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Liana distribution in response to urbanization in temperate forests [1]

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Abstract: Urbanization results in ecosystem fragmentation, habitat loss, and altered environmental conditions that usually favour pioneer and ruderal species. The objective of this study was to evaluate the impact of urban conditions on liana abundance in temperate forests. Fieldwork was conducted in 50 forests of the metropolitan Montréal area (Quebec, Canada) and focused on the 6 most common lianas of the study area, *Celastrus scandens*, *Menispermum canadense*, *Parthenocissus quinquefolia*, *Solanum dulcamara*, *Toxicodendron radicans*, and *Vitis riparia*. Potential drivers of liana distribution at the landscape scale (*e.g.*, surrounding land use, urban heat island) were quantified based on satellite images and land use maps. At the forest scale, we investigated biotic and abiotic variables in 429 sampling plots. We found that at the landscape scale, lianas benefited from urbanization, mainly through warm microclimates created by urban heat islands (UHI) as lianas are not well adapted to cold climates. At the forest scale, lianas were more abundant in disturbed forests and in edge habitats than in less disturbed forest and core habitats. Their fast growth rate enables them to quickly take advantage of high light availability on disturbed sites. Our results suggest that urbanization and ongoing climate changes will lead to an increase in liana abundance in temperate forests.
Keywords: climbing plants, edge effect, human disturbances, temperate forests, urban heat islands, woody vines.

Résumé : L'urbanisation provoque la fragmentation des écosystèmes et la perte d'habitats et altère les conditions environnementales ce qui en général favorise les espèces pionnières et rudérales. L'objectif de cette étude était d'évaluer l'impact des conditions urbaines sur l'abondance de lianes en forêt tempérée. Les travaux de terrain ont été effectués dans 50 forêts de la région métropolitaine de Montréal (Québec, Canada) et ont porté sur les 6 lianes les plus communes dans l'aire d'étude : *Celastrus scandens*, *Menispermum canadense*, *Parthenocissus quinquefolia*, *Solanum dulcamara*, *Toxicodendron radicans* et *Vitis riparia*. Les facteurs potentiellement déterminants pour la distribution des lianes à l'échelle du paysage (par exemple, l'utilisation du territoire environnant, les îlots de chaleur urbains) ont été évalués quantitativement à partir d'images satellites et de cartes d'utilisation du territoire. À l'échelle de la forêt, nous avons examiné les variables biotiques et abiotiques dans 429 parcelles d'échantillonnage. Nous avons constaté qu'à l'échelle du paysage, les lianes profitent de l'urbanisation, principalement en raison du microclimat chaud créé par les îlots de chaleur urbains puisque les lianes ne sont pas bien adaptées aux climats froids. À l'échelle de la forêt,, les lianes étaient plus abondantes dans les forêts perturbées et dans les habitats de bordure que dans les forêts moins perturbées et les habitats intérieurs. Leur taux élevé de croissance des lianes leur permet de profiter rapidement de la grande disponibilité de lumière dans les sites perturbés. Nos résultats suggèrent que l'urbanisation et les changements climatiques en cours vont mener à une augmentation de l'abondance des lianes dans les forêts tempérées.
Mots-clés : effet de bordure, forêts tempérées, îlots de chaleur urbains, perturbations humaines, plantes grimpantes, vignes ligneuses.

Nomenclature: Brouillet *et al.*, 2010.

Introduction

In urban landscapes, environmental conditions are often radically altered by human activities (Grimm *et al.*, 2008), thus reducing quality and availability of suitable habitats for sensitive plants while promoting the establishment and proliferation of ruderal and alien species (Godefroid & Koedam, 2007; Vallet *et al.*, 2010a). Several ecological filters related to adverse urban conditions yield a strong selective pressure on species traits (Williams *et al.*, 2008) and therefore promote the emergence of new distribution patterns of biodiversity (*e.g.*, Godefroid & Koedam, 2007; Knapp *et al.*, 2008; Vallet *et al.*, 2010b). Habitat fragmentation is one of the main ecological filters in urban areas (Williams *et al.*, 2008). Indeed, urban landscapes are characterized by small remnants of vegetation patches insulated from each other by an anthropized matrix, which acts on species survival and dispersal (Vallet *et al.*, 2010a; Marini *et al.*, 2012). Fragmentation also creates edge habitats, especially in forests, where abiotic conditions are altered by the surrounding inhabited matrix (Murcia, 1995; Vallet *et al.*, 2010b). The ecotones between forests and the surrounding

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matrix are subject to the effects of high solar radiation and wind (Murcia, 1995), which favour competitive, pioneer, and ruderal plants (Godefroid & Koedam, 2003; Guirado, Pino & Rodà, 2006; LaPaix, Harper & Freedman, 2012). Edges also promote alien plant introduction into forests (Cadenasso & Pickett, 2001; Guirado, Pino & Rodà, 2006), since nearby gardens and landscaped parks act as a source of propagules of naturalized and ornamental species (Williams *et al.*, 2008).

The concentration of impervious surfaces at the expense of vegetation cover promotes the formation of urban heat islands (UHI) that can induce thermal and hydric stress in sensitive organisms (Godefroid & Koedam, 2007; Grimm *et al.*, 2008). For example, Bergeron and Pellerin (2014) found that the richness of indigenous pteridophytes was lower in urban forests affected by UHI, likely because UHI reduced ground moisture essential for pteridophyte reproduction. On the other hand, in cold regions UHI could extend the growing season (Imhoff *et al.*, 2000) and thus favour species with thermophilous requirements, such as many ruderal and alien plants introduced from warmer regions (Godefroid & Koedam, 2007; Knapp *et al.*, 2008; Penone *et al.*, 2012). Phenological changes in native species (*e.g.*, bud burst, flowering period) have also been observed in urban areas associated with expansion of the growing season (White *et al.*, 2002; Zhang *et al.*, 2004).

Lianas are a functional group characterized by great morphological and anatomical plasticity, which enables them to adapt to a wide range of conditions (Rowe & Speck, 2005). They are known to increase in abundance in fragmented and disturbed forests (Schnitzer & Carson, 2001; Londré & Schnitzer, 2006; Ladwig & Meiners, 2010a). The high levels of habitat fragmentation, ambient temperature, and atmospheric carbon dioxide caused by human activities are probable main drivers responsible for the increasing abundance of lianas in ecosystems worldwide (Schnitzer & Bongers, 2011). Several liana species are vulnerable to cold (Schnitzer, 2005) and therefore could probably take advantage of UHI affecting urban forests in northern regions. Furthermore, urban forest edges offer typical habitat conditions for lianas, such as an open canopy, various supports in the form of trees and shrubs, and frequent micro-disturbances (Ibarra-Manríquez & Martínez-Ramos, 2002). Walking trails within urban forests also create canopy gaps and micro-disturbances, which are favourable for rapid spread and dominance of lianas (Ladwig & Meiners, 2010b). Although the number of studies on lianas in temperate regions has increased in the past decade (Londré & Schnitzer, 2006; Ladwig & Meiners; 2010a,b; Leicht-Young *et al.*, 2010), current knowledge is based mostly on data from tropical regions (Schnitzer & Bongers, 2002). The need to study lianas in temperate forests of North America was highlighted by Herron *et al.* (2007), who noted their traits associated with invasiveness and capacity to colonize potentially unoccupied niches. Furthermore, many native and exotic lianas appear to be problematic species worldwide (Ladwig & Meiners, 2010b) and are ubiquitous in most forest ecosystems (Schnitzer & Bongers, 2002). For instance, alien lianas with fleshy fruits were found to be a group increasingly distributed throughout the New York urban landscape over time (Aronson, Handel & Clemants, 2007).

