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Native plant turnover and limited exotic spread explain swamp biotic differentiation with urbanization

Short running title: Biotic differentiation of urban swamps

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Funding Information:
Organisme des Bassins Versants de la Capitale; Ville de Québec; Quebec Centre for Biodiversity
Science; Natural Sciences and Engineering Research Council of Canada (Discovery grants RGPIN-
2014-05367 to SP and RGPIN-2014-05663 to MP)

26 ABSTRACT

27 **Questions:** Does urbanization promote biotic differentiation or homogenization of swamp
28 plant communities? What is the contribution of natives and exotics to swamp response to
29 urbanization?

30 **Location:** Quebec City, Canada.

31 **Methods:** Plant communities of 34 swamps located in low, moderately or highly urbanized
32 landscapes were sampled, and species classified into three exclusive groups: native
33 wetland, native upland and exotic plants. Urbanization influence on the richness of each
34 plant group was assessed using mixed models. Between-site compositional similarities
35 were calculated to identify variations in beta diversity with urbanization level using tests
36 for homogeneity in multivariate dispersion. Beta diversity was further partitioned into
37 species replacement and richness difference for each plant group. Finally, the relationships
38 of ten environmental variables representing soil water saturation and microtopography with
39 plant assemblages were determined by Redundancy Analysis.

40 **Results:** Although the richness of exotics increased with urbanization intensity, revealing
41 increasing propagule pressure, it remained six to 27 times lower compared to natives,
42 whose richness remained stable with urbanization. On the other hand, beta diversity
43 increased with urbanization, with higher dissimilarities in species composition between
44 highly urbanized swamps than between low urbanized ones. This pattern resulted from
45 high species replacement among natives, while richness difference mainly contributed to
46 exotic beta diversity. Changes in plant assemblages were mostly associated with bryophyte
47 cover and soil drainage and red mottle size, suggesting that hydrological conditions likely
48 acted as a strong driver of swamp plant community response to urbanization.

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Conclusions: Swamp plant communities experienced biotic differentiation with increasing urbanization. This differentiation pattern likely was linked to the unpredictable effect of urbanization on hydrological regimes, which promoted high native turnover while limiting exotic spread. Long term monitoring is recommended to ensure that exotics do not outcompete natives through time. Designing sustainable cities requires a greater understanding of the multifaceted effect of urbanization on biodiversity.

KEYWORDS

Anoxia stress release; Assembly rules; Beta diversity; Biotic differentiation; Ecological constraints; Land use changes; Plant communities; Resistance to invasion; Species interactions; Swamps; Sustainable cities; Urbanization; Wetland conservation

INTRODUCTION

Land use transformation is a major driver of biodiversity change worldwide (Chapin et al., 2000; Thuiller, 2007). In human-altered landscapes, biological communities often experience biotic homogenization, i.e. a decrease in beta diversity (increased compositional similarity) across time or space (Olden et al., 2004, 2005; Gámez-Virúez et al., 2015; Gossner et al., 2016). Although changes in beta diversity can be related to both species replacement and richness difference (Legendre, 2014), reduced species richness has often been evidenced as a primary driver of biotic homogenization across a variety of taxonomic groups (Baeten et al., 2012; Baiser et al., 2012; Vellend et al., 2017; but see Hillebrand et al., 2018).

Urbanization, on the other hand, has been mostly associated with high species turnover among plant communities, and notably with a replacement of local plant specialists by generalists or exotics, leading to biotic homogenization (McKinney and Lockwood, 1999; Olden and Poff, 2003; McKinney, 2006; Olden and Rooney, 2006; La Sorte et al., 2014). Discrepancies in the relative contribution of exotics vs. native generalists to this homogenization process have nevertheless been reported, as previous studies have alternatively attributed declines in beta diversity to an increase of exotic species (Cadotte et al., 2017; Loiselle et al., 2020; Price et al. 2020) or to the spread of native species (Tabarelli et al., 2012; McCune and Vellend, 2013; Trentovani et al., 2013; Beauvais et al., 2016; Brice et al., 2017; Blouin et al., 2019). Furthermore, in some cases, urbanization has been shown to promote biotic differentiation (i.e., increased beta diversity; McKinney, 2008), depending on factors such as the size and composition of the initial species pool (Olden and Poff, 2003), the balance between native vs. non-native species and their residence time (Kühn and Klotz, 2006; Lososová et al., 2012, 2016) or the intensity and

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84 type of urbanization (Flynn et al., 2009; Allan et al., 2015; Newbold et al., 2015).
85 Urbanization is therefore a multifaceted process (Grimm et al., 2008) that can either
86 strengthen or release the ecological constraints shaping plant communities in urban
87 ecosystems (Pennington et al., 2010; Brice et al., 2017). Designing urban planning
88 guidelines and sustainable cities that reconcile human well-being and biodiversity
89 conservation hence requires a better understanding of plant community response to
90 urbanization.

