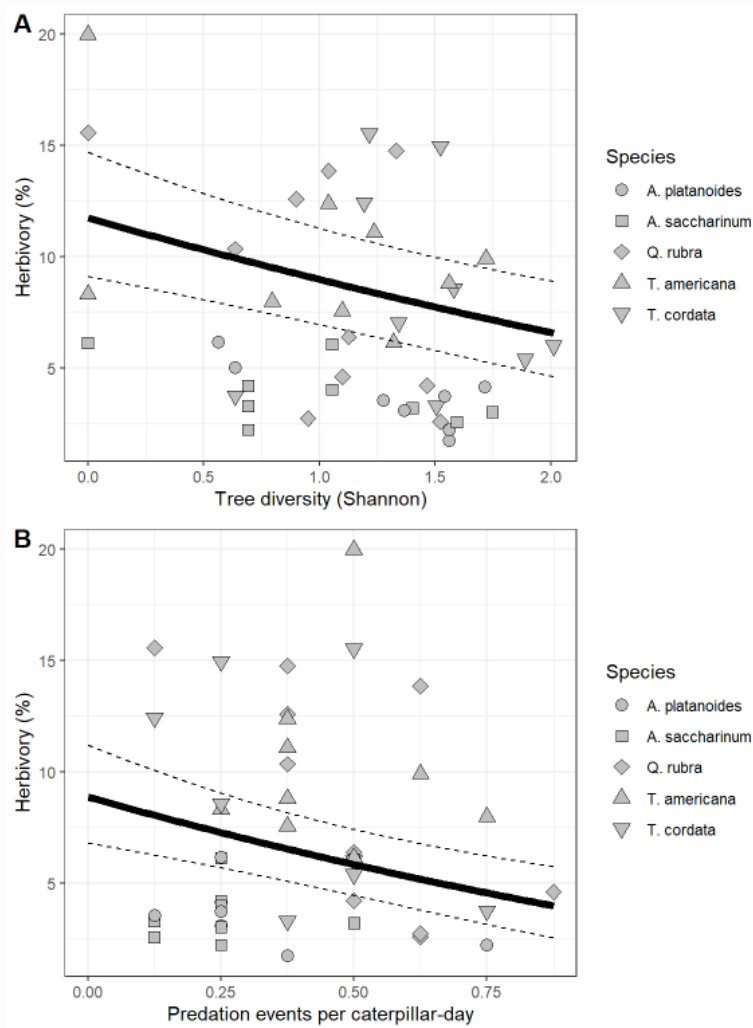| Parameter	Estimate	Adjusted SE	Confidence interval	Relative importance
(Intercept)	2.53	0.31	(1.91, 3.14)	
Diversity	-0.48	0.21	(-0.91, -0.05)	0.72
Predation	-0.47	0.22	(-0.91, -0.003)	0.64
Origin	0.19	0.71	(-1.20, 1.60)	0.31

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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.

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, Meagher, & Dale 2019;

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236 Frank 2014). However, it conflicts with other results suggesting an increase in herbivore
237 abundance with increasing plant diversity in urban environments (Mata et al., 2017), although
238 the relationship between herbivore abundance and actual herbivory is not always positively
239 correlated (Barbosa et al., 2009; Schueller, Paul, Payer, Schultze, & Vikas, 2019). Tree
240 diversity may have influenced the probability of focal trees being found and colonized by
241 herbivores. Theory predicts that specialist herbivores have greater difficulties finding their host
242 trees when they are surrounded by heterospecific neighbours (Castagneyrol et al., 2014; H.
243 Jactel, Brockerhoff, & Duelli, 2009). It is possible that non-host neighbours disrupted the
244 physical and chemical cues used by insect herbivores to locate their hosts (Damien et al., 2016;
245 H. Jactel et al., 2011; Zhang & Schlyter, 2004). However, and contrary to our expectations, we
246 did not find any significant effect of conspecific tree density on insect herbivory, thus ruling
247 out the resource concentration hypothesis in this particular case. However, because our study
248 was observational, we could not separate the effect of conspecific neighbour density from
249 heterospecific neighbour density. In the absence of data on the identity of herbivores
250 responsible for herbivory, further speculation would be hazardous.

