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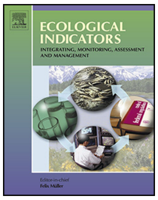

Pteridophytes as indicators of urban forest integrity

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ABSTRACT

In this study we evaluated whether pteridophytes are reliable indicators of urban forest integrity. We inventoried the total pteridophyte diversity in 82 forest patches of the Hochelaga Archipelago (Montréal area, Québec, Canada), and evaluated their level of integrity using landscape metrics (e.g., area, connectivity, matrix composition) calculated from satellite imagery and land use maps. To obtain information at microhabitat scale, we sampled pteridophyte diversity, as well as biotic and abiotic data, in 225 sample plots within these 82 patches. Relationships of pteridophyte richness to landscape metrics and to microhabitat variables were analyzed with parsimonious regression models. Variation partitioning was used to isolate the effects of each group of variables (forest area, land use, biotic/abiotic and edge effect). To enhance the interpretation of models involving richness, distance-based redundancy analyses of species composition data were performed. Indicator species of low and high levels of urban influence were then identified using the IndVal method. Results showed a strong species–area relationship that was influenced by surrounding land use. Pteridophyte richness decreased with increasing proportions of residential areas, urban heat islands (UHI) and water bodies in a 500 m-buffer zone around patches. Greater richness at the microhabitat scale was associated to greater distance from internal and external edges. Out of 38 species, 19 were significant indicators of low levels of urban influence. We conclude that pteridophytes are positive indicator of forest integrity, since they demonstrate typical plant responses to adverse urban-generated ecological conditions. Green-spored species are of particular interest, since their presence indicates low levels of UHIs. Impact of global climate changes on biodiversity can be predicted by studying UHIs, and we suggest using pteridophytes in this broader context.

1. Introduction

Urbanization is a leading cause of habitat loss and biological homogenization (McKinney, 2006). Remnant ecosystems embedded in urban areas, especially forests, provide important services such as moderating local climate, storing water, and filtering air, as well as increasing citizens' well-being (Alberti, 2010; Grimm et al., 2008). However, the balance of components ensuring ecological integrity—that is, biophysical structure, species composition and functional processes—is difficult to maintain in urban forest patches (Ordóñez and Duinker, 2012). This is because most of these components are disturbed at multiple spatial scales by human activities (Alberti, 2010). For example, ecosystem fragmentation is a landscape-level process increasing the proportion of edge habitats, which are characterized by locally-distinct biological and physico-chemical conditions (Murcia, 1995). The plant communities of edge habitats are often composed of a higher proportion of competitive, pioneer, and ruderal plants than forest cores (Godefroid and Koedam, 2004; Guirado et al., 2006; LaPaix and Freedman, 2010). The presence of edges may also favor the influx of invasive and exotic plants into forests (Cadenasso and Pickett, 2001), since the urban matrix exerts propagule pressure through its pool of naturalized and ornamental species found in wastelands, urban gardens, and managed areas (Williams et al., 2009). Observed changes in the composition of floristic assemblages of urban ecosystems are usually exacerbated by extensive areas of impervious surfaces that foster the formation of urban heat islands (UHIs) (Bechtel and Schmidt, 2011; Godefroid and Koedam, 2007; Ricotta et al., 2009, 2010), which may in turn cause thermal and hydric stress to organisms not adapted to these conditions (Grimm et al., 2008). This anthropogenic climate disturbance, the human stranglehold over nature and the novel microhabitats created in a heterogeneous matrix differentiate urban areas from the other landscapes creating a unique distribution pattern of the plants that must be understood for the preservation of remaining ecosystems (Williams et al., 2009).

Although forests in urban areas are never pristine, it is possible to establish a scale of their relative integrity and to identify the forests whose conservation should be prioritized. Landscape

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metrics (e.g., patch size, connectivity, and land use) can be used to assess structural integrity, which is known to decrease in forests that are smaller, less connected, and surrounded by a strongly anthropized matrix (Carignan and Villard, 2002; Dale and Beyeler, 2001). Biological indicators that have either a negative (e.g., exotic organisms) or a positive (e.g., native organisms) response to ecological integrity can also be used (Carignan and Villard, 2002). For example, the extinction of native and specialist species in some forests shows the carrying incapacity of the system, and thus a decrease in the functional component of integrity (McKinney, 2006; Ordóñez and Duinker, 2012). Species richness estimates calculated from judiciously chosen guilds or functional groups, can effectively represent patterns and processes related to many components of ecosystems (Dale and Beyeler, 2001), but efficacy varies with sampling unit size (Dufrêne and Legendre, 1997) and a method to control this confounding effect is usually necessary (e.g., Bräuniger et al., 2010). Furthermore, the choice of biological indicators should be guided by their ability to respond in a predictive manner to the stresses or disturbances being studied (Dale and Beyeler, 2001; McGeoch, 1998). Mosses and lichens are often used as indicators, but they have paradoxical responses to urbanization because their diversity decreases at high levels of air pollution (e.g., LeBlanc and De Sloover, 1970), and occasionally increases under conditions of dense construction or heavy human use (Bräuniger et al., 2010). Amphibians are also frequently used as indication of integrity, but their richness is usually low in urban areas (Gagné and Fahrig, 2007) impeding the development of a practical scale of integrity. A single species approach can address a range of concerns related to species richness; in addition, it can provide more accurate information on habitats (De Cáceres and Legendre, 2009; Dufrêne and Legendre, 1997). However, to be useful, the response of the species in question should be representative of at least a few other species; otherwise, more exceptions than general trends concerning the objectives of the bioindicator will be identified (McGeoch, 1998).

In this paper, our main goal was to evaluate whether pteridophytes (ferns and their allies: horsetails, club mosses) are positive indicators of urban forest integrity. Considered to be among the earliest land plants, pteridophytes are globally a diversified group (Kreft et al., 2010; Tryon, 1986). Therefore, they are ubiquitous and, above all, have a combination of attributes advantageous for bioindicator studies. First, most herbivores (vertebrates, insects) avoid consuming them. Second, they have no mechanism of biotic pollination or zoochory. Finally, their spores allow them to be pioneers in isolated pristine habitats. Their distribution therefore closely reflects abiotic habitat conditions, facilitating analysis of other taxa group patterns (Barrington, 1993). Indeed, pteridophytes are among the best surrogates for native biodiversity; their richness has been shown to predict overall species richness (Leal et al., 2010), and their presence–absence can distinguish floristic patterns from main forest types (Salovaara et al., 2004). Some taxa or groups of pteridophytes have been studied in urbanized landscapes, but the influence of disturbances has received little attention. Some authors have suggested that a heat island effect could partly explain their distribution patterns (Daniel and Lecamp, 2004; Murakami et al., 2005). In this context, our specific objectives were to determine: (1) how pteridophyte diversity (including species richness and composition) in urban forest patches is influenced by landscape metrics, and (2) what major biological and physicochemical factors (soil pH, landform, edge gradient, etc.) affect pteridophyte diversity in the immediate local environment of the species. Our study particularly focused on typical urban influences, such as those associated with matrix composition, heat islands, and edge effects. Using these factors, we defined integrity levels in order to examine whether some species have an ecological preference for either patches or microhabitats that are weakly disturbed.

