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

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Abstract

1. Urban trees provide important ecological services to urban ecosystems, including cooling, pollution filtering or improvement of human well-being. Urban trees can be more at risk to be damaged by herbivores than their rural counterparts. But not all urban trees suffer from the same amount of insect damage and intra-urban gradients of herbivory have been observed, although underlying drivers 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, and linked herbivory and predation with tree density and tree diversity in the vicinity of focal trees.
3. Leaf insect herbivory decreased with increasing tree diversity, and predator attack rate on artificial larvae increased with tree density around focal trees. Insect herbivory was negatively correlated with predator attack rate.
4. Our findings indicate that tree diversity and density are determinants of multitrophic interactions among trees, herbivores and predators in urban environments and that managing tree diversity and density could contribute to pest regulation in cities.

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

Introduction

Insect herbivores have a major impact on tree growth and survival, henceforth 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; Hervé Jactel et al., 2017). Most of studies reported negative relationship between tree diversity and herbivory (*i.e.*, associational resistance, Barbosa et al., 2009), although the opposite was also found (Haase et al., 2015; Schuldt et al., 2011). Recently, the interest about tree diversity effects on 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). However, given the numerous peculiarities of the urban environment, it is still unclear how and why tree diversity might influence insect herbivory on urban trees.

By determining the amount and the quality of food and habitat resources available to herbivores and their enemies, both the density and diversity of trees 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). On the contrary, 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 this hypothesis in forest is controversial (Muiruri et al., 2016; Riihimäki, Kaitaniemi, Koricheva, & Vehviläinen, 2005) 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 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, Brockerhoff, Castagneyrol, Orazio, & Jactel, 2015). Non-native tree species can also provide habitats to predatory birds or 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, tree origin, and predator activity on insect herbivory in urban trees of the city of Montreal (Quebec, Canada). We measured leaf area removed or 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 (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.

Materials and methods

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 experiment 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 trees 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 ± SD: 18.38 ± 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).

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

Species	**Angrignon** (45°26'N, -73°36')	**Marguerite-Bourgeoys** (45°47'N, -73°36'W)	**Ignace-Bourguet** (45°45'N, -73°60'W)
Acer saccharinum	37.55 (n = 2)	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 opposite 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; 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 background leaf insect herbivory (Kozlov et al., 2017) as the percentage of leaf area removed or impacted by insect herbivores. 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 much 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), whom was blind to tree identity.

Tree neighbourhood

We used two 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) and tree species diversity (Shannon diversity index). 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 target trees were also within the neighbourhood of another target tree.

Statistical analyses

Tree density was correlated with tree diversity (Pearson's correlation: $r = 0.71$), as could be expected. Including them both as predictors in the same model would have caused collinearity issues resulting in spurious model coefficient parameter estimates (Graham, 2003). We therefore built separate models for tree density and tree diversity.

We first tested the effect of tree neighbourhood (tree diversity or density) on predation rate. We ran two separate Linear Mixed-effect Models (LMM) with *Origin* (native or exotic focal tree species), *Season* and tree density (*Density*) or diversity (*Diversity*) as fixed effects, and *Park*, tree species (*Species)* and individual *Tree ID* (nested within park) as random factors. We log-transformed predation rate to satisfy model assumptions of normality and homogeneity of residuals.

We used a two-step approach to test the effect of tree neighbourhood on insect herbivory. First, we ran two separate LMM with *Origin* and tree *Density* or *Diversity* as fixed effects and *Park* and *Species* as random factors. Because tree density or diversity may have had an effect on predation rate, we then tested whether accounting for predation rate in models predicting herbivory modified our conclusions about the effect of tree neighbourhood. We considered that if the effect of tree neighbourhood on herbivory was indirectly mediated by its effect on predation rate, then its statistically significant effect on herbivory would turn non-significant after predation rate was introduced as a predictor in the model. We therefore built a second set of models with *Origin*, predation rate (*Predation*) and tree *Density* or *Diversity* as fixed effects and *Park* and *Species* as random factors. Herbivory was measured only once, right after the

second predation survey, in early summer. Thus, herbivory estimate accumulated damage made by herbivores since leaf unfolding, i.e. mainly in spring. We considered that early summer predation rate was thus less representative of predation pressure experienced by herbivores responsible for observed damaged and therefore decided to limit the test of predation effect on herbivores to predation measured earlier, in late spring. We used a square-root transformation of insect herbivory to satisfy model assumptions.

