

1 **INSECT HERBIVORY ON URBAN TREES:**
2 **COMPLEMENTARY EFFECTS OF TREE**
3 **NEIGHBOURS AND PREDATION**

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19
20 **Abstract**

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

35
36 **Keywords** : Artificial prey, Insect herbivory, [Tree diversity](#), Top-down control, Urban
37 biodiversity

Commenté [H1]: unclear what this means.
You evaluated the relationships between herbivory,
predation, and local tree diversity?

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39 Introduction

40 Insect herbivores have a major impact on tree growth and survival, hence, on the functioning
41 of forest ecosystems (Metcalfé et al., 2014; Visakorpi et al., 2018; Zvereva, Zverev, & Kozlov,
42 2012). Tree diversity significantly influences insect herbivory in forest ecosystems
43 (Castagneyrol, Jactel, Vacher, Brockerhoff, & Koricheva, 2014; Jactel et al., 2017). Most
44 studies report that herbivory declines as tree diversity increases (*i.e.*, associational resistance,
45 Barbosa et al., 2009), although the opposite pattern has also been found (Haase et al., 2015;
46 Schuldt et al., 2011). Recently, the interest in how tree diversity affects insect herbivory has
47 expanded to include urban forests (Clem & Held, 2018; Dale & Frank, 2018; Frank, 2014),
48 where pest damage can compromise the ecological and aesthetic values of urban trees (Nuckols
49 & Connor, 1995; Tooker & Hanks, 2000; Tubby & Webber, 2010). Urban forests differ from
50 natural forests in many ways. For example, most of the trees in cities are planted, found in
51 lower density and/or mixed with native and exotic ornamental species, that are rarely
52 encountered in natural forests. Thus, given these specific characteristics of urban forests, it is
53 still unclear how and why tree diversity might influence insect herbivory on urban trees.

54 The density and diversity of trees determine the amount and the quality of food and habitat
55 resources available to herbivores and their enemies, and thus can have strong impact on the
56 bottom-up and top-down forces acting upon insect herbivores (Haase et al., 2015; Muiruri,
57 Rainio, & Koricheva, 2016; Setiawan, Vanhellemont, Baeten, Dillen, & Verheyen, 2014). For
58 example, some insect herbivores, in particular generalist species, could take advantage of tree
59 diversity to acquire more abundant, complementary food resources or benefit from a more
60 balanced food mix, thus causing more damage in mixed forests (Lefcheck, Whalen, Davenport,
61 Stone, & Duffy, 2013). In contrast, insect herbivores generally find it easier to identify and
62 orientate towards the signals emitted by their host trees when the latter are more concentrated
63 (*the resource concentration hypothesis*, Hambäck & Englund, 2005; Root, 1973) while non-
64 host trees can emit volatile compounds that interfere with the ability of herbivores to detect
65 their preferred host (Jactel, Birgersson, Andersson, & Schlyter, 2011). Finally, the abundance
66 and diversity of predatory birds and arthropods generally increases with plant density and
67 diversity, which would result in a better top-down regulation of insect herbivores (*the enemies
68 hypothesis*, Risch, Andow, & Altieri, 1983; Root, 1973). However, the evidence available to
69 support the *resource concentration hypothesis* in forest is controversial (Muiruri et al., 2016;
70 Riihimäki, Kaitaniemi, Koricheva, & Vehviläinen, 2005) and the contribution of natural
71 enemies to the control of herbivores in urban area remains poorly explored.

72 Tree diversity and density vary widely between and within cities (Ortega-Álvarez, Rodríguez-
73 Correa, & MacGregor-Fors, 2011; Sjöman, Östberg, & Bühler, 2012). A consequence of this
74 variability is that even within a common urban environment, herbivory may be reduced in some
75 tree species and increased in others (Clem & Held, 2018; Frank, 2014), and the relative
76 importance of bottom-up and top-down forces responsible for these effects may also differ. In
77 addition, non-native trees have been widely planted in urban habitats (Cowett & Bassuk, 2014;
78 Moro, Westerkamp, & de Araújo, 2014). While they often escape from herbivory by native

Commenté [H2]: Henceforth means, 'from here on out' or 'from this time forward' and is not the same as therefore, or thus, or hence

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Commenté [H3]: is that what you're referring to when you say "this"

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

Commenté [H4]: predatory birds generally refers to hawks, owls, and the like, but I think you mean birds that eat insects or other arthropods, right?