2. Materials and methods

2.1. Study area

The study was conducted on four of the largest islands (Montréal, 482.8 km^2; Bizard, 22.8 km^2; Perrot, 41.9 km^2; and Nun's Island, 3.7 km^2) of the Hochelaga Archipelago (45°28′ N; 73°45′ W) in southern Québec, Canada. The islands are in close proximity to each other as only about 250 m (shore to shore) separates the two most remote islands. The region has a humid continental climate with cold, snowy winters and hot, humid summers. The average annual temperature is 6.2 °C, but temperature reaches 21 °C in July, the warmest month. The average annual precipitation is 979 mm; 22% of which falls as snow (Environment Canada, 2011). The regional forests belong to the sugar maple-bitternut hickory bioclimatic domain. The forest floor consists primarily of geophytes and sciophytes, such as spring-flowering plants and ferns (Grandtner, 1966).

The study area is within Canada's second most populous metropolitan area, with a population of about 3.6 million (Statistics Canada, 2011), and within a port area that is an important gateway for exotic plants (Lavoie et al., 2003). An extant examination of historical aerial photos of the study area shows that considerable land use changes occurred around the 1960s (Bergeron, unpubl. data). Prior to that period, agricultural activities occupied over 50% of the territory. The conversion of land to urban use began at the center of Montréal Island, as well as along its shores and those of the other islands under study. Currently, the area is predominantly residential, but rural sectors are still present, mostly in the western part, which includes the largest forests. The area's other important forests are found mostly along the Prairies River, except of the one in Mount Royal Park, adjacent to Montréal's downtown.

2.2. Forest patch selection and field sampling

All forests in the Hochelaga Archipelago are considered seminatural because they naturally regenerate after tree logging. While most of the forests of the area have been logged at least once since European colonization, most have been left unmanaged during the last 30–40 years. Forest patches were selected using satellite imagery (1:5000) and field reconnaissance surveys based on size (area > 0.5 ha), horizontal structure (wooded vegetation cover >80%) and understory composition (no turf grass cover). Managed green spaces and urban wastelands were not considered. A total of 116 patches met the criteria (about 3111 ha). Only two selected patches included silvicultural plantations, but only on 20% and 40% of their surfaces. We retained 82 patches (0.7–245.2 ha, mean = 31 ha; Fig. 1), covering about 2545 ha or 5% of the study area, to create a network of interconnected patches that avoid spatial discontinuities among those nearest neighbors. Distances (centroid to centroid) between nearest neighbor patches range between 295 and 4502 m (mean = 1188 m). Most excluded patches were located in the western and southern extremes of Bizard and Perrot islands, respectively.

Field sampling was conducted during the growing seasons of 2009 and 2010. The number of species per patch was obtained by a single sampling of each patch between June and August, as pteridophytes are perennials emerging in April-May under this climate. One or two observers searched on foot for pteridophyte individuals within each patch for a maximum period of 10 min of active search per hectare of forest, divided by the number of observers. Throughout species inventories, care was taken to sample as many microhabitats as possible.

2.3. Sample plot selection and field sampling

During forest patch sampling, the geographic coordinates of all sites with pteridophytes (670 sites) were taken using a GPS device. The total cover of pteridophytes at each site was roughly estimated for a 100 m^2 area according to three classes: 0.1–15%, 16–50% and 51–100%. From the 670 sites, 225 were randomly selected for sampling, i.e., 75 from each cover class. The 225 sites were scattered within 46 patches. These sites consisted mainly of mesic forests (50% of sites) dominated by sugar maple, transition zones or rocky woods (30% of sites) dominated by red maple–red oak and arboreal swamps (20% of sites) dominated by silver maple (Bergeron, unpubl. data).

On each site, a 10 m × 10 m sample plot was delineated. In each plot, we noted the presence of all species of pteridophytes. We also estimated the total cover occupied by herb and shrub strata using 7 classes: <1%, 1–5%, 6–25%, 26–40%, 41–60%, 61–80% and 81–100%, and measured the diameter at breast height (DBH) of all trees ($\geq$1 cm DBH). DBHs were used to calculate the total basal area per plot. The percentage of canopy openness was calculated by averaging four readings of a Lemmon's model C spherical densiometer, one from each corner of the plot. The proportion of stones on the forest floor surface (stoniness) was estimated visually (size classes of 20% each). The thickness of the A horizon (i.e., top mineral horizon mixed with humified matter) was measured from holes dug at eastern and western sides of the plot, and a sample of its soil was collected. In the laboratory, soil samples were air dried and passed through a 2 mm sieve. Soil pH and electrical conductivity were determined in 1:10 soil/water suspensions using an Orion 4-star pH/conductivity meter. In the field, we also estimated the topographic relative moisture index (TRMI), which ranges from 0 (most xeric conditions) to 60 (most hygric conditions). The TRMI is computed by summing scores related to the topographic position, steepness, aspect, and configuration of the dominant slope in the plot (Parker, 1982). In addition, we evaluated the number of micro-landform types (flat, depression, mound, down slope, mid-slope, ledge, up slope and steep slope) in the plot according to two classes: 1 type or $\geq$2 types. Finally, to consider the effect of internal edges, the distance to nearest open area (e.g., trails, ditches, roads, grasslands) was measured and grouped in two classes: $\leq$30 m or >30 m. Eighty-seven percent of the internal edges located at less than 30 m were walking trails.