The aim of our study was to understand liana distribution and abundance in urban temperate forests. Specifically, the objectives were to evaluate 1) the influence of environmental factors on the distribution and abundance of lianas at the landscape scale and 2) the influence of biotic interactions, abiotic factors, and edge effects at the local forest scale. Although lianas are ubiquitous in vacant lots and wastelands in cities, we focused on forests since they are important conservation units for urban native biodiversity.

Methods

Study area

The study was conducted on 4 of the largest islands (Montréal, 482.8 km^2; Île Bizard, 22.8 km^2; Île Perrot, 41.9 km^2; Île des Sœurs, 3.7 km^2) of the Hochelaga Archipelago (45°28'N, 73°45'W; Figure 1). The region has a humid continental climate with cold, snowy winters and hot, humid summers. The average annual temperature is 6.8 °C, ranging from –10 °C in January to 21 °C in July. The average annual precipitation is 1000 mm, 20% of which falls as snow (Environment Canada, 2014). The regional forests belong to the sugar maple–bitternut hickory bioclimatic domain. The forest understory consists primarily of geophytes and sciophytes, such as spring-flowering plants and ferns, but some groups, such as exotic shrubs and animal-dispersed species, are increasing due to ornamental planting (Bergeron & Pellerin, 2014).

The study area is located within Canada's second most populous metropolitan region, with a population of about 3.8 million inhabitants (Statistics Canada, 2014). A review of historical aerial photographs showed that, until the 1960s, more than 50% of the study area was devoted to agriculture (Bergeron & Pellerin, 2014). Around this period, the conversion of agricultural land to urban use

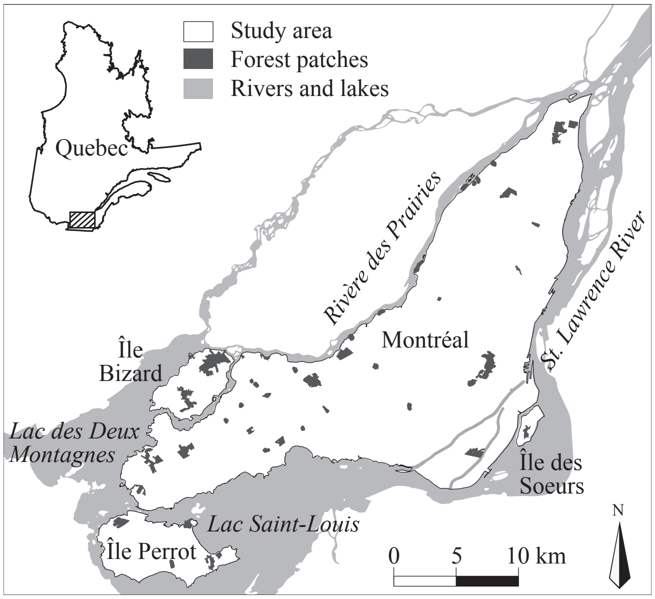

Figure 1. Location of the 50 sampled forest patches in the Hochelaga Archipelago, Quebec, Canada.

was initiated in the centre of the island of Montréal, as well as along its shores and those of the other studied islands. Currently, the area is mostly residential, but some rural sectors persist, especially in the western part, where the largest forests remain. All other large forests, with the exception of Mount Royal Park near downtown Montréal, are found along the Rivière des Prairies (Figure 1).

SITE SELECTION AND SAMPLING DESIGN

Forest patches were selected using satellite imagery (2010; 1:5 000) and field reconnaissance surveys, according to their size (area > 0.5 ha), horizontal structure (wooded vegetation cover > 80%), and understory composition (no turf grass cover). A total of 116 forests met these criteria (total area 3111 ha). We retained 50 patches (1−216 ha, mean = 28 ha, total = 1397 ha; Figure 1) that represented a compromise among gradients of forest sizes, spatial positions, and proportions of residential land use (Table I).

The number of plots (*n*) was determined to obtain a sampling effort of about 1% of the area of a forest patch (area), with *n* being slightly greater for smaller patches. Using a pre-validated equation ($n = 0.1656 \cdot \text{area [ha]} + 4$), we allocated 429 plots within 50 patches. In each patch, the randomly assigned plots were stratified in major vegetation communities and then equally redistributed between edge and core habitats. We considered edges to comprise the first 50 m inside the forest, as most studies have found evidence of edge effects within that range (*e.g.*, Vallet *et al.*, 2010b; LaPaix, Harper & Freedman, 2012). Accordingly, 1 of the forests sampled was considered all edge with no interior.

VEGETATION AND ENVIRONMENTAL DATA SAMPLING

Field sampling was conducted during the growing seasons of 2011 and 2012. To calculate the total tree basal area at each sampling location, the diameter at breast height of each tree (≥10 cm) in a 20-m × 20-m plot was estimated using the mid-point of 4 classes (10–20 cm; 21–30 cm; 31–40 cm; 41–50 cm) and measured directly for individuals >50 cm. Simpson's index, which integrates both richness and a measure of evenness (Simpson, 1949), was also calculated on tree data to determine whether tree composition influences the liana distribution. Liana, shrub, and herb covers were evaluated in a 10 × 10-m sub-plot according to 7 classes: presence (0.01%), <1%; 1–5%; 6–25%; 26–50%; 51–75%; and 76–100%.

TABLE I. Frequency of forest patches in the different selection criteria classes selected to study liana distribution and abundance in the Hochelaga archipelago.