Supprimé: predatory

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

Commenté [H5]: is this correct? See below.

114 Materials and methods

115 Study site

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

121 Tree selection

122 Every tree in Angrignon, Ignace-Bourget and Marguerite-Bourgeoys parks had been
123 previously geolocalized and identified to the species level. This information was accessible
124 through the city database for urban trees (<http://donnees.ville.montreal.qc.ca/dataset/arbres>).
125 We selected a total of 45 trees of five deciduous species (Table 1). Three species are native to
126 the study area (*Acer saccharinum* L., *Tilia americana* L., *Quercus rubra* L.) while two are
127 exotics, from Europe (*Acer platanoides* L., *Tilia cordata* Mill.). These species are amongst the
128 most abundant tree species in the city of Montreal where together they represent 37% of all the
129 tree species of the public domain. In agreement with the city of Montreal administration, we
130 only selected trees with a diameter at breast height (DBH) greater than 8 cm (mean \pm SD: 18.38
131 \pm 9.36) (to withstand the sampling of leaves required for the experiment) and with low
132 branches that could be easily accessed using a stepladder (for safety).

Commenté [H6]: It appears to me that there are only 45 in Table 1.

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Table 1. Mean (\pm SD) diameter at breast height (in cm) and number of trees 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-Bourguet (IB) (45°45'N, -73°60'W)
<i>Acer saccharinum</i>	37.55 (n = 2)	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 \pm 1.45 (n = 5)

135 Predation rate assessment

136 We used artificial caterpillars made with modelling clay to estimate predation rate on sampled
 137 trees (Ferrante, Lo Cacciato, & Lovei, 2014; Howe, Lövei, & Nachman, 2009). We installed
 138 15 artificial caterpillars per tree. We haphazardly selected three low (2.5-3.5 m from ground)
 139 branches facing different directions and installed five artificial caterpillars per branch (total:
 140 720 caterpillars). Caterpillars were 3 cm long, and modelled to match the approximate form
 141 and size of real caterpillars. They were modelled using a 1-cm ball of non-toxic and odourless
 142 green modelling clay (*Sculpey III String Bean colour*) and secured on thin branches using a 12-
 143 cm long, 0.5 mm diameter, non-shiny metallic wire.

144 We exposed artificial caterpillars for 11 days in late spring (from May 29th to June 9th, 2018)
 145 and for 6 days in early summer (from July 18th to July 24th, 2018). These seasons were chosen
 146 to cover the main activity period of both predators and herbivores. Artificial caterpillars were
 147 left untouched for the full duration of each survey. We estimated total predator attack rate as
 148 the number of artificial larvae with any predation mark, divided by the total length of the
 149 observation period in days. There were uncertainties regarding predator identity responsible
 150 for predation marks. Most of the marks were attributable to birds or arthropods, while very few
 151 were attributable to small mammals, therefore, we chose to combine predation marks primarily
 152 attributed to birds or arthropods into a single category, which we refer to as total predation.

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

Commenté [H7]: I don't see how three can all be opposite each other. I suggest changing "opposite" to different.

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157 Leaf insect herbivory

158 We estimated insect herbivory on leaves (Kozlov et al., 2017) as the percentage of leaf area
159 removed or impacted by insect herbivores through other modes of feeding such as
160 skeletonization or mining. We collectively call this leaf area damaged. At the end of the second
161 predation survey, we collected 10 leaves per branch on the same branches on which we had
162 exposed artificial caterpillars, starting with the most apical, fully-developed, leaf to the 10th
163 leaf down to branch basis (Total: 30 leaves per tree). We estimated total herbivory (i.e., total
164 leaf area consumed or impacted by herbivores, regardless of their identity) as well as damage
165 made by chewing, mining and sap-feeding herbivores at the level of individual leaves by using
166 an ordinal scale of eight percentage classes of defoliation: 0%; 0-1%, 1-5%; 6-10%; 11-25%;
167 26-50%; 51-75% and 76-100%. We counted the number of galls per leaf. Most damage was
168 made by leaf chewers, while other damage had a skewed distribution, preventing detailed
169 analyses for each type of damage separately. We therefore analysed total herbivory by
170 averaging herbivory at the level of individual trees and using the median of each class of
171 defoliation. Herbivory was scored by a single observer (BC), who was blind to tree identity.