91 Wetlands are receiving increasing attention due to the multiple ecosystem services they
92 provide (MEA, 2005; Maltby and Acreman, 2011), especially in urban areas where they
93 act as critical green infrastructures for flood control, water purification, aesthetics, cooling
94 effect and recreation (Taha, 1997; Bolund and Hunhammar, 1999; Lee and Scholz, 2006;
95 Sun et al., 2012; McLaughlin and Cohen, 2013). Empirical evidence shows that wetland
96 ecosystem services related to water quality are generally improved by higher plant
97 diversity, including increased nitrogen removal as well as reduced phosphorus loss and
98 methane efflux (Engelhardt and Ritchie, 2001; Bouchard et al., 2007; Brisson et al., 2020).
99 Yet, wetlands are generally highly vulnerable to invasion by exotics (Zedler and Kercher,
100 2004; Loiselle et al., 2020; Price et al., 2020) and wetland plants are more widely
101 distributed than upland ones (Santamaría, 2002; Ricklefs et al., 2008), which suggests that
102 these ecosystems are prone to biotic homogenization. Changes in ecological conditions due
103 to urbanization indeed generally promote the dispersal of exogenous species, either native
104 generalists or exotics, from surrounding heterogeneous urban lands to open wetlands
105 (Ehrenfeld and Schneider, 1991; Findlay and Bourdages, 2000; Ehrenfeld, 2008; Cutway
106 and Ehrenfeld, 2009). Wetland types might differ in their response to urbanization,

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3 107 however, based on their natural stress regimes. Some previous studies have indeed
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5 108 evidenced biotic differentiation of wetland communities following environmental changes
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8 109 (Ehrenfeld and Schneider, 1991; Favreau et al., 2019).
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10 110 Forested wetlands (i.e., wetlands characterized by the presence of trees) which include
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12 111 swamps or riparian forests for example are characterized by harsh ecological constraints
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14 112 that strongly filter the establishment of plant species (Battaglia et al., 2000; Lin et al.,
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16 113 2004). Compared to open wetlands or mesic forests, in forested wetlands, low light
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18 114 availability combines with periodic anaerobic soil conditions during the growing season to
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20 115 simultaneously shape plant assemblages (Conner et al., 1981; Mitsch and Gosselink, 2000;
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22 116 Colmer and Voeselek, 2009). Given these intense ecological constraints filtering out
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24 117 poorly adapted species, alterations of natural hydrological regimes by urban sprawl could
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26 118 promote the establishment of new species (Azous and Horner, 1997; Groffman et al., 2003;
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28 119 Kentula et al., 2004; Pennington et al., 2010), thereby leading to the biotic differentiation
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30 120 of forested wetlands. Such a pattern was previously evidenced in riparian forests, where
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32 121 urbanization has been associated with a decrease of flooding period and duration, a stress
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34 122 release process that led to a greater variation in species composition across sites (Brice et
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36 123 al., 2017). Despite recent investigations (Loiselle et al., 2020), swamp vegetation response
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38 124 to urbanization still remains to be explored to generalize the impact of urbanization on
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40 125 forested wetland flora.
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46 126 In this study, we examine how plant species richness and beta diversity of swamps vary
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48 127 with urbanization in the Quebec City metropolitan area, Canada. More precisely, we
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50 128 addressed the following questions: (i) Is urbanization associated with biotic
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52 129 homogenization or differentiation in swamp flora? (ii) How does urbanization affect
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species composition of swamps? (iii) What is the specific response of wetland and upland species as well as exotics to an urbanization gradient? Because we expected a variable intensity of stress release after urbanization, we hypothesized that it generates biotic differentiation. We predicted greater beta diversity and more divergent species composition among swamps surrounded by urbanized landscapes compared to less disturbed ones. We also anticipated that urbanization would foster upland and exotic species richness.