Selection criteria	Number of patches
Area (ha)	
1–9	23
10–29	16
53–216	11
Longitude	
73°58'–73°52'W	15
73°51'–73°42'W	16
73°43'–73°32'W	18
Residential (%)	
0–40	17
41–60	17
61–84	16

In each 400-m^2 plot, we estimated the Relative Site Moisture Index (RSMI), ranging from 0 for xeric environments to 70 for hydric environments. The RSMI is expressed as the sum of scores attributed to topographic position, steepness, aspect, configuration of the dominant slope in the plot, and soil texture (Van de Grift, 1996). For this index, soil texture was evaluated qualitatively as the relative proportions of sand, silt, and clay. We estimated the percentage of canopy openness by averaging 4 readings, 1 from each corner of the 100-m^2 sub-plot, on a Lemmon model C spherical densiometer (Rapid City, SD, USA). The proportion of stones on the forest floor (stoniness) was estimated visually using 6 classes: presence (0.01%); ≤3%; 4–15%; 16–50%; 51–90%, and 91–100%. The number of micro-landforms (flat, depression, mound, down slope, mid-slope, ledge, upslope, steep slope) in the sub-plot was recorded, and the distance to nearest open area (mostly trails, but also ditches, roads, grasslands, etc.) was assessed using 2 classes: ≤30 m or >30 m. The presence of human micro-disturbances (vandalism, garbage, litter) was also noted. The A horizon thickness was then measured at 2 opposite corners of the sub-plot, and a sample of its soil was collected. In the laboratory, soil samples were air-dried and sieved (2-mm mesh). Soil pH and electrical conductivity were determined in a 10:1 water:soil suspension using a Thermo Scientific Orion Star A215 meter (Waltham, MA, USA).

LANDSCAPE FEATURES

Landscape features were extracted from GeoEye and DigitalGlobe satellite imagery (2000 and 2009) and from the Montréal Metropolitan Community's Master Plans. The perimeter of the 50 forest patches was delineated in ESRI ArcGIS 9.3 software and used to compute the forest patch area and perimeter:area ratio. Within each forest patch, a digital elevation model (grid resolution: 8–23 m; Canadian Digital Elevation Model, 2007) was used to calculate the range between maximum and minimum values of slope as a proxy of topographic heterogeneity. To assess the isolation of each of the 50 forests, we measured the edge-to-edge distance from a selected patch to its nearest neighbour among the 116 forests.

To assess the effects of the surrounding urban matrix on forests, we established a 500-m buffer zone around each patch (in accordance with Duguay, Eigenbrod & Fahrig, 2007; Bräuniger *et al.*, 2010). In this buffer zone, we assessed patch density (*i.e.*, the number of patches divided by the area of the buffer) based on the 116 preselected forest patches. We also computed street and population density (Statistics Canada, 2014) and the proportions of each major type of land use (residential, agricultural, public utility, landscaped green space, water body). Water bodies in the buffers relate mainly to the proportion of large rivers (des Prairies and St. Lawrence) and large lakes (Deux Montagnes and Saint-Louis), small ponds being rare in the study area (Figure 1). Commercial/industrial areas, accounting for less than 10% of all buffer zones, were not included, because they reflect a Zoning By-law rather than the physical composition of the urban matrix.

The proportion of heat islands in the buffer zone was assessed using a Landsat 5 (band 6) image of the Montréal Metropolitan Community, taken on 27 June 2005, which was preprocessed by the Heat Island Research Group (Université du Québec à Montréal). After removing clouds, we reclassified the image pixels (range of 17.0–42.5 °C) following the standard deviation method (Martin, 2008). The proportion of heat islands was computed as the proportion of pixels larger than 1σ of the mean temperature class (μ = [26.8–29.4] °C) in the 500-m buffer zone. Finally, we measured the distance of each plot to the nearest shore on the island's perimeter and sorted each plot into 2 groups, <60 m or ≥60 m. This distance was previously found to be significant in explaining pteridophyte communities in forests of the same area (Bergeron & Pellerin, 2014).

STUDY ORGANISMS

Liana species (woody vines) were the focus of this research. Two rare species (occurring in less than 10% of the sampling plots) and herbaceous vines were excluded from analysis. Six species were therefore retained: *Celastrus scandens*, *Menispermum canadense*, *Parthenocissus quinquefolia*, *Solanum dulcamara*, *Toxicodendron radicans*, and *Vitis riparia*. This functional group of ligneous and light-demanding species climb by means of adhesive discs, adventitious roots, tendrils, or twining stems and are characterized by berry-like fruits that are dispersed by zoochory, mainly by birds (Haines, 2011). All species are native except for *S. dulcamara*, which is a thoroughly naturalized species from Eurasia. This species was introduced for horticultural purposes around the 18th century (Lavoie *et al.*, 2012) and is now so common that it is often thought to be native (Burnham, 2013). *Parthenocissus quinquefolia* is considered a native species of eastern temperate forests (USDA & NRCS, 2013), but its establishment status in Quebec is somewhat obscure and subject to debate (Brouillet *et al.*, 2010; Lavoie *et al.*, 2012), likely because cultivars, widely used for ornamental purposes, could have escaped from culture. All inventoried species except for the poisonous *T. radicans* are used in horticulture, but *V. riparia* and *P. quinquefolia* are those most commonly encountered in the managed habitats (walls, fence, gardens, etc.) of the study area (M. H. Brice, pers. obs.).

DATA ANALYSIS

Liana distribution was analyzed at 2 distinct spatial scales: landscape (broad scale, n = 50) and local forest (fine scale, n = 429). As a response variable, we used liana abundance (cover) instead of diversity, because the latter is low in temperate forests (Schnitzer, 2005). Using the mid-point of each cover class, we calculated the total abundance of all species per plot as the response variable at the forest scale and the mean abundance of all plots per forest as the response variable at the landscape scale. To separate the sources of variation in the data for each spatial scale, explanatory variables were sorted into 5 subsets: I) forest features and II) land use at the landscape scale; and III) habitat features, IV) edge effect, and V) spatial effect at the forest scale (Table II). In exploratory

TABLE II. Subsets of explanatory variables sampled at the landscape and forest patch scales.

Subsets	Variables	Description (units)
Landscape scale (broad spatial scale)		
I Forest features	area	Forest patch area (m^2)
	PAR	Perimeter:area ratio
	slope	Difference between maximum and minimum slope (°)
II Land use	isolation	Edge-to-edge distance to the nearest forest (m)
	street	Street density in a 500-m buffer zone ($m \cdot m^{-2}$)
	pop	Population density in a 500-m buffer zone ($\# \cdot m^{-2}$)
	resid	Proportion of residential areas in a 500-m buffer zone (%)
	utility	Proportion of public infrastructures in a 500-m buffer zone (%)
	rural	Proportion of rural areas in a 500-m buffer zone (%)
	green	Proportion of green areas in a 500-m buffer zone (%)
	water	Proportion of water bodies in a 500-m buffer zone (%)
	UHI	Proportion of urban heat islands in a 500-m buffer zone (%)
Forest patch scale (fine spatial scale)		
III Habitat features	shrub	Shrub cover in a 100-m^2 plot (%)
	herb	Herb cover in a 100-m^2 plot (%)
	basal.area	Total tree basal area in a 400-m^2 plot ($m \cdot ha^{-1}$)
	simpson	Simpson's diversity index for tree species
	canopy	Mean canopy openness in a 100-m^2 plot (%)
	stoniness	Stoniness of soil surface in a 100-m^2 plot (%)
	pH	Soil pH
	EC	Soil electrical conductivity ($\mu S \cdot cm^{-2}$)
	A.horiz	Mean A horizon thickness (cm)
	RSMI	Relative site moisture index (0–70)
	relief	Number of microrelief types (1 or ≥2)
	disturbance	Presence of garbage, litter, or vandalism (0 or 1)
IV Edge effect	dist.open	Plot distance to the nearest opening (≤30 or >30)
	edge	Plot distance to the nearest forest edge (≤50 or >50)
	shore	Plot distance to the nearest stream (≤60 or > 60)
V Spatial effect	XY	Third-order polynomial of XY coordinates (*i.e.*, x, y, x^2, xy, y^2, x^3, x^2y, xy^2, y^3)