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Commenté [H8]: or call it herbivory, as you like, but just be clear about that.

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172 Tree neighbourhood

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

184 Statistical analyses

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

Commenté [H9]: I've always seen this referred to as a full model (e.g. Burnham & Anderson 2002 and Grueber et al. 2011) but maybe “beyond optimal” is a new way of phrasing it or I am misunderstanding what is meant? If you mean something other than the full model, please define it clearly and provide a reference for the terminology. Thanks.

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$$\begin{aligned} 191 \quad Y_{ij} \sim & \beta_0 + \beta_1 \times \text{Density}_{ij} + \beta_2 \times \text{Diversity}_{ij} + \\ 192 & \beta_3 \times \text{Conspecific}_{ij} + \beta_4 \times \text{Origin}_{\text{exotic}, ij} + \beta_5 \times \text{Park}_{\text{IB}, ij} + \\ 193 & \beta_6 \times \text{Park}_{\text{MB}, ij} + \beta_6 \times \text{Predation}_{ij} + \\ 194 & \gamma_j + \varepsilon_{ij} \end{aligned} \quad (1)$$

$$Y \sim N(0; \sigma_{\text{species}}^2) \quad \varepsilon \sim N(0; \sigma_e^2)$$

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

Commenté [H10]: or percent leaf area damaged

202 To ease the interpretation of parameter estimates after model averaging, we standardized the
203 input variables using Gelman's approach (Gelman, 2008). We then applied a procedure of
204 model selection based on the Akaike's criterion corrected for small sample size (AICc) by
205 running every model nested within the full model. As tree density and tree diversity were
206 correlated (Pearson's correlation: $r = 0.71$), we excluded all sub-models that included these
207 predictors together. We ranked all models based on difference in AICc between each model
208 and the top ranked model with the lowest AICc (ΔAICc). Models with a $\Delta\text{AICc} < 2$ are
209 generally considered equally supported by the data or not differentiable from the top ranked
210 model. Finally, we estimated model fit by calculating marginal (R^2_m) and conditional (R^2_c) R^2
211 values, corresponding to variance explained by fixed effects only (R^2_m) and by fixed and
212 random effects (R^2_c) (Nakagawa & Schielzeth, 2013). When multiple models had a $\Delta\text{AICc} <$
213 2 , we used a model averaging approach to build a consensus model including all variables
214 found in the set of best models. We considered that a given predictor had a significant effect if
215 its 95% confidence interval did not overlap zero. When only one model had a $\Delta\text{AICc} < 2$, we
216 used it as the best model. We used a square-root transformation of insect herbivory to satisfy
217 model assumptions of normality and homogeneity of residuals.

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

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$$\begin{aligned} 223 \quad Y_{ijk} \sim & \beta_0 + \beta_1 \times \text{Density}_{ijk} + \beta_2 \times \text{Diversity}_{ijk} + \\ 224 & \beta_3 \times \text{Conspecific}_{ijk} + \beta_4 \times \text{Origin}_{\text{exotic},ijk} + \beta_5 \times \text{Park}_{\text{IB},ijk} + \\ 225 & \beta_6 \times \text{Park}_{\text{MB},ijk} + \beta_6 \times \text{Season}_{\text{summer},ijk} + \\ 226 & \gamma_j + \tau_{kij} + \varepsilon_{ijk} \quad (2) \\ 227 \quad Y \sim & N(0; \sigma_{\text{species}}^2) \quad \tau \sim N(0; \sigma_{\text{individual}}^2) \quad \varepsilon \sim N(0; \sigma_e^2) \end{aligned}$$

228
229 Statistical analyses were performed using the R software version 3.4.4 (R Core Team 2019)
230 with packages *lme4* (Bates, Mächler, Bolker, & Walker, 2015) and *MuMIn* (Barton 2019).