2.4. Landscape metrics

Landscape metrics were extracted from GeoEye and Digital-Globe satellite imagery (2000 and 2009) and from layers (2003 and 2010) of the Montréal Metropolitan Community's (MMC) Master Plans. We first delineated the perimeter (forest edge) of the 82 forest patches in ESRI ArcGIS 9.3 software, and then created a 500 m-buffer zone around each patch (in accordance with Bräuniger et al., 2010; Duguay et al., 2007). We then computed the forest patch area, obtained the geographic coordinates of the patch centroid and measured the distance to nearest forest edge for each sample plot to consider the effect of external edges caused by the forest-matrix interface. In the buffer zone, we included the 116 preselected patches to obtain the patch density (i.e., number of patches divided by the area of the buffer). We also calculated the street density and proportions of each major type of land use: residential, public utility, agricultural, landscaped green space and water body. Water bodies in the buffers relate mainly to the proportion of large rivers (Prairies and St. Lawrence) and large lakes (Two Mountains and St. Louis) of the study area (Fig. 1). Commercial/industrial areas, accounting for less than 10% of all buffer zones,

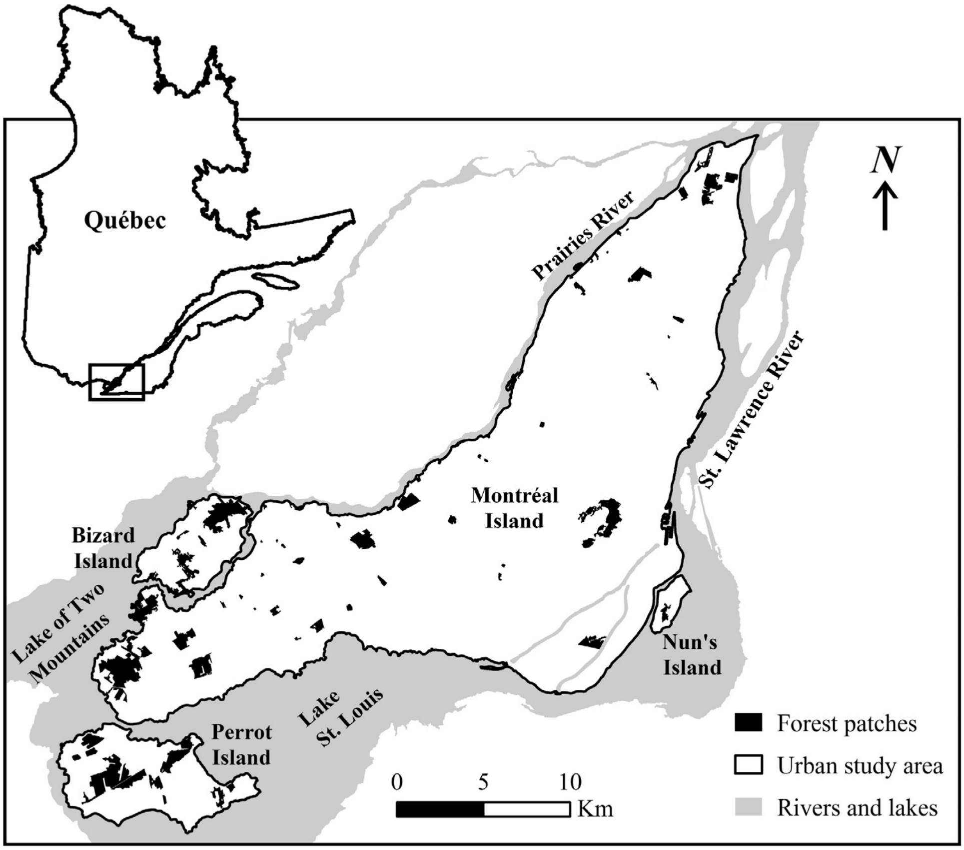

Fig. 1. Location of the 82 forest patches sampled in the Hochelaga Archipelago, southern Québec, Canada.

were discarded, because they reflected a Zoning By-Law rather than the physical composition of the urban matrix. To generate surface temperature data, we used a Landsat 5 (band 6) image of the MMC, taken on June 27th 2005, which was preprocessed and resampled (1:50,000) by the Heat Island Research Group (UQAM University). We first removed clouds and then reclassified the image's pixels (range of 17.0–42.5 °C) by the standard deviations method (σ) suggested by Martin (2008). Finally, pixels greater than 1σ of the mean temperature class (μ = [26.8–29.4] °C) were retained to calculate the proportion of heat islands inside each 500 m-buffer zone.

2.5. Data analysis

Data on presence–absence and richness of fern taxa and their allies were based on plant identification to the rank of distinct species, and followed the nomenclature of the VASCAN database (Brouillet et al., 2010). The presence–absence data were preferred to abundance data, because the latter often need to be analyzed separately according to the habit (caespitose or rhizomatous) of each species (e.g., Richard et al., 2000). All statistical tests were carried out in R 2.15 (R Core Team, Vienna, Austria) with appropriate open source packages.

To evaluate the spatial structure of pteridophyte distribution throughout the network of forest patches, we created explanatory variables using principal coordinates of neighbor matrices (PCNM) for modeling positive autocorrelation (Dray et al., 2006). PCNM analysis uses the geographic coordinates of sampling sites (here, each patch centroid) to generate a distance matrix, on which eigenfunctions are computed, and eventually introduced into a regression model to explain response variables (here, pteridophyte richness). From the 'pcnm 2.1-2' R package, the distance matrix was determined by a minimum spanning tree (truncation distance: 6242 m), which represents a network of patches based on least-cost links. After detrending response data, these latter were regressed against all eigenfunctions to detect significant spatial structures (Borcard and Legendre, 2002). The overall *F-test* (9999 permutations) was not significant. Thus, we selected any eigenfunction as explanatory variable for subsequent stages of the modeling of pteridophyte richness. To verify whether this absence of spatial structure in the richness data was related to the lack of spatial structure among the elements of the urban areas, we performed a second PCNM analysis using each landscape metric as response variable. Of the nine variables, four were detrended (D.PATCH, D.STREET, UTILIT and UHI) prior to individual analyses. For each analysis, only an overall *F-test* keeping all the eigenfunctions with positive autocorrelation was run.