analyses, we verified the spatial structure of liana data at both scales with Moran's I permutation tests on connectivity networks (minimum spanning trees). No autocorrelation ($I = -0.013$, $P = 0.938$) was found at the landscape scale. Thus, spatial effect was evaluated only at the forest scale, using the third-degree polynomial function of the centred geographic coordinates of each plot (x, y, x^2, xy, y^2, x^3, x^2y, xy^2, y^3) in order to generate trend surface variables (Legendre & Legendre, 2012). To meet statistical assumptions, the UHI (square) and slope (square root) variables were transformed, after which we standardized all explanatory variables to z-scores ($\mu = 0$ and $\sigma = 1$). All statistical analyses were performed in the R environment version 3.0.1 (Vienna, Austria).

To obtain parsimonious regression models, each subset of variables was subjected to a forward selection procedure (9999 permutations of residuals) using the packfor package of R. Forward selection was carried out using the pre-selected alpha level ($\alpha = 5\%$) as the stopping criterion. This procedure retained 1 variable from subset I (slope), 5 from subset II (UHI, street, utility, water, and isolation), 4 from subset III (shrub, canopy, A.horiz, and pH), 2 from subset IV (shore and edge), and 1 from subset V (Y). All variance inflation factors of the selected variables were less than 2, indicating negligible multicollinearity. We then computed multiple linear regressions for each subset using the selected explanatory variables, using the ape package of R. Parametric tests of significance of the equation parameters were used for the landscape-scale models because residuals were normal and homoscedastic (Shapiro-Wilk, $W = 0.964$, $P = 0.130$; Breusch-Pagan, $BP = 6.13$, $P = 0.409$), while permutation tests were used for forest-scale models (9999 permutations) because residuals might be subject to spatial autocorrelation, which could have biological significance. In the latter case, an F test of R^2 and a two-tailed t test of the regression coefficients were performed by permutations of the full model residuals.

For each spatial scale, we computed a final model by gathering together each subset of explanatory variables and then isolating both the variation shared between them (shared fraction) and the unshared variation (unique fraction) using variation partitioning analysis. This approach enabled us to estimate the relative contributions of different sets of explanatory variables representing complementary hypotheses explaining the distribution patterns of vegetation (Legendre & Legendre, 2012). More precisely, we partitioned the variation explaining liana abundance (vegan package; for details see Legendre & Legendre, 2012) between the 2 subsets of the landscape-scale models (1 shared and 2 unique fractions) and the 3 subsets of the forest-scale models (4 shared and 3 unique fractions). Finally, we tested the unique fractions using partial regressions (9999 permutations under the reduced model), which enabled us to better assess the significance of each group of environmental factors (here, the subsets) and consistent relationships between them.

Results

Lianas were omnipresent in the 50 forests studied, found in 100% of the patches and in 88% of the plots. The most frequent species at both spatial scales were *Vitis riparia*, *Parthenocissus quinquefolia*, and *Toxicodendron radicans* (Figure 2), whereas the species that had the highest mean abundance across all the forests was *T. radicans*.

LIANA DISTRIBUTION AT THE LANDSCAPE SCALE

The land use subset was the most powerful predictor of liana abundance at the landscape scale, explaining almost 50% of the variation (Model II; Table III). Liana

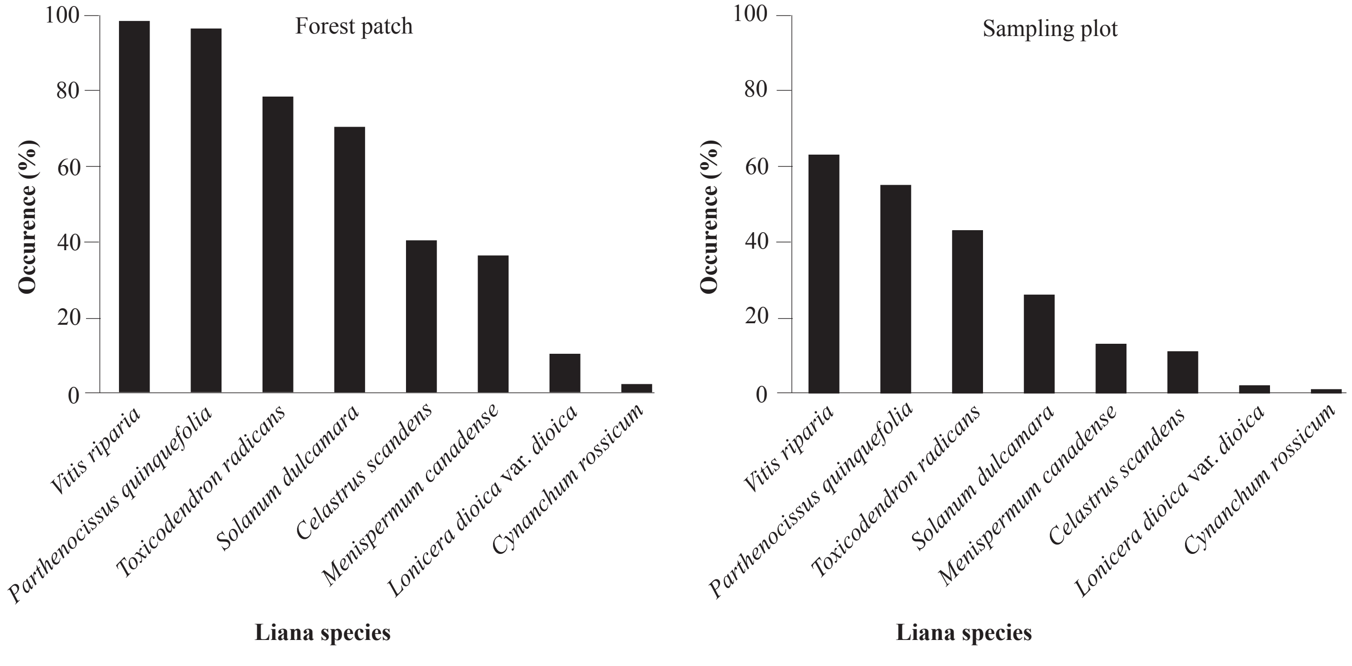

FIGURE 2. Occurrence of liana species in the Hochelaga Archipelago (Quebec, Canada). Occurrence is expressed as the percentage of forest patches or sampling plots in which each species appears.

abundance strongly increased with the proportion of UHI (Figure 3), public utilities, and water bodies in the surrounding matrix, as well as with the degree of isolation. In contrast, abundance decreased with street density in the surrounding matrix. According to the forest feature model (Model I; Table III), which represents 7.4% of the variation explained, there was a negative relationship between slope range within a patch and liana abundance, indicating that lianas were more abundant on flat than on rugged sites.