231 Results

232 *Insect herbivory* – Leaf area damaged was on average (\pm SE) 7.19 ± 0.70 % ($n = 48$). Leaf
233 damage was lower in *Acer platanoides* (3.53 ± 0.54) and *A. saccharinum* (3.86 ± 0.47) than in
234 *Quercus rubra* (8.77 ± 1.65), *Tilia americana* (10.3 ± 1.37) and *T. cordata* (8.75 ± 1.75) (Fig.
235 1A).

Commenté [H11]: If you decide to use herbivory above, this should be changed to that, otherwise people will be confused and wonder if this is some portion of herbivory or what.

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There were six models competing with the top ranked model in a range of 2 units of $\Delta AICc$ (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). Others predictors had no significant effect on insect herbivory. 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.

Commenté [H12]: See the below comment under predation. I think this sentence should be removed.

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 rate is the number of caterpillars attacked per day in late spring.

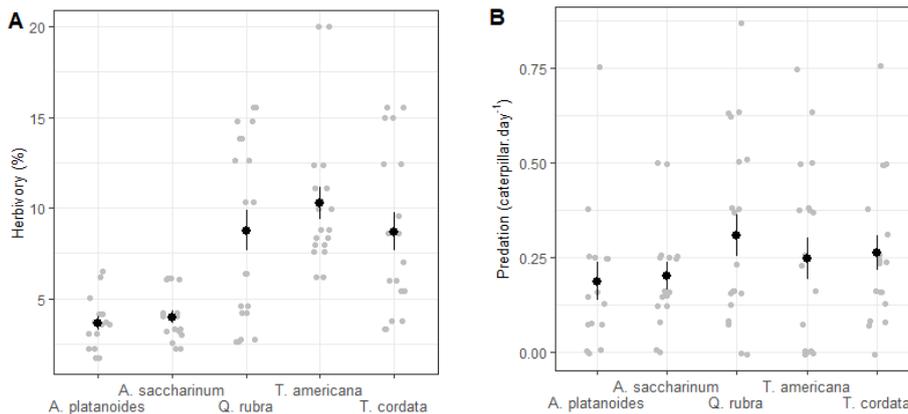
Commenté [H13]:

Commenté [H14R13]: It would be useful if the order on this figure were re-arranged to show native-non-native pairs in the same order, and the oak at the end. For herbivory, the trend is in the predicted direction – A platanoides and T cordata have lower herbivory than their native congeners, respectively.

You could run a paired analyses to evaluate that more rigorously, or you could just mention it in the discussion.

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Commenté [H15]: The Y axis label should be changed to something like, "Predation events per caterpillar-day" The dot between caterpillar and day doesn't have a standard meaning that I know of. If that's common usage, ignore, but I don't think it is. To me it looks leftover from an analysis column for usage in R.



250 **Predation** – Of the 1,315 artificial caterpillars that we installed, 198 displayed marks
251 unambiguously attributable to predators (*i.e.*, 15%). Predation rate varied between 0 and 0.87
252 per caterpillar-day (Fig. 1B).
253 Only one model had a $\Delta AICc < 2$ and was thus selected as the best model. This best model
254 included only Season, with predation rate two times higher in late spring (mean \pm CI: $0.44 \pm$
255 $[0.31, 0.58]$ caterpillars \cdot day⁻¹) than in early summer ($0.20 \pm [0.16, 0.24]$ caterpillars \cdot day⁻¹).
256 Other predictors had no significant effects on predation rate. Season explained 56 % of
257 variability in predation rate and, collectively, fixed and random effects explained 59 % of
258 variability in predation rate.

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Commenté [H16]: I think this should be deleted. Using a model selection approach, you've already stated that Season is the only factor in the best model, so it is redundant to say the others weren't significant. It also confounds the information theoretic approach and a frequentist approach, which should be avoided if possible.