For every model, we first ran the complete model and then applied backward model simplification by sequentially dropping non-significant terms. Model parameters were fitted using restricted maximum likelihood (REML). The significance of fixed effects was tested based on the *F*-distribution estimating degrees of freedom with Kenward-Roger methods (Kuznetsova, Brockhoff, & Christensen, 2017). We estimated model coefficient parameters of the simplified models and estimated model fit by calculating marginal (R^2m) and conditional (R^2c) R^2 values, corresponding to variance explained by fixed effects only (R^2m) and by fixed and random effects (R^2c) (Nakagawa & Schielzeth, 2013). Statistical analyses were performed using the R software version 3.4.4 (R Core Team 2019) with packages *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017) and *MuMIn* (Barton 2019).

Results

Predation – Of the 1,360 artificial caterpillars that we installed, 198 displayed marks unambiguously attributable to predators (*i.e.*, 15%). There was a statistically significant, albeit weak, increase in predation rate with increasing tree density (slope estimate ± SE: [8.96 ± 4.01] $\times 10^{-3}$ caterpillars·day^{-1}, Fig. 1, Table 2), in both seasons. There was no effect of tree diversity on predation rate (Table 2). Mean predation rate (± SE) on artificial caterpillars was significantly higher in late spring (0.40 ± 0.03 caterpillars·day^{-1}) than in early summer (0.10 ± 0.01 caterpillars·day^{-1}, Fig. 1, Table 2). The origin of the tree had no effect on predation rate (Table 2). Collectively, fixed effects explained more than 54% of variability in predation rate (Table 2), while random factors accounted for less than 7% of variability (Table 2).

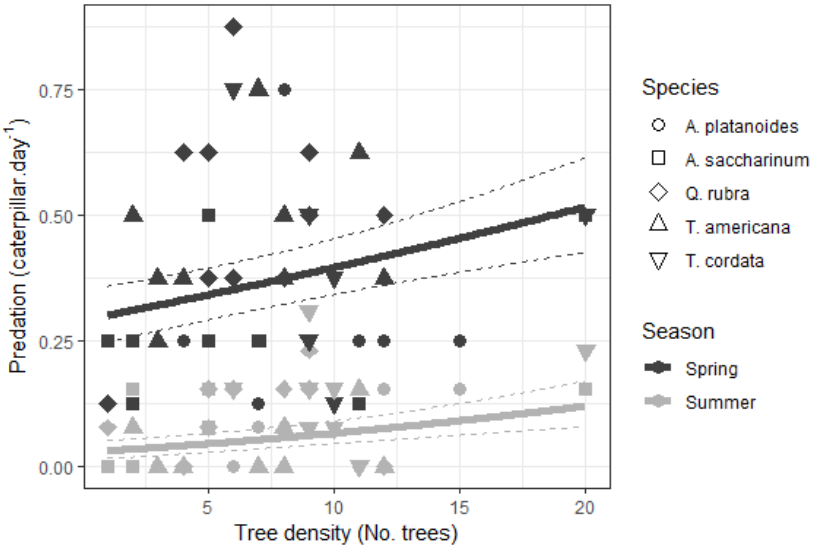

Figure 1. Effects of tree density and season on predation rate. Solid and dashed lines represent model predictions ± SE from *Model 1* in Table 2.

Table 2. Summary of linear mixed effect models (LMM) testing the effects of the origin (native *vs* exotic focal tree species), season (late spring *vs* early summer) tree density (*Density*, number of trees), tree species richness (*Richness*) and tree diversity (*Diversity*) on predation rate. R^2m and R^2c represent R^2 of fixed and fixed *plus* random factors, respectively. σ_{park}, $\sigma_{species}$ and σ_{tree} are the estimated standard deviation of the Park, Species and Tree ID random factors. Values in bold characters indicate significant effects.

Predictors	*F*-value (df)	*P*-value	R^2_m (R^2_c)	σ_{park}	$\sigma_{species}$	σ_{tree}
Density	4.99 (1, 78.9)	**0.028**				
Season	121.54 (1, 77.5)	< **0.001**	0.56 (0.63)	5.6×10^{-2}	3.2×10^{-2}	6.2×10^{-5}
Origin	0.15 (1, 4.1)	0.715				
Shannon	2.23 (1, 70.8)	0.139				
Season	116.43 (1, 78.3)	< **0.001**	0.54 (0.61)	5.3×10^{-2}	3.6×10^{-2}	$< 0.1 \times 10^{-5}$
Origin	0.08 (1, 3.9)	0.792				

Insect herbivory – Damaged leaf area was on average (± SE) 7.19 ± 0.70 % (*n* = 48). Leaf damage were 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). There was a significant decrease of insect herbivory with increasing tree diversity (–0.47 ± 0.22, Fig. 2A, Table 3). However, this effect turned non-significant after predation rate was accounted for in the model (Table 3). Insect herbivory decreased significantly with increasing predation rate, regardless of tree diversity or density (–1.37 ± 0.58) (Fig. 2B, Table 3). The origin of the tree had no effect on insect herbivory (Table 2). Collectively, fixed effects only accounted for 7% of variability in insect herbivory while random factors explained 49% of total variability (Table 3).