251 Insect herbivory varied across tree species but did not differ between native and non-native
252 species, thus not providing support for predictions of the enemy release hypothesis (Cincotta,
253 Adams, & Holzapfel, 2009; Meijer, Schilthuizen, Beukeboom, & Smit, 2016). One possible
254 explanation for this result could be that native herbivores spilled over exotic tree species from
255 neighbouring native tree species, as it was recorded in previous studies (Branco et al., 2015).
256 This would have been facilitated by the fact that exotic tree species (from Europe) had
257 congeneric species in Canada. Although we only surveyed a handful of native and exotic
258 species, making any generalization hazardous, we can speculate on the lack of difference
259 between native and non-native species. It is also important to note that a large part of the
260 variability in leaf insect damage was attributable to the species on which leaf samples were
261 collected. In particular, both *Acer platanoides* and *A. saccharinum* were far less damaged than
262 *Tilia cordata*, *T. americana* and *Quercus rubra*. In a recent study in Michigan, Schueller et al.,
263 (2019) also reported greater insect herbivory (and herbivore diversity) on *Quercus* species as
264 compared to *Acer* species, which is consistent with the view that plant species identity can
265 drive arthropods community and abundance on forest host trees (Burghardt, Tallamy, &
266 Gregory Shriver, 2009; Pearse & Hipp, 2009).

267 We found a significant negative correlation between predator attack rate and insect herbivory
268 measured later in the season. This finding suggests a potential relationship between herbivory
269 and predation in urban environments (Faeth, Warren, Shochat, & Marussich, 2005; Kozlov et
270 al., 2017 but see Long & Frank, 2020). However, we refrain from concluding that predation
271 was the main driver of insect herbivory for several reasons. First, the effect size of the
272 herbivory-predation relationship was small, as was model R^2 (Table 3). Second, concerns
273 remain about how well predation on artificial prey represents of actual predation (Lövei &
274 Ferrante, 2017; Rößler, Pröhl, & Lötters, 2018). In particular, artificial caterpillars used to
275 assess predation rate modelled lepidopteran-like leaf chewing caterpillars and thus, caution is
276 needed when it comes to extrapolate predator attack rates to other herbivore feeding guilds.
277 Third, we had no information on actual natural prey density in focal and neighbouring trees.

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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, Dunn, Sexton, & Frank, 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 and 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, Buyung-Ali, Knight, & Pullin, 2010; Nowak, Hirabayashi, Bodine, & Greenfield, 2014).

Authors' contributions

BC and AP conceived the study. YK selected trees and coordinated field work. YK and BC acquired data. AS, MLB and BC analysed the data. AS, MLB and BC wrote the first draft. All authors contributed critically to the final manuscript.

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Data accessibility

Data and script available from the Data INRAE repository: https://doi.org/10.15454/R4NESA

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.

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. doi: 10.1007/s10530-008-9312-4

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *In: Second International Symposium on Information Theory (B.N. Petrov & F. Csaki, eds), pp. 267–281. Akademiai Kiado, Budapest.*

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. doi: 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). doi: 10.18637/jss.v067.i01

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. doi: 10.3390/ijerph110303453

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*, 456. doi: 10.1186/1471-2458-10-456

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. doi: 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. doi: 10.1111/1365-2664.12175

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. doi: 10.1007/s10530-008-9255-9

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. doi: 10.1093/ee/nvy071

Coley, P. D. (1980). Effects of leaf age and plant life history patterns on herbivory. *Nature*, *284*, 545–546. doi: 10.1038/284545a0

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. doi: 10.1016/j.ufug.2014.02.001

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. doi: 10.1016/j.cois.2018.06.001

Dale, A. G., & Frank, S. D. (2014). Urban warming trumps natural enemy regulation of herbivorous pests. *Ecological Applications: A Publication of the Ecological Society of America*, *24*(7), 1596–1607. doi: 10.1890/13-1961.1

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

13

380   density and host apparency at different spatial scales. *Forest Ecology and Management*,
381   *378*, 103–110. doi: 10.1016/j.foreco.2016.07.025

382 Doherty, E. M., Meagher, R. L., & Dale, A. G. (2019). Turfgrass Cultivar Diversity Provides
383   Associational Resistance in the Absence of Pest Resistant Cultivars. *Environmental*
384   *Entomology*, *48*(3), 623–632. doi: 10.1093/ee/nvz026

385 Faeth, S. H., Warren, P. S., Shochat, E., & Marussich, W. A. (2005). Trophic Dynamics in
386   Urban Communities. *BioScience*, *55*(5), 399–407. doi:
387   10.1641/0006-3568(2005)055[0399:TDIUC]2.0.CO;2

388 Ferrante, M., Lo Cacciato, A., & Lövei, G. (2014). Quantifying predation pressure along an
389   urbanisation gradient in Denmark using artificial caterpillars. *European Journal of*
390   *Entomology*, *111*(5), 649–654.