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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

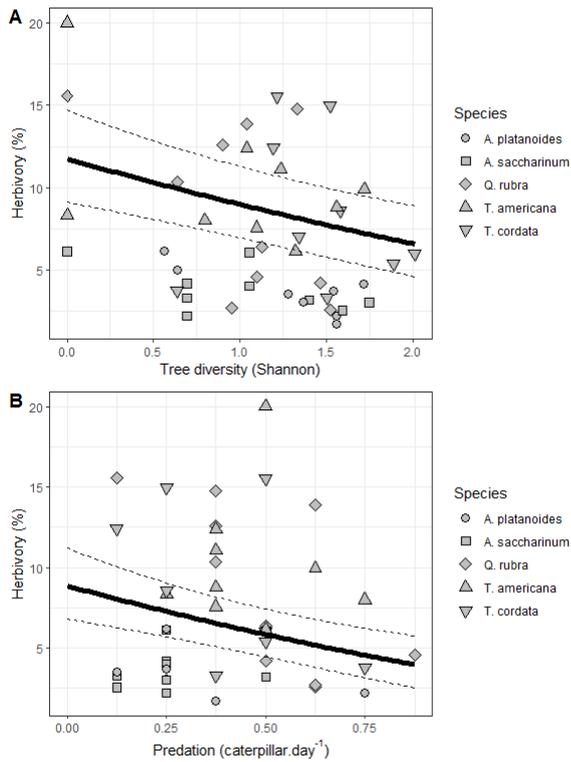


Figure 2. Effects of tree diversity (A) and predation rate (B) on insect herbivory. Solid and dashed lines represent prediction and adjusted standard error of the average model respectively (Table 3). Herbivory is the percentage of leaf area removed or impacted by herbivores in early summer. Tree diversity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

269 **Discussion**

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

276 Our results are in line with several studies having reported reduced herbivory in trees
 277 surrounded by heterospecific neighbours (reviewed by Castagneyrol et al., 2014; Jactel et al.,
 278 2017). It also adds to the growing number of studies documenting diversity-resistance
 279 relationships in urban environments (Clem & Held 2018; Doherty, Meagher, & Dale 2019;

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

Commenté [H17]: You didn't evaluate vegetation volume, did you?

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299 Insect herbivory varied across tree species but did not differ between native and non-native
300 species, thus not providing support for predictions of the enemy release hypothesis (Cincotta,
301 Adams, & Holzapfel, 2009; Meijer, Schilthuizen, Beukeboom, & Smit, 2016). One possible
302 explanation for this result could be that native herbivores spilled over exotic tree species from
303 neighbouring native tree species, as it was recorded in previous studies (Branco et al., 2015).
304 This would have been facilitated by the fact that exotic tree species (from Europe) had
305 congeneric species in Canada. It is also important to note that a large part of the variability in
306 leaf insect damage was attributable to the species on which leaf samples were collected. In
307 particular, both *Acer platanoides* and *A. saccharinum* were far less damaged than *Tilia cordata*,
308 *T. americana* and *Quercus rubra*. In a recent study in Michigan, Schueller et al., (2019) also
309 reported greater insect herbivory (and herbivore diversity) on *Quercus* species as compared to
310 *Acer* species, which is consistent with the view that plant species identity can drive arthropods
311 community and abundance on forest host trees (Burghardt, Tallamy, & Gregory Shriver, 2009;
312 Pearse & Hipp, 2009).

Commenté [H18]: see comment on figure one.

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Commenté [H19]: Your power to test the hypothesis is very low, with only 3 native and 2 introduced species, and an analysis that does not take the phylogenetic paring into account. Both these things should be mentioned here.

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

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

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

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

356 Conclusion

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

366 Authors' contributions

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

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Commenté [H20]: what data make you suggest this?
Is the decrease only seen in certain locations? Above,
in a sentence I suggest deleting (perhaps not a good
suggestion after all) you say other predictors aren't
significant.

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391 **Data accessibility**

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

393 **Conflict of interest disclosure**

394 The authors of this article declare that they have no financial conflict of interest with the content
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