To separate sources of variations in pteridophyte data at both spatial scales investigated (forest patch and microhabitat), explanatory variables were split into four subsets (Table 1), namely: (i) forest area; (ii) land use; (iii) biotic/abiotic; and (iv) edge effect. Since variables were expressed in different units, they were standardized to *z*-scores ($\mu = 0$ and $\sigma = 1$) prior to analysis. To perform univariate parsimonious models, forward-selection tests (9999 permutations of residuals; 'packfor 0.0-7' package) were conducted on all variables, except AREA. Selection procedures were cut off at $\alpha = 5\%$ and at an adjusted coefficient of determination (R_a^2), resulting from a multiple regression on all variables belonging to a given subset (i.e., $R_a^2 = 28\%$, 32%, 7% for the ii, iii and iv subsets, respectively). Based on forward-selection, three explanatory variables were selected from subset ii (RESID, WATER and UHI), five from subset iii (micro-landform, moisture, pH, EC and shrub cover), while both variables related to subset iv (D.open and D.edge) were retained. At this step, all variance inflation factors (VIF) were less than 2, indicating negligible multicollinearity while the correlation coefficients between the explanatory variables ranged from −0.43 to 0.60 (Table 1S). We also verified polynomial relationships and interaction terms between predictors, but none were better than the parsimonious models described below. We then computed four linear regression models with the variables selected, using the 'ape 2.8' package. Species-forest area (Model I) and species-land use (Model II) regressions used pteridophyte richness in patches as a response variable, while species-biotic/abiotic (Model III) and species-edge effect (Model IV) regressions used pteridophyte richness in sample plots as a response. All models were tested for significance of equation parameters with 9999 permutations. An *F*-test of R-square was conducted on full model residuals, and a two-tailed *t*-test was performed on regression coefficients. Hence, the resulting four models designated the relationships between variables in their natural state. In a second step, we analyzed how the variation explained by pteridophyte richness changes with the presence of covariates held constant. With the partial regression method available in the 'vegan 2.0-1' package, we thus partitioned variation in richness data among the two groups of variables retained from subsets i and ii, and performed the same procedure

Table 1
Subsets of explanatory variables sampled at the scales of forest patch and microhabitat.

Subsets	Variables	Description and units
(i) Forest area	AREA	Area of forest patch (m^2)
(ii) Land use	D.PATCH	Patch density (i.e., a patch count) in 500 m-buffer (#/m^2)
	D.STREET	Street density (i.e., a length measure) in 500 m-buffer (m/m^2)
	RESID	Proportion of residential areas (e.g., 3-storey building) in 500 m-buffer (%)
	UTILIT	Proportion of public utility (e.g., transport infrastructures) in 500 m-buffer (%)
	RURAL	Proportion of agricultural areas (e.g., cultivated fields) in 500 m-buffer (%)
	GREEN	Proportion of landscaped green areas (e.g., managed parks) in 500 m-buffer (%)
	WATER	Proportion of water bodies (e.g., rivers, lakes, large ponds) in 500 m-buffer (%)
	UHI	Proportion of urban heat islands (i.e., surface above 29.7 °C) in 500 m-buffer (%)
(iii) Biotic/abiotic	Herb cover	Total cover of herb stratum in 100 m^2 (%)
	Shrub cover	Total cover of shrub stratum in 100 m^2 (%)
	Basal area	Total basal area of trees in 100 m^2 (m^2/ha)
	Light	Canopy openness in 100 m^2 (%)
	Stoniness	Stoniness on the soil surface in 100 m^2 (%)
	pH	Potential Hydrogen of soil in 100 m^2 ($-\log[H^+]$)
	EC	Electrical conductivity of soil in 100 m^2 ($\mu S\,cm^{-2}$)
	A.horizon	Thickness of A horizon in 100 m^2 (cm)
	Moisture	Topographic Relative Moisture Index in 100 m^2 (TRMI scores: 0–60)
	Micro-landform	Number of micro-landform types in 100 m^2 (1 or $\geq$2)
(iv) Edge effect	D.edge	Sample plot distance to nearest forest edge (m)
	D.open	Sample plot distance to nearest open area ($\leq$30 or >30 m)

Table 2
Clustering of variables related to forest patches (WATER, UHI and RESID) and microhabitats (D.edge and D.open) into groups characterized by low or high levels of urban influence. The number of observations and mean (±SD) of each variable defining the groups are shown. For abbreviations see Table 1. NA = not applicable.

Groups	Low	High	Low		High	
	N	*N*	Mean	SD	Mean	SD
WATER	21	61	37%	±12	3%	±5
UHI	57	25	9%	±9	55%	±13
RESID	37	45	23%	±13	64%	±12
D.edge	59	166	203 m	±57	63 m	±34
D.open	125	100	>30 m	NA	≤30 m	NA

Table 3
Linear models of pteridophyte richness by explanatory variables at the scales of forest patch and microhabitat: (a) species-forest area regression, (b) species-land use regression, (c) species-biotic/abiotic regression, (d) species-edge effect regression. For abbreviations see Table 1.

	Coefficient	*P*
(a) Model I ($R_a^2 = 0.598$; $P = 0.0001$; $N = 82$)		
Intercept	7.4512	0.0001
AREA	5.8229	0.0001
(b) Model II ($R_a^2 = 0.281$; $P = 0.0001$; $N = 82$)		
Intercept	7.4512	0.0001
WATER	−2.5720	0.0022
RESID	−2.5568	0.0040
UHI	−2.4458	0.0106
(c) Model III ($R_a^2 = 0.313$; $P = 0.0001$; $N = 225$)		
Intercept	3.5689	0.0001
Micro-landform	0.9251	0.0001
Moisture	0.4364	0.0006
pH	−0.3406	0.0040
EC	−0.2702	0.0253
Shrub cover	−0.2613	0.0242
(d) Model IV ($R_a^2 = 0.073$; $P = 0.0001$; $N = 225$)		
Intercept	3.5689	0.0001
D.edge	0.4656	0.0007
D.open	0.2920	0.0312

for the variables retained from subsets iii and iv. The variation associated to the resulting individual fractions (i.e., the “pure” effect of a given group of variables on the richness) was tested with 9999 permutation tests under the reduced model.

To better interpret models involving pteridophyte richness, we examined the patterns associated to the composition of ecological assemblages. With species data, we computed two distance-based redundancy analyses (db-RDA; Legendre and Anderson, 1999) in the ‘vegan 2.0-1’ package. For each spatial scale, the db-RDA was done on a Sørensen dissimilarity matrix calculated from the multispecies table of presence–absence (Legendre and Legendre, 2012). In this analysis, we adopted a less rigid approach by integrating all the explanatory variables and by failing to distinguish the covariates. The overall canonical relationships and first constrained axes were validated by significance tests with 9999 permutations. Interpretation of percentages of variance explained by the univariate and multivariate models was based on Ezekiel’s R_a^2 (Legendre and Legendre, 2012).

To identify pteridophytes that could be indicators of habitat integrity, we used explanatory variables of Models II and IV. With the *k*-means algorithm iterated 100 times, each variable was partitioned into $k = 2$, and the resulting classification vector was used to form groups of sites (forest patches or sample plots), with low and high levels of urban influence (Table 2). Indicator species were searched using the Indicator Value approach (IndVal; Dufrêne and Legendre, 1997) from the ‘indicspecies 1.5.2’ package. We chose the “group-equalized” version of IndVal, which allows comparison of groups with unbalanced observations (De Cáceres and Legendre, 2009). The significance of associations between species (here, presence–absence of a pteridophyte) and groups was tested with 9999 permutations. The *P* values used were corrected by Sidák’s method (Legendre and Legendre, 2012).