METHODS

Study area

The study was conducted in the Quebec City metropolitan area (46°48'52"N 71°12'28"W; hereafter referred to as Quebec City), the seventh most populous urban area in Canada (569 717 inhabitants; Statistics Canada, 2016). Across this 548 km² territory, 50% of land use consists of remnants of natural habitats, 39% of built-up areas and 11% of agricultural lands. Built-up areas, which have increased by 79% in the last 35 years (Nazarnia et al., 2016), correspond to residential (24%), industrial/commercial (5.5%), road networks and mining areas (5%), and vacant lots (4.5%; Cimon-Morin and Poulin, 2018). Yet, nearly 4 921 ha of wetlands (8% of the landscape) are still present across Quebec City metropolitan area, including 2 394 ha of swamps (Beaulieu et al., 2014)

Site selection

Sites were selected based on a map of Quebec City that situates wetlands larger than 0.3 ha according to seven classes identified by photointerpretation (bog, fen, forested peatland, marsh, swamp, wet meadow and shallow water). Among them, 102 swamps were retained according to the following criteria: 1) an area ranging from 1 to 6 ha, to avoid

biases due to size effect; 2) a distance of at least 300 meters between sites; 3) a balance between riparian and isolated swamps (i.e., not directly connected to a permanent watercourse); and 4) a surrounding landscape not dominated by agricultural fields. These 102 swamps were then visited, to exclude bush-dominated, degraded and misclassified swamps (such as forested peatlands). Thirty-four swamps met all criteria. For each swamp, we then characterized landscape composition in a 100 m buffer zone using nine land use categories (Appendix S1) obtained from photointerpretation in QGIS 3.0.0 (QGIS Development Team, 2018). In the surrounding of the sampled swamps, urbanization had mostly taken place from the 1960s to the 1980s (Raimbault, 2019). Land use composition was then used to group swamps according to three levels of landscape urbanization based on the optimum of a non-hierarchical k-means clustering (Legendre and Legendre, 2012). This clustering approach allowed us to account for different land-use classes simultaneously, and therefore better represent the complexity of urbanization process which is hardly synthesized by a single continuous landscape variable (Grimm et al., 2008). Nine low, 14 intermediate and 11 highly urbanized swamps were identified (i.e., swamps respectively located in surrounding landscapes with low, intermediate and high urbanization levels). These urbanization levels increased with decreasing cover of forests and wetlands in the landscape surrounding each site (87% cover at low urbanization level, 57% at intermediate urbanization level and 25% at high urbanization level), and with increasing cover of impervious surfaces including residential and commercial areas, industrial sites, highways and secondary roads (8% cover at low urbanization level, 23% at intermediate urbanization level and 50% at high urbanization level; Appendix S1-2).

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Vegetation surveys

Vascular plant communities in the 34 selected swamps were sampled during the summer of 2016 (end of June-beginning of September). Two to five sampling plots each measuring 400-m² (20 × 20 m) were established per swamp, depending on its size, in order to uniformize sampling intensity per swamp area, for a total of 92 plots (i.e., 25, 38 and 29 plots sampled in swamps respectively corresponding to low, intermediate and high urbanization level) . These plots were randomly positioned within each swamp while respecting a 30-meter distance between plots to limit spatial autocorrelation and a 25-meter distance from the edge to avoid edge effect (Alignier et al., 2014). In each plot, the cover of each plant species was visually estimated using seven classes: <1%, 1–5%, 6–10%, 11–25%, 26–50%, 51–75%, 76–100%. Nomenclature follows VASCAN (Brouillet et al., 2019). Plant cover was averaged at the site scale for analyses. A preliminary analysis detected no significant correlation between swamp area and species richness ($r = -0.06$; $P = 0.74$), nor between sampling area and species richness ($r = 0.18$; $P = 0.31$), indicating that the sampling method did not induce species-area bias.

Species groups

To better determine the impacts of urbanization level on plant communities, all inventoried species were classified into three mutually exclusive plant groups: native wetland, native upland and exotic plants (Appendix S3). We first distinguished between species based on their origin (native or exotic to the Quebec province) following VASCAN (Brouillet et al., 2019). Then, all native species were sorted based on their habitat preference (wetland or upland species) following Bazoge et al. (2014) and the PLANT

database (USDA, 2019). “Obligate” and “facultative wetland” were classified as wetland species (i.e., specialist plants preferentially occurring in wetlands), and “facultative,” “facultative upland” and “upland” as upland species (i.e., generalist plants equally occurring in wetland and terrestrial habitats as well as plants occurring preferentially in terrestrial habitats). Only two species, *Lythrum salicaria* and *Lysimachia nummularia*, were both exotics and wetland species, but neither was frequent (present in 15% and 9% of the sites, respectively) or abundant (<1% of cover in each site for both species) and they were thus classified as exotics exclusively.