391 Frank, Steven D. (2014). Bad neighbors: urban habitats increase cankerworm damage to
392   non-host understory plants. *Urban Ecosystems*, *17*(4), 1135–1145. doi:
393   10.1007/s11252-014-0368-x

394 Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations.
395   *Statistics in Medicine*, *27*(15), 2865–2873. doi: 10.1002/sim.3107

396 Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in
397   ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*,
398   *24*(4), 699–711. doi: 10.1111/j.1420-9101.2010.02210.x

399 Hambäck, P. A., & Englund, G. (2005). Patch area, population density and the scaling of
400   migration rates: the resource concentration hypothesis revisited. *Ecology Letters*, *8*(10),
401   1057–1065. doi: 10.1111/j.1461-0248.2005.00811.x

402 Howe, A., Lövei, G. L., & Nachman, G. (2009). Dummy caterpillars as a simple method to
403   assess predation rates on invertebrates in a tropical agroecosystem. *Entomologia*
404   *Experimentalis et Applicata*, *131*(3), 325–329. doi: 10.1111/j.1570-7458.2009.00860.x

405 Huberty, A. F., & Denno, R. F. (2004). Plant Water Stress and Its Consequences for
406   Herbivorous Insects: A New Synthesis. *Ecology*, *85*(5), 1383–1398.

407 Jactel, H., Birgersson, G., Andersson, S., & Schlyter, F. (2011). Non-host volatiles mediate
408   associational resistance to the pine processionary moth. *Oecologia*, *166*(3), 703–711. doi:
409   10.1007/s00442-011-1918-z

410 Jactel, H., Brockerhoff, E., & Duelli, P. (2009). A Test of the Biodiversity-Stability Theory:
411   Meta-analysis of Tree Species Diversity Effects on Insect Pest Infestations, and
412   Re-examination of Responsible Factors. In M. Scherer-Lorenzen, C. Körner, & E.-D.
413 Schulze (Eds.), *Forest Diversity and Function: Temperate and Boreal Systems* (pp. 235–
414   262). doi: 10.1007/3-540-26599-6_12

415 Staab, M., & Schuldt, A. (2020). The Influence of Tree Diversity on Natural Enemies—a
416   Review of the "Enemies" Hypothesis in Forests. *Current Forestry Reports*.
417   doi: 10.1007/s40725-020-00123-6

418 Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., … Brockerhoff,
419   E. G. (2017). Tree Diversity Drives Forest Stand Resistance to Natural Disturbances.
420   *Current Forestry Reports*, *3*(3), 223–243. doi: 10.1007/s40725-017-0064-1

421 Keane, R., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis.
422   *Trends in Ecology & Evolution*, *17*(4), 164–170. doi: 10.1016/S0169-5347(02)02499-0

423 Kozlov, M. V., Lanta, V., Zverev, V., Rainio, K., Kunavin, M. A., & Zvereva, E. L. (2017).
424   Decreased losses of woody plant foliage to insects in large urban areas are explained by
425   bird predation. *Global Change Biology*, *23*(10), 4354–4364. doi: 10.1111/gcb.13692

426 Kozlov, M. V., Zverev, V., & Zvereva, E. L. (2017). Combined effects of environmental
427   disturbance and climate warming on insect herbivory in mountain birch in subarctic
428   forests: Results of 26-year monitoring. *Science of The Total Environment*, *601–602*, 802–
429   811. doi: 10.1016/j.scitotenv.2017.05.230