3. Results

3.1. Pteridophyte diversity at the forest patch scale

A total of 38 species of pteridophytes (Table 2S), all of native origin (Brouillet et al., 2010), were recorded in the 82 forest patches. The number of pteridophytes per patch ranged from 0 to 29. Hochelaga Archipelago seems an area particularly rich in pteridophyte for northern temperate regions of North America. In comparison, the Wayne County (Michigan, USA) also supports 38 species of pteridophytes, but on an area three times larger (Reznicek et al., 2011).

Across the sampled patches, taxa with the highest percentage of occurrence were *Equisetum arvense* (81%), *Onoclea sensibilis* (74%), *Athyrium filix-femina* (60%), *Matteuccia struthiopteris* (50%) and *Dryopteris carthusiana* (45%). All pteridophytes sampled are typical forest species for Montréal region, although *E. arvense* and *O. sensibilis* may occupy more urban open habitats. None of the 38 sampled species are designated threatened or vulnerable in Québec, although four taxa were observed only once (*Botrychium dissectum*, *Cystopteris fragilis*, *Lycopodium clavatum* and *Woodwardia virginica*). These four taxa are associated to specific habitats (rocky escarpments and peaty woods) rare in the study area, and found only in some of the largest patches.

Results of the PCNM global tests showed that the variation in richness among patches of the network was not spatially structured ($P = 0.0750$) whereas the spatial distribution of ecological conditions in the study area was significantly autocorrelated ($P < 0.05$) for six landscape metrics (D.PATCH, D.STREET, RESID, UTILIT, GREEN and UHI). At the same time, a random spatial pattern was found for RURAL ($P = 0.1150$) as well as for AREA ($P = 0.3000$) and WATER ($P = 0.1350$), both involved in the parsimonious regression models.

A positive relationship was found between pteridophyte richness and AREA, meaning that large forest patches had more species than smaller ones (Table 3a). In contrast, richness decreased when proportions of water bodies (WATER), residential areas (RESID) and urban heat islands (UHI) increased in the surrounding matrix (Table 3b). The best-fit model was the species-forest area regression (Model I), which explained about 60% of the variance in richness data. However, partitioning analysis showed that an important part of this variation was influenced by the other landscape metrics (Fig. 2a). The greatest variation was explained solely by the AREA (forest area subset: 38.5%; $P = 0.0001$), but 21.3% was shared with the parsimonious variables from the land use subset. Although the variation explained solely by land use variables was 6.8%, the fraction was highly significant ($P = 0.0001$).

The canonical relationship between species composition data and landscape metrics explained 21.2% of the variation ($P = 0.0001$). The first axis (13.9% of variance, $P = 0.0001$) mostly showed a pattern of species accumulation along the AREA vector, while the second axis (6% of variance, $P = 0.0001$) was mostly related to the WATER and UHI vectors (Fig. 3a). In the ordination diagram, *O. sensibilis*, *E. arvense* and *M. struthiopteris* (Onse-Eqar-Mast) were apparently segregated from other species and, among other things, negatively correlated to the UHI vector. Finally, 19 species were found significant indicators at the forest patch scale (Table 4). Patches with small percentages of RESID and UHI zones in their surrounding had respectively 18 and 10 indicator species (Table 4). No significant indicator species was found for the group of patches defined by the WATER variable.

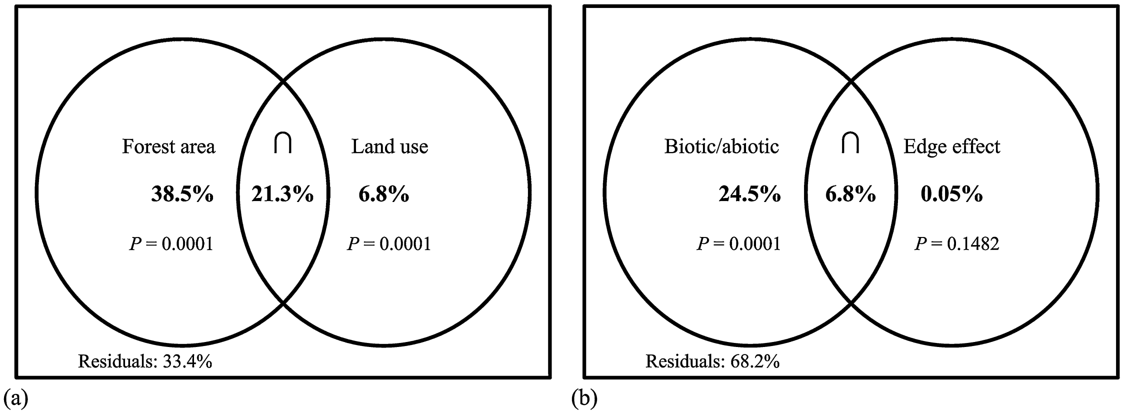

Fig. 2. Variation partitioning of pteridophyte richness explained by parsimonious variables from (a) the subsets forest area (AREA) and land use (RESID, WATER, UHI) and (b) the subsets: biotic/abiotic (micro-landform, moisture, pH, EC, shrub cover) and edge effect (D.open, D.edge). The *P* values are from tests of individual fractions. The joint fraction (∩) is not testable.