Variation partitioning showed that the land use subset alone captured most of the variation of liana abundance data (R^2_a = 40.4%), while the forest feature subset did not add any explanation (Figure 4). In fact, the variation explained by the latter was entirely shared with the land use variables (R^2_a = 8.49%).

LIANA DISTRIBUTION AT THE FOREST PATCH SCALE

According to the habitat feature model (Model III; Table III), which explained 16% of the variation, liana abundance at the forest scale increased with canopy openness, shrub cover, and pH, while it decreased with thickness of the A horizon. The edge effect model, accounting for about 2% of the variation, underlined the fact that lianas were more abundant in edge than in core habitats, and particularly in forest patches close to a shore (Model IV; Table III). Finally, the spatial model, explaining 2% as well, indicated a weak positive trend in liana abundance along a longitudinal gradient inside the studied forests, *i.e.*, lianas were slightly more abundant in the eastern part of a forest than in the western part (Model V; Table III).

TABLE III. Parsimonious multiple linear regression models of liana abundance explained by the variables from the subsets of forest features and land use at the landscape scale ($n = 50$) and the subsets of habitat features, edge effect, and spatial effect at the forest patch scale ($n = 429$).

Models	β	*P*
Landscape scale models		
Model I: Forest features ($R^2_a = 0.07$, $F = 4.9$, $P = 0.031$)		
Intercept	6.034	<0.001
slope	–2.168	0.031
Model II: Land use ($R^2_a = 0.49$, $F = 10.4$, $P < 0.001$)		
Intercept	6.034	<0.001
UHI	3.864	<0.001
street	–3.450	<0.001
utility	2.675	0.003
water	2.310	0.007
isolation	1.613	0.045
Forest patch scale models		
Model III: Habitat features ($R^2_a = 0.16$, pseudo-$F = 20.7$, $P < 0.001$)		
Intercept	5.165	<0.001
shrub	2.818	<0.001
canopy	2.769	<0.001
A.horiz	–1.822	0.001
pH	1.554	0.004
Model IV: Edge effect ($R^2_a = 0.02$, pseudo-$F = 5.9$, $P = 0.006$)		
Intercept	5.165	<0.001
shore	1.459	0.017
edge	1.328	0.022
Model V: Spatial effect ($R^2_a = 0.02$, pseudo-$F = 10.6$, $P = 0.001$)		
Intercept	5.165	<0.001
Y	1.903	0.001

Variation partitioning indicated that the minimal explanation provided by both the edge and the spatial effect subsets (R^2_a = 1.53% and 1.78%, respectively) arises from their shared effect with the habitat feature variables (Figure 4). Indeed, the unique fraction of the edge effect was negligible (R^2_a = 0.3%), while that of the spatial effect was null, meaning that the latter was induced by spatial variation of habitat variables. The largest proportion of the variation in liana abundance was thus explained solely by the habitat feature subset (R^2_a = 11.8%).

Discussion

Overall, our results suggest that lianas benefit greatly from disturbances associated with urbanization. Most notably, they thrive in forests subjected to significant heat islands, a well-known proxy of urbanization. Most lianas are not physiologically well adapted to cold climates due to the wide and long vessels of their vascular system, which increases the risk of freezing-induced xylem embolism (Ewers, Fisher & Fichtner, 1991; Schnitzer, 2005). To reduce this mortality risk, several temperate lianas in the genera *Vitis*, *Parthenocissus*, and *Toxicodendron* display early bud set and leaf senescence, which result in a shorter active growth season compared to other woody species of the same climate (Stiles, 1982). Warmer winters and longer growing seasons related to UHI effects (Imhoff *et al.*, 2000) could thus have contributed to increase liana survival and abundance in the studied urban temperate forests. Studies on the effects of temperature increase on lianas are almost nonexistent. Wang *et al.* (2011) however have shown that the germination rate and the biomass of the tropical herbaceous vine *Ipomoea cairica* increase with elevated temperature.

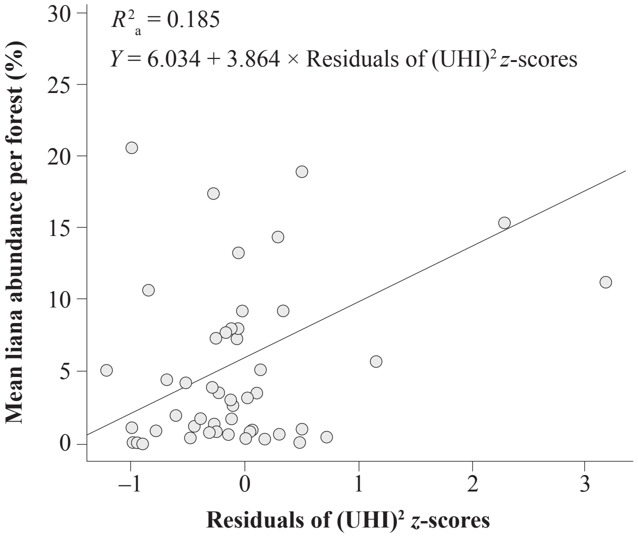

FIGURE 3. Scatterplot of liana abundance on UHI while controlling for the effects of the other land use variables. To obtain this figure we first computed a multiple regression of UHI on all other land use variables (street, utility, water, isolation) to remove their effect on lianas and keep only the UHI effect. Standardized values of variables were used. The UHI residuals were then used in a simple regression with lianas to obtain the variance of liana abundance explained only by the heat island effect.