430   Lefcheck, J. S., Whalen, M. A., Davenport, T. M., Stone, J. P., & Duffy, J. E. (2013).
431   Physiological effects of diet mixing on consumer fitness: a meta-analysis. Ecology, 94(3),
432   565-572.
433   Long, L. C., & Frank, S. D. (2020). Risk of bird predation and defoliating insect abundance
434   are greater in urban forest fragments than street trees. *Urban Ecosystems*. doi:
435   10.1007/s11252-020-00939-x
436   Lövei, G. L., & Ferrante, M. (2017). A review of the sentinel prey method as a way of
437   quantifying invertebrate predation under field conditions. *Insect Science*, *24*(4), 528–542.
438   doi: 10.1111/1744-7917.12405
439   Mata, L., Threlfall, C. G., Williams, N. S. G., Hahs, A. K., Malipatil, M., Stork, N. E., &
440   Livesley, S. J. (2017). Conserving herbivorous and predatory insects in urban green
441   spaces. *Scientific Reports*, *7*. doi: 10.1038/srep40970
442   Mattson, W. J. (1980). Herbivory in Relation to Plant Nitrogen Content. *Annual Review of*
443   *Ecology and Systematics*, *11*(1), 119–161. doi: 10.1146/annurev.es.11.110180.001003
444   Meijer, K., Schilthuizen, M., Beukeboom, L., & Smit, C. (2016). A review and meta-analysis
445   of the enemy release hypothesis in plant-herbivorous insect systems. *PeerJ*, *4*, e2778. doi:
446   10.7717/peerj.2778
447   Meineke, E. K., Dunn, R. R., Sexton, J. O., & Frank, S. D. (2013). Urban warming drives
448   insect pest abundance on street trees. *PloS One*, *8*(3), e59687. doi:
449   10.1371/journal.pone.0059687
450   Meineke, E. K., & Frank, S. D. (2018). Water availability drives urban tree growth responses
451   to herbivory and warming. *Journal of Applied Ecology*, *55*(4), 1701–1713.
452   doi:10.1111/1365-2664.13130
453   Metcalfe, D. B., Asner, G. P., Martin, R. E., Espejo, J. E. S., Huasco, W. H., Amézquita, F. F.
454   F., … Malhi, Y. (2014). Herbivory makes major contributions to ecosystem carbon and
455   nutrient cycling in tropical forests. *Ecology Letters*, *17*(3), 324–332. doi:
456   10.1111/ele.12233
457   Mooney, K.A. & Singer, M.S. (2012). Plant effects on herbivore-enemyinteractions in natural
458   systems. InTrait-Mediated Indirect Interactions:Ecological and Evolutionary
459   Perspectives (eds Ohgushi, T., Schmitz, O.,Holt, R.D.). Cambridge University Press,
460   Cambridge, pp. 107–130.
461   Moreira, X., Abdala-Roberts, L., Teran, J. C. B. M. y, Covelo, F., Mata, R. de la, Francisco,
462   M., Tack, A. J. M. (2019). Impacts of urbanization on insect herbivory and plant
463   defences in oak trees. *Oikos*, *128*(1), 113–123. doi: 10.1111/oik.05497
464   Moro, M. F., Westerkamp, C., & de Araújo, F. S. (2014). How much importance is given to
465   native plants in cities' treescape? A case study in Fortaleza, Brazil. *Urban Forestry &*
466   *Urban Greening*, *13*(2), 365–374. doi: 10.1016/j.ufug.2014.01.005
467   Muiruri, E. W., Rainio, K., & Koricheva, J. (2016). Do birds see the forest for the trees?
468   Scale-dependent effects of tree diversity on avian predation of artificial larvae.
469   *Oecologia*, *180*(3), 619–630. doi: 10.1007/s00442-015-3391-6
470   Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from
471   generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–
472   142. doi: 10.1111/j.2041-210x.2012.00261.x
473   Nell, C., Abdala-Roberts, L., Parra-Tabla, V. & Mooney, K. (2018).Tropical tree diversity
474   mediates foraging and predatory effects ofinsectivorous birds.Proc. R Soc. B, 285,
475   20181842
476   Nowak, D. J., Hirabayashi, S., Bodine, A., & Greenfield, E. (2014). Tree and forest effects on
477   air quality and human health in the United States. *Environmental Pollution (Barking,*
478   *Essex:1987)*, *193*, 119–129. doi: 10.1016/j.envpol.2014.05.028
479   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. doi: 10.1111/j.1365-2311.1995.tb00455.x

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*, doi: 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. doi: 10.1073/pnas.0904867106

QGIS Development Team (2019). QGIS Geographic Information System. Open Source Geospatial Foundation Project.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raupp, & Denno. (1983). Leaf age as a predictor of herbivore distribution and abundance [Herbivorous insects including the willow leaf beetle]. In *Academic Press*. *Variables Plants and Herbivores in Natural and Managed Systems*.

Revision of World Urbanization Prospects | Multimedia Library - United Nations Department of Economic and Social Affairs Retrieved May 30, 2019, from https://www.un.org/development/desa/publications/2018-revision-of-world-urbanization-prospects.html

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. doi: 10.1007/s00442-004-1696-y

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. doi: 10.2307/1942161

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. doi: 10.1016/j.ufug.2011.09.004

Sustainable use of pesticides. Retrieved May 30, 2019, from https://ec.europa.eu/food/plant/pesticides/sustainable_use_pesticides_en

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. doi: 10.1093/forestry/cpq027

Visakorpi, K., Gripenberg, S., Malhi, Y., Bolas, C., Oliveras, I., Harris, N., … 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. doi: 10.1111/nph.15338

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. doi: 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. doi: 10.1111/j.1600-0706.2012.20688.x