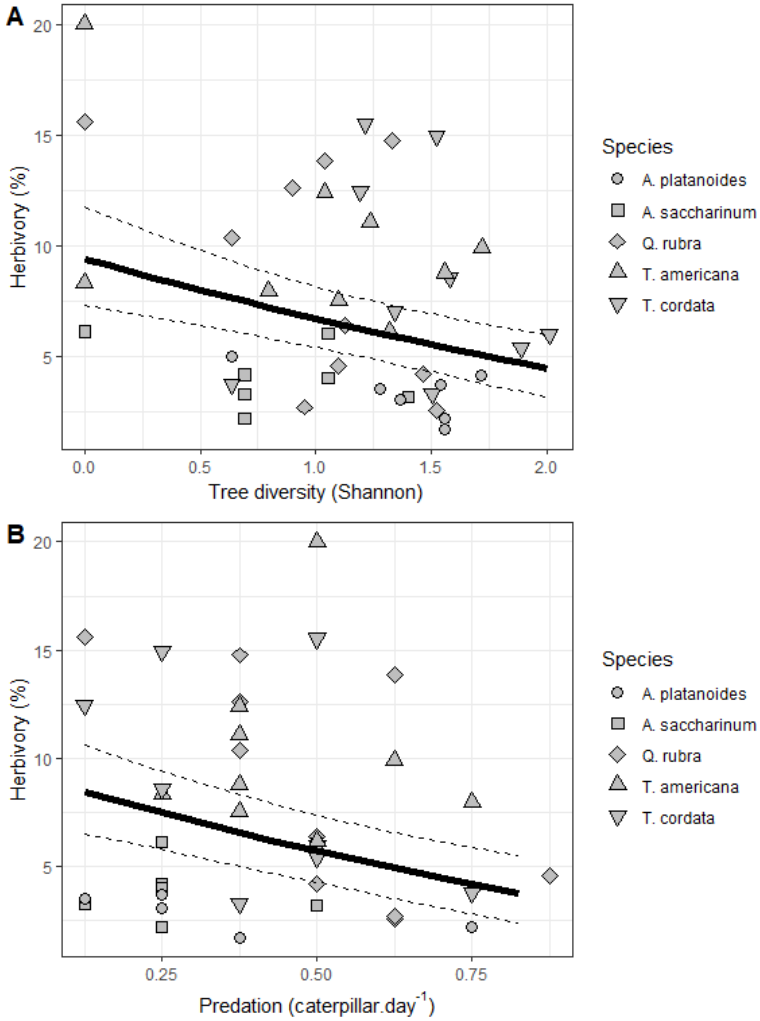

Figure 2. Effects of tree diversity (A) and predation rate (B) on insect herbivory. Solid and dashed lines represent prediction and standard error of LMM (A: Model 3, Table 3; B: Model 6, Table 3). Herbivory is the percentage of leaf area removed or impacted by herbivores in early summer. Tree diversity is represented by Shannon's diversity index. Predation rate is the number of caterpillars attacked per day in late spring.

Table 3. Summary of linear mixed effect models (LMM) testing the effects of the origin (native *vs* exotic focal tree species) and tree density (*Density*, number of trees) or tree diversity (*Diversity*) in a radius of 20 m centred on focal trees on herbivory (Models 1-2) or together with predation rate (*Predation*, Model 3-4). R^2m and R^2c represent R^2 of fixed and fixed *plus* random factors, respectively, and were calculated after model simplification. σ_{park} and $\sigma_{species}$ are the estimated standard deviation of the Park and Species random factors. Values in bold characters indicate significant effects.