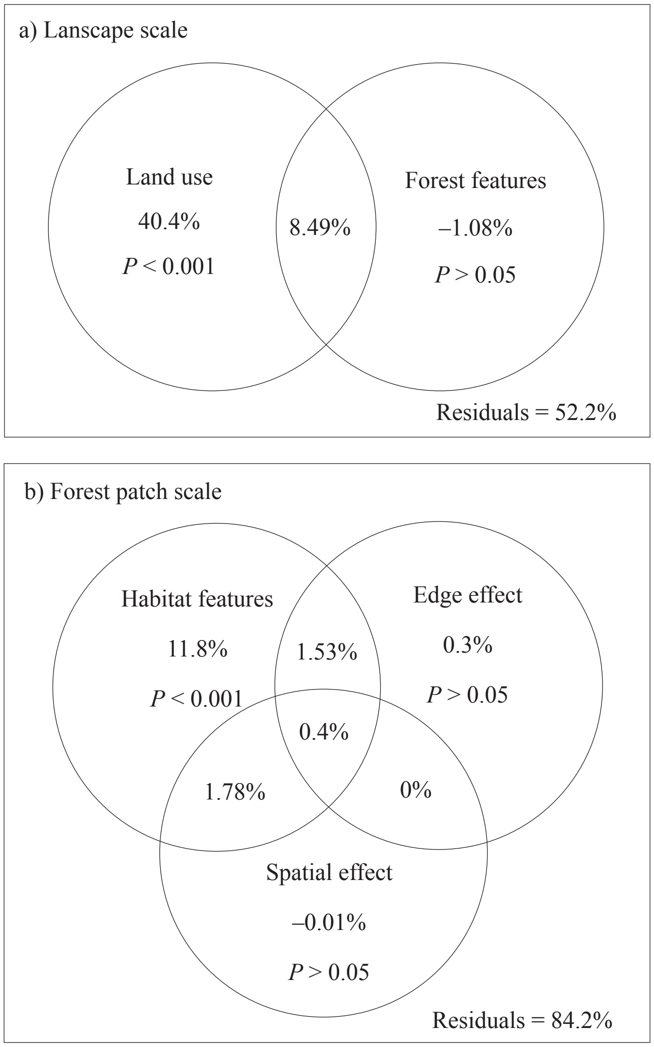

FIGURE 4. Variation partitioning of liana abundance explained by parsimonious variables from a) the subsets of forest features (slope) and land use (UHI, street, utility, water, isolation) and b) the subsets of habitat features (canopy, shrub, A.horiz, pH), edge effect (shore, edge), and spatial effect (Y). The P values are from tests of unique fractions. The shared fraction (∩) is not testable. Negative value should be interpreted as 0%.

Recent modeling studies show that lianas and herbaceous vines could experience range expansion, especially northward spread, in temperate regions under warmer conditions (*e.g.*, Sasek & Strain, 1990; Bradley, Wilcove & Oppenheimer, 2010). Observation of the climbing form of *Toxicodendron radicans* in the studied forests (M. H. Brice, pers. obs.), usually absent in the northern United States and Canada due to cold temperatures (Voss, 1985), is likely further evidence of UHI warming effects on lianas in the study area. On the other hand, UHI usually induce soil dryness (Godefroid & Koedam, 2007), resulting in water stress for many indigenous plants (Godefroid, Monbaliu & Koedam, 2007; Bergeron & Pellerin, 2014). Lianas are not physiologically drought-resistant species (van der Sande *et al.*, 2013). However, they usually have a deep and extensive root system that enables them to get water from deeper sources of ground water, which could give them an advantage in dry periods (*e.g.*, Jackson *et al.*, 1995; Schnitzer, 2005).

In light of the positive trend between lianas and UHI, which indicated that liana abundance increased with urbanization, we expected that they would also increase with street density. Contrary to that expectation, we found that lianas were more abundant in forests surrounded by low street density. In the study area, low street densities are found both in rural and slightly industrial areas, which often contain many vacant lots and wastelands. As lianas are fast-growing in high light conditions (Schnitzer & Bongers, 2002), these open environments may have promoted their establishment in the vicinity of forest patches and thus facilitated further invasions, especially in forest edges. Several liana species can spread horizontally over open ground and remain self-supporting until conditions change (*e.g.*, increased light and support availability; Selaya & Anten, 2008). This plasticity allows them to rapidly colonize open fields, such as abandoned agricultural lands (Dewalt, Schnitzer & Denslow, 2000; Schnitzer & Bongers, 2002) and to dominate herbaceous forest communities. This is the case for *P. quinquefolia* and *T. radicans*, for example, which can grow and spread successfully as ground cover in the absence of supports (Ladwig & Meiners, 2010a).

According to our results, lianas were also more abundant in geographically isolated forests than in more continuous woodlands. Colonization from one forest patch to another therefore does not seem to be limited by distance between patches, probably because zoochorous species are generally less affected by habitat isolation than abiotically dispersed species (Marini *et al.*, 2012). Animal dispersal, especially by birds, is a long-distance and directional process (Montoya *et al.*, 2008; Penone *et al.*, 2012) and could contribute to the ability of lianas to establish in isolated forests, where urban-related disturbances are more severe. On the other hand, extensive and intensive human disturbances in urban areas likely increase the availability of suitable habitats for lianas (Schnitzer & Bongers, 2002; 2011), reversing the usual negative isolation effects. As observed in areas of low street density, open habitats highly suitable for lianas (*e.g.*, railway and road verges) are more abundant around isolated forest patches. This phenomenon likely increases the connections between liana populations to levels of contact not possible in patches located in more closed woodland landscapes.

At the landscape level, our results also indicated that liana abundance was higher in forests near shorelines than in forests located in the central part of the islands. This pattern is likely related to light availability, as riparian forests often contain extensive sunny edge habitats due to their position along large open-water corridors. Finally, our results suggested that forests with a homogeneous topography (small slope range) were more favourable for lianas than forests with a more uneven landscape. However, the effect of this variable was entirely shared with the land use subset, meaning that this pattern is a byproduct of the adjacent matrix conditions rather than a result of the forest features *per se*. In the study area, forests located in a highly urbanized matrix were in fact usually characterized by flat topography, probably due to levelling work inherent in urban sprawl (M. H. Brice, unpubl. data).

At the forest scale, we found that lianas were mostly associated with open and sunny habitats with high shrub cover and alkaline and compacted soils, all of which are typical of young or disturbed forests and edges (Vallet *et al.*, 2010b). The habitat feature variables were almost entirely shared with the edge effect, suggesting that edges offer conditions favourable to liana growth. For example, in urban areas, edges often have high cover of shrubs, which can be used as supports for liana growth, because shrubs tend to be more resistant to disturbances than many herbaceous species (Moffatt & McLachlan, 2004; Bergeron & Pellerin, 2014). As well, soil pH is usually higher in edge than in core habitats or undisturbed forests due to pollutants leaching from construction rubble (Godefroid, 2001; Godefroid, Monbaliu & Koedam, 2007) and deicing salt commonly used in temperate regions (Czerniawska-Kusza, Kusza & Duzyński, 2004). The soils in edge habitats are also often compacted, due to intensive human frequentation (Godefroid & Koedam, 2004; Godefroid, Monbaliu & Koedam, 2007). Such soil attributes are often associated with highly disturbed habitats and edges (Moffatt, McLachlan & Kenkel, 2004), where lianas were found. Overall, our results concur with those of other studies that have shown that lianas thrive in edges (Londré & Schnitzer, 2006; Ladwig & Meiners, 2010b) and in young secondary forests (Madeira *et al.*, 2009; Ladwig & Meiners, 2010b). These types of habitats probably provide a good compromise between host availability and light, which have opposite trends during succession (Madeira *et al.*, 2009). The adaptations that allow lianas to compete in forests subject to intense heat islands could also enable them to proliferate in disturbed habitats (Schnitzer, 2005; Schnitzer & Bongers, 2011). The relatively high temperatures and low humidity in canopy gaps, young forests, and edges (Murcia, 1995; Collinge, 1996) result in elevated evapotranspiration pressure, which is deleterious to the survival of many plants, especially those adapted to shady and stable understory conditions (Moffatt & McLachlan, 2004; Bergeron & Pellerin, 2014), thus giving lianas a competitive advantage.