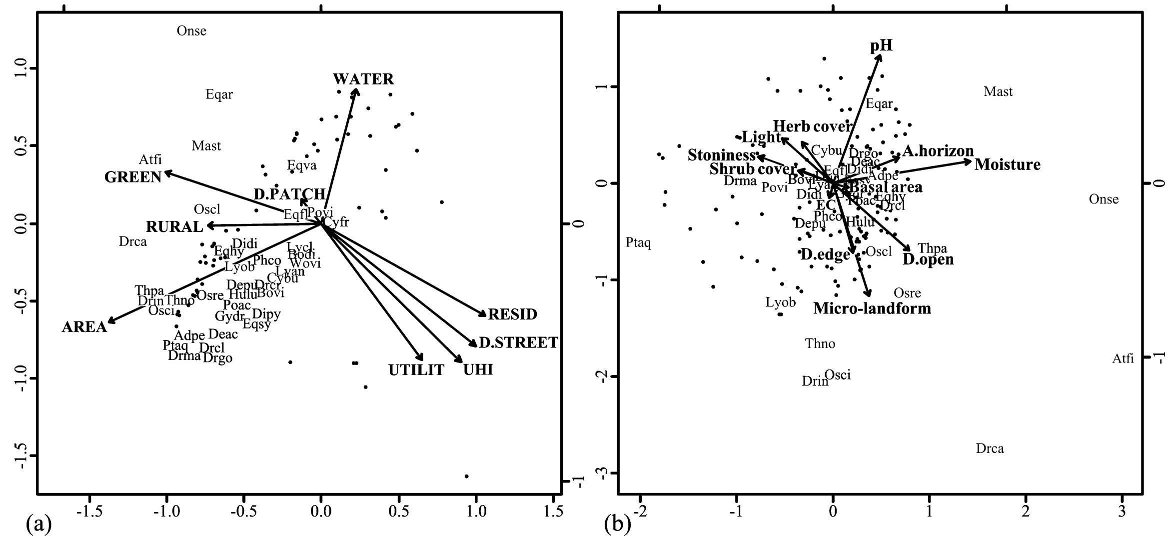

Fig. 3. Ordination diagram of the first (horizontal scale) and second (vertical scale) axes based on a db-RDA of the composition of pteridophytes assemblages (Sørensen index) following (a) the landscape metrics sampled at the forest patch scale; and (b) variables sampled at the microhabitat scale. The arrows are environmental vectors; points are sites (forest patches or sample plots). See Table 2S for species names.

3.2. Pteridophyte diversity at the microhabitat scale

A total of 33 pteridophytes (out of 38 species composing the landscape pool) were recorded in the 225 sample plots. The most common taxa across the microhabitats were the same as those observed for the forest patch scale, but their ranks were slightly different; for example, *A. filix-femina* ranked first in occurrence (61%; Table S2). The number of pteridophytes per plot ranged from 1 to 10.

The relationships between pteridophyte richness and micro-landform and moisture were positive, while the relationships between richness and pH, EC and shrub cover were negative (Table 3c). A positive relationship was also found between richness and each variable from the edge effect subset (Table 3d), meaning that there were a greater number of pteridophytes in plots located at remote distances from forest edges (external edges) and open areas (internal edges). Explanatory variables from the species-biotic/abiotic regression (Model III) explained the main fraction of variation in richness data after their introduction in the partitioning analysis (24.5%; $P = 0.0001$), and 6.8% of variance was shared with the edge effect subset (Fig. 2b). The remaining fraction of explained variation was negligible and not significant (0.05%; $P = 0.1482$).

The db-RDA explained only 15.7% of the variation ($P = 0.0001$) in the composition data constrained by the microhabitat conditions. The first axis (4.7% of variance, $P = 0.0001$) showed a gradient dominated by moisture vector, where *O. sensibilis* (Onse) and *M. struthiopteris* (Mast) were at the hygric end and *Pteridium aquilinum* (Ptaq) at the xeric end (Fig. 3b). The second axis (3.8% of variance; $P = 0.0001$) segregated several pteridophytes by pH and micro-landform vectors, and in particular a cluster of species (Osre-Osci-Thno-Drin) was correlated to a high number of micro-landform.

At the microhabitat scale, only four species were found to be significant indicators of urban influence (Table 5). *E. arvense* and *P. aquilinum* were associated with plots located close to open areas, while *A. filix-femina* and *D. carthusiana* were strongly associated with plots located far from open areas. *D. carthusiana* was also an indicator of plots located far from forest edges.

4. Discussion

No evidence of spatial autocorrelation was found in pteridophyte richness data of Hochelaga Archipelago forest patches. This absence of spatial effect could be related to pteridophytes'

Table 4
Indicator Values on the presence–absence data of pteridophytes for the groups of forest patches characterized by low or high levels of urban influence (based on WATER, UHI and RESID variables). The values are expressed as the square root of the original IndVal. Only significant indicator species are shown. Percentage of patches (occurrence) where a species was observed is also indicated ($N = 82$). For abbreviations see Table 1.

	Occurrence (%)	WATER		UHI		RESID	
		Low	High	Low	High	Low	High
Equisetum arvense	80.5	0.67	0.61	0.73^{**}	0.49	0.76^{**}	0.52
Onoclea sensibilis	74.4	0.65	0.58	0.76^{***}	0.38	0.77^{***}	0.47
Athyrium filix-femina	59.8	0.45	0.61	0.73^{***}	0.28	0.73^{***}	0.38
Matteuccia struthiopteris	50.0	0.52	0.49	0.64^{*}	0.30	0.59	0.42
Dryopteris carthusiana	45.1	0.32	0.57	0.61^{*}	0.27	0.77^{***}	0.20
Dryopteris intermedia	42.7	0.28	0.58	0.59^{*}	0.28	0.66^{**}	0.28
Dryopteris marginalis	30.5	0.20	0.51	0.47	0.27	0.54^{*}	0.25
Thelypteris palustris	29.3	0.26	0.46	0.52^{*}	0.17	0.59^{**}	0.20
Pteridium aquilinum	26.8	0.21	0.46	0.50	0.18	0.57^{**}	0.18
Osmunda regalis	25.6	0.28	0.41	0.48	0.18	0.59^{**}	0.15
Osmundastrum cinnamomeum	24.4	0.15	0.47	0.50^{*}	0.13	0.60^{***}	0.12
Thelypteris noveboracensis	20.7	0.09	0.47	0.41	0.20	0.57^{**}	0.10
Osmunda claytoniana	18.3	0.17	0.38	0.46^{*}	0.07	0.60^{***}	0.04
Lycopodium obscurum	14.6	0.10	0.38	0.40	0.08	0.57^{***}	0.00
Equisetum sylvaticum	12.2	0.11	0.33	0.42^{*}	0.00	0.47^{**}	0.04
Diphasiastrum digitatum	12.2	0.11	0.33	0.30	0.17	0.52^{***}	0.00
Phegopteris connectilis	9.8	0.00	0.36	0.30	0.10	0.46^{**}	0.00
Huperzia lucidula	9.8	0.12	0.28	0.37	0.00	0.46^{**}	0.00
Dennstaedtia punctilobula	8.5	0.12	0.26	0.35	0.00	0.43^{**}	0.00

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

long-dispersal potential (Barrington, 1993; Kreft et al., 2010; Tryon, 1986). Nonetheless, most of the spores produced annually by several species are expelled just a few meters from the mother plant (Peck et al., 1990; Tryon, 1986) while several other species disperse mainly vegetatively and thus form clumped colonies (Richard et al., 2000). The detection of contagious distribution patterns would therefore be more probable at local scales. For instance, Karst et al. (2005) found that spatial autocorrelation in pteridophyte data was much stronger at a small spatial scale (1 ha) than at an intermediate scale (1000 ha), and that environmental factors explained most of the variation found at an intermediate scale. This indicates that the role of processes related to dispersal history (chance) versus that resulting from environmental control (deterministic) is not constant from one spatial scale to another. We did not test processes related to geographic distance at the microhabitat scale, due to the broad spatial discontinuities imposed by our random sampling design. The large amount of residuals (68%) in our partitioning analysis of microhabitat factors may, however, suggest a small scale effect of limited dispersion involving pteridophytes (Legendre and Legendre, 2012).