Predictors	***F*-value**	***P*-value**	R^2_m (R^2_c)	σ_{park}	$\sigma_{species}$
Density	1.87 (1, 35.8)	0.180			
Origin	0.1 (1, 3.2)	0.766	- (0.46)	0.22	0.55
Shannon	4.51 (1, 24.7)	**0.044**			
Origin	0.04 (1, 3.1)	0.860	0.08 (0.46)	0.22	0.55
Density	0.68 (1, 33.8)	0.415			
Predation	5.48 (1, 28.2)	**0.026**			
Origin	0.24 (1, 3.1)	0.657	0.07 (0.56)	0.08	0.67
Shannon	2.72 (1, 35.6)	0.108			
Predation	5.48 (1, 28.2)	**0.026**			
Origin	0.11 (1, 3.2)	0.766	0.07 (0.56)	0.08	0.67

Discussion

We confirmed that tree density and diversity can both influence insect herbivory and predator activity on urban trees. Specifically, we found that insect herbivory decreased with increasing tree diversity (i.e. associational resistance) and that predator attack rate on artificial caterpillars increased with increasing tree density. We also found a negative correlation between predator attack rate and insect herbivory. Although further analysis are needed to confirm this trend, our findings provide some support to the view that increasing tree diversity can enhance regulation of insect herbivores by natural enemies in urban forests.

Herbivory slightly decreased with increasing tree species diversity in 20m radius circular buffers centred on focal trees, which is in line with several studies having reported reduced herbivory in trees surrounded by heterospecific neighbours (reviewed by Castagneyrol et al., 2014; Hervé 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; Frank 2014). However, it conflicts with other results suggesting an increase in herbivore abundance with increasing plant diversity and vegetation volume 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, Paul, Payer, Schultze, & Vikas, 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; H. Jactel, Brockerhoff, & Duelli, 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; H. Jactel et al., 2011; Zhang & Schlyter, 2004). However, 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, which contradicts the predictions of the enemy release hypothesis (Cincotta, Adams, & Holzapfel, 2009; Meijer, Schilthuizen, Beukeboom, & Smit, 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. 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 (Table 3). In particular, both *Acer platanoides* and *Acer saccharinum* were far less damaged than *Tilia cordata*, *Tilia 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, Tallamy, & Gregory Shriver, 2009; Pearse & Hipp, 2009).

Predator activity increased with increasing tree density in 20m radius buffers centred on focal

trees. Although it is clear from the literature that the urban environment can alter the structure of predator communities and the top-down control they exert upon herbivores as compared to rural areas (Cupitra-Rodriguez, Cruz-Bernate, & Montoya-Lerma, 2018; Kozlov et al., 2017; Turrini, Sanders, & Knop, 2016), few studies to date have addressed predation within intra-urban gradients (Frey et al., 2018; Long & Frank, 2020; Mata et al., 2017; Philpott & Bichier, 2017). The positive effect of tree density on predation could be explained by the fact that higher numbers of adequate nesting or resting places for predators such as birds or parasitoids can be provided by a greater abundance of trees(Langellotto & Denno, 2004; Shrewsbury et al., 2004). Insectivorous birds in particular might show preferences for foraging areas hosting a greater density of trees (Whelan & Maina, 2005). Likewise, insect-eating arthropods respond positively to the vegetation volume in urban areas (Schuh & Slater 1995). Even though they do not directly interact with the vegetation component of their habitat, these predators might use it as hunting grounds or could, in the case of parasitoids, feed on pollen or honeydew to acquire nutritive elements missing from their diet (Leius, 1963; Mata et al., 2017). Focal tree origin did not affect predation rate on artificial caterpillars, which strengthen the idea that predatory birds or arthropods can use native and exotic trees alike as foraging ground in city (Gray & van Heezik, 2016). Finally, contrary to our expectations, predation rate was not affected by tree diversity. Yet, the "natural enemies hypothesis" predicts that more diverse ecosystems sustain more prey and hosts throughout the year, allowing their enemies to maintain their populations (Letourneau, 1987; Root, 1973; Russell, 1989). We could not verify the premises of this hypothesis and might have overlooked the longer-term effect of tree species diversity on predation, which would deserve further attention. In particular, we suggest that particular attention should be paid to the spatial and temporal characteristics of the abundance and diversity of birds that nest and feed in urban trees.

We found a significant negative association 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, Warren, Shochat, & Marussich, 2005; Kozlov et al., 2017 but see Long & Frank, 2020). However, we refrain from concluding that, in our system, 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 much predation on artificial prey is representative of actual predation (Lövei & Ferrante, 2017; Rößler, Pröhl, & Lötters, 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. 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).

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 more scattered tree vegetation cover in spring, making it easier for predators to target artificial caterpillars, or by greater predators

activity matching the phenology of actual caterpillars and feeding period of chicks (Coley, 1980; Raupp & Denno, 1983).

Conclusion

Our study highlights several ecological factors driving leaf insect herbivory in the urban trees of the Montreal city. In particular, we found that insect herbivory decreased with increasing tree diversity and was probably affected by predator activity, which increased with tree density. While biological invasions and global warming are increasing the risk upon 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, densifying and 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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