Conclusion

This study shows that, at both landscape and forest spatial scales, liana abundance tends to increase with environmental disturbances arising from urbanization. These species, both native and exotic, are plastic, opportunistic, and competitive, characteristics often attributed to invasive plants, enabling them to thrive in new niches created by urban sprawl. With intensifying urbanization, lianas will likely become more abundant in northern cities and could therefore potentially be used as an indicator of disturbance intensity caused by human activities in urban ecosystems. Although our study was able to reveal the broad patterns of liana occurrence in urban forests, further studies will be needed to better understand their segregation patterns within temperate forests (*e.g.*, upper canopy, lower canopy, trunk, etc.) and their use of open habitats as dispersal corridors in the vicinity of forests. Finally, as cities are often regarded as microcosms of climate change (Grimm *et al.*, 2008) and as liana abundance increases with urban heat islands, lianas are likely to spread further in temperate regions, where they were formerly uncommon.

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Literature cited

Aronson, M. F. J., S. N. Handel & S. E. Clemants, 2007. Fruit type, life form and origin determine the success of woody plant invaders in an urban landscape. Biological Invasions, 9: 465–475.

Bergeron, A. & S. Pellerin, 2014. Pteridophytes as indicators of urban forest integrity. Ecological Indicators, 38: 40–49.

Bradley, B. A., D. S. Wilcove & M. Oppenheimer, 2010. Climate change increases risk of plant invasion in the Eastern United States. Biological Invasions, 12: 1855–1872.

Bräuniger, C., S. Knapp, I. Kühn & S. Klotz, 2010. Testing taxonomic and landscape surrogates for biodiversity in an urban setting. Landscape and Urban Planning, 97: 283–295.

Brouillet, L., F. Coursol, M. Favreau, M. Anions, P. Bélisle & P. Desmet, 2010. VASCAN, the Database of Vascular Plants of Canada. Online [URL] http://data.canadensys.net/vascan (Accessed on 9 December 2013).

Burnham, R. J., 2013. Censusing lianas in mesic biomes of eastern regions (CLIMBERS). Online [URL] http://climbers.lsa.umich.edu/ (Accessed on 6 May 2013).

Cadenasso, M. L. & S. T. A. Pickett, 2001. Effect of edge structure on the flux of species into forest interiors. Conservation Biology, 15: 91–97.

Canadian Digital Elevation Model, 2007. Online [URL] http://www.geobase.ca (Accessed on 11 November 2011).

Collinge, S. K., 1996. Ecological consequences of habitat fragmentation: Implications for landscape architecture and planning. Landscape and Urban Planning, 36: 59–77.

Czerniawska-Kusza, I., G. Kusza & M. Duzyński, 2004. Effect of deicing salts on urban soils and health status of roadside trees in the Opole region. Environmental Toxicology, 19: 296–301.

Dewalt, S. J., S. A. Schnitzer & J. S. Denslow, 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. Journal of Tropical Ecology, 16: 1–19.

Duguay, S., F. Eigenbrod & L. Fahrig, 2007. Effects of surrounding urbanization on non-native flora in small forest patches. Landscape Ecology, 22: 589–599.

Environment Canada, 2014. Climate Normals and Averages 1981–2010. Montréal/Pierre Elliott Trudeau Intl A. Online [URL] http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=5415&lang=e&StationName=montreal&SearchType=Contains&stnNameSubmit=go&dCode=1 (Accessed on 11 January 2014).

Ewers, F. W., J. B. Fisher & K. Fichtner, 1991. Water flux and xylem structure in vines. Pages 127–160 in F. E. Putz & H. A. Mooney (eds). The Biology of Vines. Cambridge University Press, Cambridge.

Godefroid, S., 2001. Temporal analysis of the Brussels flora as indicator for changing environmental quality. Landscape and Urban Planning, 52: 203–224.

Godefroid, S. & N. Koedam, 2003. Distribution pattern of the flora in a peri-urban forest: An effect of the city–forest ecotone. Landscape and Urban Planning, 65: 169–185.

Godefroid, S. & N. Koedam, 2004. The impact of forest paths upon adjacent vegetation: Effects of the path surfacing material on the species composition and soil compaction. Biological Conservation, 119: 405–419.

Godefroid, S. & N. Koedam, 2007. Urban plant species patterns are highly driven by density and function of built-up areas. Landscape Ecology, 22: 1227–1239.

Godefroid, S., D. Monbaliu & N. Koedam, 2007. The role of soil and microclimatic variables in the distribution patterns of urban wasteland flora in Brussels, Belgium. Landscape and Urban Planning, 80: 45–55.

Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu, X. Bai & J. M. Briggs, 2008. Global change and the ecology of cities. Science, 319: 756–760.

Guirado, M., J. Pino & F. Rodà, 2006. Understorey plant species richness and composition in metropolitan forest archipelagos: Effects of forest size, adjacent land use and distance to the edge. Global Ecology and Biogeography, 15: 50–62.

Haines, A., 2011. Flora Novae Angliae: A Manual for the Identification of Native and Naturalized Higher Vascular Plants of New England. New England Wild Flower Society, Yale University Press, Framingham.

Herron, P. M., C. T. Martine, A. M. Latimer & S. A. Leicht-Young, 2007. Invasive plants and their ecological strategies: Prediction and explanation of woody plant invasion in New England. Diversity and Distributions, 13: 633–644.

Ibarra-Manríquez, G. & M. Martínez-Ramos, 2002. Landscape variation of liana communities in a Neotropical rain forest. Plant Ecology, 160: 91–112.

Imhoff, M. L., C. J. Tucker, W. T. Lawrence & D. C. Stutzer, 2000. The use of multisource satellite and geospatial data to study the effect of urbanization on primary productivity in the United States. IEEE Transactions on Geoscience and Remote Sensing, 38: 2549–2556.

Jackson, P. C., J. Cavelier, G. Goldstein, F. C. Meinzer & N. M. Holbrook, 1995. Partitioning of water resources among plants of a lowland tropical forest. Oecologia, 101: 197–203.