At the forest patch scale, the species-area relationship explained most of the variation found in the pteridophyte richness. The absence of contagious distribution of richness between patches and the random distribution of patch sizes over the study area suggest that pteridophyte diversity is mainly controlled by deterministic processes underlying the integrity of ecological conditions inside each patch. As a proxy of habitat heterogeneity, patch size has often been identified as the driver of biodiversity changes in fragmented landscapes (Bräuniger et al., 2010), especially for vulnerable plants (Guirado et al., 2006) like many pteridophytes (Murakami et al., 2005). In addition, it appears that in several urban areas, the recurrence of anthropogenic disturbances (habitat loss, biological invasions, etc.) breaks the spatial organization of environmental variables and prevents the establishment of structured dispersion processes for several species, even in mobile groups (Sattler et al., 2010). In our study, the metrics typically related to concentric patterns of urbanization were autocorrelated (e.g., RESID and UHI), but despite this organization, an induced spatial dependence in pteridophyte response was not observed. In fact, the adjacent land use conditions of a forest act mostly by altering the relationship of patch size to species richness (Guirado et al., 2006), which is evident in the large shared effect (21%) our data shows between the forest patch area and land use variables. Compared to rural areas, small patches of urban areas are more seriously affected by disturbances, such as pedestrian frequentation, the pattern of which is shaped by human activities around forests (Guirado et al., 2006). Small urban patches contribute less evaporative cooling from trees, and are therefore more affected than large forests by the diffusion of dry and warm microclimatic conditions from the matrix to the forest interior (Grimm et al., 2008; Memon et al., 2008). In our study, most of the relationship between patch area and land use is likely determined by UHIs, as our results showed that an increase in surface temperature in the surrounding matrix was detrimental to pteridophyte richness. Since UHIs can reduce the availability of ground moisture (Memon et al., 2008), it has been suggested that the sexual reproduction of pteridophytes (gametophyte stage), which requires a water film for sperm motility on the prothallus, could be diminished in the presence of UHIs (Murakami et al., 2005). Green-spored species, such as six of the ten species (Table S2) found to be indicators of low UHIs (*E. arvense*, *E. sylvaticum*, *M. struthiopteris*, *O. sensibilis*, *Osmundastrum cinnamomeum* and *Osmunda claytoniana*), are likely even more sensitive to habitat dryness, because the viability of their spores is brief (ca. 48 days) and their chloroplasts

Table 5
Indicator Values on the presence–absence data of pteridophytes for the groups of sample plots characterized by low or high levels of urban influence (based on D.edge and D.open variables). The values are expressed as the square root of the original IndVal. Only significant indicator species are shown. Percentage of plots (occurrence) where a species was observed is also indicated ($N = 225$). For abbreviations see Table 1.

	Occurrence (%)	D.edge		D.open	
		Low	High	Low	High
Athyrium filix-femina	60.9	0.63	0.51	0.65^{***}	0.44
Dryopteris carthusiana	41.8	0.64^{***}	0.35	0.57^{**}	0.33
Equisetum arvense	20.4	0.25	0.36	0.21	0.44^{**}
Pteridium aquilinum	12.9	0.26	0.25	0.14	0.38^{*}

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

burst without adequate moisture (Lloyd and Klekowski, 1970). This prevents germination and makes them vulnerable to local extinction, unlike non-chlorophyllous spore species that can reappear after a disturbance because of their soil spore banks. In contrast, species with green spores are quick to colonize new habitats when conditions are favorable (Lloyd and Klekowski, 1970; Mehltreter, 2010).

Some properties of the urban matrix may also induce new biological interactions detrimental to pteridophytes in forest patches (Williams et al., 2009). The environmental conditions typical of an urban matrix usually favor urban-adapted species (Ricotta et al., 2009) such as thermophilous (Bechtel and Schmidt, 2011; Godefroid and Koedam, 2007) or exotic plants (Ricotta et al., 2010). Forests in urban residential sectors also tend to include a high proportion of ligneous plants escaped from gardens (Godefroid and Koedam, 2007). Space and resources of forest habitats in which pteridophytes are normally established could thus be monopolized by these invading plants. For instance, in the Ottawa region, 150 km west of our study area, forest patches in urbanized areas have been found to contain 40% more exotic plants than landscapes with few residential sectors in the same region (Duguay et al., 2007). Maintaining species colonies at demographic levels that ensure a wide diversity can thus be difficult in urban forest patches limited in space, because the geophyte life form of pteridophytes does not allow growth rates fast enough to respond to these climatic changes and to interact with invading plants (Grime, 1985; Page, 2002).

High water availability usually stimulates pteridophyte growth and controls the diversity of favorable habitats (Greer et al., 1997; Karst et al., 2005; Kreft et al., 2010; Richard et al., 2000). Contrary to such expectations, we found lower pteridophyte richness in forest patches surrounded by large proportions of water bodies than in patches surrounded by few water bodies. This is likely due, at least in part, to the fact that patches located near the shores of this archipelago's islands are subjected to the area's largest human footprint, since urbanization initiates at these locations. Currently, Montréal's open riverbanks are covered with wasteland-type vegetation composed of about 50% exotic plants (Morin et al., 1989). Often adjacent to these riverbanks, riparian forests are subject to strong human pressure due to recreational use that results in compacted and bare soils, garbage presence, and poor herbaceous diversity in the understory (Cole and Marion, 1988; Moffatt et al., 2004). In Hochelaga Archipelago, the shrub and herb layers of several forest patches near water bodies are dominated by exotic plants *Frangula alnus*, *Lythrum salicaria* and *Rhamnus cathartica* (Vincent et al., 1986) which could explain in part the lower richness associated to water bodies. However, monospecific colonies of *O. sensibilis* or *M. struthiopteris* are often found in riparian forests of the area, especially in forest where the shrub layer is absent (Vincent et al., 1986). The predominance of these two ferns could also partly explain the lower richness associated to water bodies. Therefore, although water is a key element for pteridophytes to thrive, the recurrence of anthropogenic disturbances in ecosystems located near water bodies, as is the case for our study area, could have caused a cumulative population decline, and eventually the local extinction of a large number of pteridophytes. Actually, some of the highest rates of extinction have been found for native herbaceous plants living in urban riparian forests, while the introduction of exotic plants continues year after year, leaving floristically degraded sites (DeCandido et al., 2004).