Knapp, S., I. Kühn, R. Wittig, W. A. Ozinga, P. Poschlod & S. Klotz, 2008. Urbanization causes shifts in species' trait state frequencies. Preslia, 80: 375–388.

Ladwig, L. M. & S. J. Meiners, 2010a. Liana host preference and implications for deciduous forest regeneration. Journal of the Torrey Botanical Society, 137: 103–112.

Ladwig, L. M. & S. J. Meiners, 2010b. Spatiotemporal dynamics of lianas during 50 years of succession to temperate forest. Ecology, 91: 671–680.

LaPaix, R., K. Harper & B. Freedman, 2012. Patterns of exotic plants in relation to anthropogenic edges within urban forest remnants. Applied Vegetation Science, 15: 525–535.

Lavoie, C., A. Saint-Louis, G. Guay & E. Groeneveld, 2012. Les plantes vasculaires exotiques naturalisées: une nouvelle liste pour le Québec. Le Naturaliste canadien, 136: 6–32.

Legendre, P. & L. Legendre, 2012. Numerical Ecology. 3rd English Edition. Elsevier, Amsterdam.

Leicht-Young, S. A., N. B. Pavlovic, K. J. Frohnapple & R. Grundel, 2010. Liana habitat and host preferences in northern temperate forests. Forest Ecology and Management, 260: 1467–1477.

Londré, R. A. & S. A. Schnitzer, 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years. Ecology, 87: 2973–2978.

Madeira, B. G., M. M. Espírito-Santo, S. D. Neto, Y. R. F. Nunes, G. A. Sánchez-Azofeifa, G. W. Fernandes & M. Quesada, 2009. Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. Plant Ecology, 201: 291–304.

Marini, L., H. H. Bruun, R. K. Heikkinen, A. Helm, O. Honnay, J. Krauss, I. Kühn, R. Lindborg, M. Pärtel & R. Bommarco, 2012. Traits related to species persistence and dispersal explain changes in plant communities subjected to habitat loss. Diversity and Distributions, 18: 898–908.

Martin, P., 2008. Analyse diachronique du comportement thermique de Montréal en période estivale de 1984 à 2005. MSc thesis. Université du Québec à Montréal, Montréal, Quebec.

Moffatt, S. F. & S. M. McLachlan, 2004. Understorey indicators of disturbance for riparian forests along an urban–rural gradient in Manitoba. Ecological Indicators, 4: 1–16.

Moffatt, S. F., S. M. McLachlan & N. C. Kenkel, 2004. Impacts of land use on riparian forest along an urban–rural gradient in southern Manitoba. Plant Ecology, 174: 119–135.

Montoya, D., M. A. Zavala, M. A. Rodríguez & D. W. Purves, 2008. Animal versus wind dispersal and the robustness of tree species to deforestation. Science, 320: 1502–1504.

Murcia, C., 1995. Edge effects in fragmented forests: Implications for conservation. Trends in Ecology & Evolution, 10: 58–62.

Penone, C., N. Machon, R. Julliard & I. Le Viol, 2012. Do railway edges provide functional connectivity for plant communities in an urban context? Biological Conservation, 148: 126–133.

Rowe, N. & T. Speck, 2005. Plant growth forms: An ecological and evolutionary perspective. New Phytologist, 166: 61–72.

Sasek, T. H. & B. R. Strain, 1990. Implications of atmospheric CO_2 enrichment and climatic change for the geographical distribution of two introduced vines in the U.S.A. Climatic Change, 16: 31–51.

Schnitzer, S. A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist, 166: 262–276.

Schnitzer, S. A. & F. Bongers, 2002. The ecology of lianas and their role in forests. Trends in Ecology & Evolution, 17: 223–230.

Schnitzer, S. A. & F. Bongers, 2011. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. Ecology Letters, 14: 397–406.

Schnitzer, S. A. & W. P. Carson, 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology, 82: 913–919.

Selaya, N. G. & N. P. R. Anten, 2008. Differences in biomass allocation, light interception and mechanical stability between lianas and trees in early secondary tropical forest. Functional Ecology, 22: 30–39.

Simpson, E. H., 1949. Measurement of diversity. Nature, 163: 688.

Statistics Canada, 2014. Population and dwelling counts, for census metropolitan areas, 2006 and 2011 censuses - 100 % data. Online [URL] http://www12.statcan.gc.ca/census-recensement/2011/dp-pd/hlt-fst/pd-pl/Table-Tableau.cfm?T=201&S=3&O=D&RPP=150 (Accessed on 11 January 2014).

Stiles, E. W., 1982. Fruit flags: Two hypotheses. American Naturalist, 120: 500–509.

USDA & NRCS, 2013. The PLANTS Database. National Plant Data Team, Greensboro, North Carolina. Online [URL] http://plants.usda.gov (Accessed on 9 December 2013).

Vallet, J., H. Daniel, V. Beaujouan, F. Rozé & S. Pavoine, 2010a. Using biological traits to assess how urbanization filters plant species of small woodlands. Applied Vegetation Science, 13: 412–424.

Vallet, J., V. Beaujouan, J. Pithon, F. Rozé & H. Daniel, 2010b. The effects of urban or rural landscape context and distance from the edge on native woodland plant communities. Biodiversity and Conservation, 19: 3375–3392.

Van de Grift, J., 1996. The relative site moisture index: An expansion of the topographic relative moisture index. Honors thesis, University of Wisconsin–Madison, Madison, Wisconsin.

van der Sande, M. T., L. Poorter, S. E. Schnitzer & L. Markesteijn, 2013. Are lianas more drought-tolerant than trees? A test for the role of hydraulic architecture and other stem and leaf traits. Oecologia, 172: 961–972.

Voss, E. G., 1985. Michigan Flora. II. Dicots. Cranbrook Institute, Bloomfield Hills, Michigan.

Williams, N. S. G., M. W. Schwartz, P. A. Vesk, M. A. McCarthy, A. K. Hahs, S. E. Clemants, R. T. Corlett, R. P. Duncan, B. A. Norton, K. Thompson & M. J. McDonnell, 2008. A conceptual framework for predicting the effects of urban environments on floras. Journal of Ecology, 97: 4–9.

Wang, R. L., R. S. Zeng, S. L. Peng, B. M. Chen, X. T. Liang & X. W. Xin, 2011. Elevated temperature may accelerate invasive expansion of the liana plant *Ipomoea cairica*. Weed Research, 51: 574–580.

White, M. A., R. T. Nemani, P. E. Thornton & S. W. Running, 2002. Satellite evidence of phenological difference between urbanized and rural areas of the eastern United States deciduous broadleaf forest. Ecosystems, 5: 260–273.

Zhang, X., M. A. Friedl, C. B. Schaaf, A. H. Strahler & A. Schneider, 2004. The footprint of urban climates on vegetation phenology. Geophysical Research Letters, 31: L12209, DOI: 10.1029/2004GL020137