At the microhabitat scale, abundant shrub cover was negatively correlated to pteridophyte richness, indicating that sample plots dominated by shrubs had a lower number of pteridophyte species. In Eastern Canada, urbanization promotes the understory establishment of shrubs whose seeds are dispersed by birds, such as *Prunus virginiana*, a native plant used in horticulture, and *R. cathartica* (Duguay et al., 2007; Moffatt et al., 2004; Moffatt and McLachlan, 2004), a species capable of establishing in shady sites and known for outcompeting other plants for space (Charles-Dominique et al., 2012). These two species, especially *R. cathartica*, dominated the shrub stratum in several of our plots (Table S3). In general, pteridophytes are poor competitor against ligneous plants (Grime, 1985), which are more tolerant of anthropogenic disturbances in urban areas (Godefroid and Koedam, 2007; LaPaix and Freedman, 2010; Moffatt and McLachlan, 2004). Despite the impact of biological interactions, the number of pteridophyte species in assemblages was essentially controlled by physicochemical conditions associated to topographic and edaphic properties. Moisture and soil pH are two parameters recognized as important gradients along which ferns are distributed in temperate forests (Greer et al., 1997; Karst et al., 2005; Richard et al., 2000), and this is supported by our results. Interestingly, the cluster of species including *Osmunda regalis*, *O. cinnamomeum*, *Thelypteris novaeboracensis* and *D. intermedia* (Osre-Osci-Thno-Drin) was strongly related to the micro-landform vector at the microhabitat scale and to the AREA vector at the forest patch scale. A large forest patch usually features a great heterogeneity of micro-landforms, and more particularly, a wide range of soil moisture regimes, allowing the coexistence of several species. Although short-distance dispersal affects diversity of ferns in their immediate environment (Richard et al., 2000), it appears that the control exerted by the moisture gradient is predictable at multiple spatial scales, at least between 1 ha up to 1000 ha according to Karst et al. (2005). One of the most important drivers of pteridophyte richness in Japan was the diversity of micro-landforms in large patches, while those of a small size, less than 1 ha, often exhibited topographic homogeneity (Murakami et al., 2005). In our study, the positive effects of patch size and micro-landforms on richness are likely interrelated. This may promote resource availability and mechanisms of ecological niche partition within some species associations, thereby increasing pteridophyte richness.

Our results also showed an important edge effect on pteridophyte distribution, both by external and internal conditions, as less richness was found near edges or open areas. Disturbances in edge habitats, such as wind throw, pedestrian traffic and soil compaction, are known to be detrimental to several native herbaceous plants (Godefroid and Koedam, 2004; LaPaix and Freedman, 2010; Murcia, 1995), and particularly to ferns, since individuals are not resistant to defoliation of their fronds (Grime, 1985). However, almost all variance explained by the variables related to edge effect was shared with the parsimonious variables from the biotic/abiotic subset, meaning that it was essentially the biological and physicochemical conditions found near edges that were harmful to pteridophytes. For instance, our results showed that pteridophyte richness was negatively correlated with shrub cover, but positively correlated to soil moisture. Shrub density in edge habitats is often high, while air and soil moisture are low, due to lateral exposure to solar radiation (Murcia, 1995). These conditions may have induced higher interspecific competition, influenced fertility during the gametophyte stage, and caused hydric stresses on the fronds, as several pteridophytes have no physiological mechanism effective to control water loss (Page, 2002). Moreover, the two species identified as indicators of edges, *E. arvense* and *P. aquilinum*, are known to tolerate dry soil, intense light, competition and disturbances (Greer et al., 1997; Grime, 1985; Richard et al., 2000), while those found to be indicators of plots far from edges, *A. filix-femina* and *D. carthusiana*, are species typical of moist and shady habitats (Greer et al., 1997). Also, according to our results, pteridophyte richness is positively correlated to moderately low values of soil pH and electrical conductivity. These values of the latter are usually higher in urban forest edges than in forest cores due to the spread of calcic debris (e.g., $Ca(OH)_2$) from construction (Godefroid and Koedam, 2004, 2007; Murcia, 1995), and, in northern regions, to deicing salt (e.g., NaCl, $CaCl_2$) used on nearby roads (Charbonneau, 2006). Ionic concentration and pH imbalances in cells may cause physiological gaps (Bryson and Barker, 2002). Surprisingly, several species of pteridophytes tolerate high salt concentrations in their mature aerial organs (Bryson and Barker, 2002), but their prothallus cells may be intolerant to salts (Bogdanović et al., 2012). This phenomenon illustrates the limitations engendered by the two distinct stages (gametophyte and sporophyte) in the pteridophyte life cycle (Page, 2002; Peck et al., 1990). Finally, the edges of urban forests and inside trails are often flat lands, leveled artificially by humans, which has the effect to homogenize the micro-landforms and contributes probably to the deterioration of the global abiotic conditions of a forest patch.

5. Conclusion

Overall, our results highlights that most variables causing pteridophyte diversity to decline in the forests we studied were related to conditions typical of urbanization, indicating that pteridophyte presence is a positive indicator of urban forest integrity. As pteridophytes are good surrogates for biodiversity pattern (Leal et al., 2010) and since urban habitats disturbed by heat islands and edge effects promote extirpation of native plants (McKinney, 2006), pteridophytes could be consider as an integrative bioindicators of integrity. They are also cost-effective, since their presence can be established rapidly in the field (Dale and Beyeler, 2001). Many biologists are indeed capable of identifying ferns and their allies *in situ* by their leaves throughout most of the growing season. From a methodological point of view, pteridophytes are frequent and abundant enough to observe a modulation of responses to processes operating at different spatial scales which therefore allow the development of a practical scale of ecological integrity. Furthermore, our results suggested that the more common pteridophyte taxa are adequate for monitoring general trends, as they are not opportunistic and have ecological preferences for weakly disturbed sites, while green-spored species could indicate more specific patterns related to urban heat island. Finally, urban ecology studies that consider factors related to temperature extremes can improve our understanding of the possible future response of biodiversity to global climate changes (Grimm et al., 2008). The use of pteridophytes as model organisms predictive of ecological integrity is an example of such an approach.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2013.10.015. These data include Google maps of the most important areas described in this article.

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