Environmental variables

Ten environmental variables were evaluated in each plot. Soil texture and drainage were evaluated using a semi-quantitative scales ranging from 1 (sand) to 12 (clay) for texture and from 0 (excessive) to 6 (very bad) for drainage (Saucier, 1994). The size (1: < 5 mm; 2: 5-15 mm; 3: > 15 mm), depth (cm) and abundance (1: <2%; 2: 2-20%; 3: > 20%) of soil mottles as well as the thickness of humus or peat (cm) were quantified as proxies of water table depth and near-surface water saturation, given that humus degrades more rapidly in aerobic conditions (Zoltai and Vitt, 1995; Mitsch and Gosselink, 2015). No significant correlation between soil mottle abundance and sampling date was detected ($r = 0.25$; $P = 0.16$), suggesting that our sampling design did not induce biases in soil conditions, and evidencing that soil mottles are relatively stable through time as previously reported (Vepraskas and Craft, 2016). Similarly, no significant correlation was detected between soil type (organic vs. non-organic) and soil mottle abundance ($r = -0.27$; $P = 0.12$). Microtopographic variation was assessed using a four-class index based on the elevation

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223 difference between pits and mounds (0: flat, 1: <0.5 m, 2: 0.5-1 m, 3: more than 1 m of
224 amplitude). The cover of bryophytes (largely dominated by *Sphagnum* spp.), vernal pools
225 and bare ground surfaces was additionally estimated using the same classes as for plant
226 cover to approximate hydric conditions at soil surface (Goguen and Arp, 2017).

227
228 **Statistical analysis**

229 Changes in plant richness per site between levels of urbanization intensity were first
230 evaluated using a linear mixed model including urbanization levels (low, intermediate,
231 high) and species groups (native wetland, native upland, exotic) as fixed effects. As a
232 significant interaction between urbanization level and species group was detected, the
233 individual effect of each factor was tested for each level of the other factor using least
234 square means comparisons. Richness values were square root-transformed to meet residual
235 normality and variance homogeneity, and back-transformed for result presentation.

236 Second, changes in swamp beta diversity between levels of urbanization intensity were
237 investigated using tests of homogeneity for multivariate dispersions (Anderson et al., 2006)
238 to reveal biotic homogenization or differentiation processes. This method uses
239 permutations to compare groups of sites based on the average distance between sites and
240 their associated group centroid in an ordination space, as a measure of beta diversity. For
241 this, the cover of each species in the site-by-species matrix was first transformed into its
242 importance value (IV; Barbour et al., 1987), to account for differences in sampling effort
243 between sites (i.e., 2 to 5 plots sampled per swamp). The IV of a species corresponded
244 more precisely to the mean of its relative frequency (number of plots per swamp in which
245 the species occurred relative to the total number of occurrences of all species) and relative
246 dominance (cover of the species per swamp relative to the total cover of all species, using

the median of the cover classes). Species IV therefore allow to take into account differences in sampling intensity by rescaling species cover according to the number of plots surveyed per swamp through the use of species relative frequency. A site-by-site Euclidean distance matrix based on Hellinger transformation (Legendre and Gallagher, 2001) was then computed for calculating the centroids of low, moderately and highly urbanized swamps. Hellinger transformation (which corresponds to the square root of the cover/frequency of a species i at site j divided by the sum of species cover/frequency at site j) is advised prior to compute Euclidean distance-based ordinations such as PCA, PCoA or RDA as it accurately preserves Euclidean distances among sites (Legendre and Gallagher, 2001). Finally, the distances of each site to its associated group centroid were subjected to an ANOVA with 9,999 permutations to determine whether beta diversity differed within urbanization levels. To reveal differences in species composition between urbanization levels, we additionally compared the three centroid locations using a PERMANOVA (9,999 permutations; Anderson, 2001) interpreted from a PCoA biplot (Anderson and Walsh, 2013). Given that changes in beta diversity can relate to both species turnover and richness difference, these two mechanisms were further investigated for a thorough understanding of the drivers of biotic homogenization or differentiation. We partitioned beta diversity into these two components using Sørensen dissimilarity on presence-absence data (Legendre, 2014; Borcard et al., 2018) given we were interested in richness difference rather than abundance as a proxy of ecological niche diversity and competitive interactions potentially leading to species exclusion. For this, four partitionings were conducted for each urbanization level, one for the entire pool of species and one for each plant ecological group (native wetland, native upland, and exotic species).

Finally, we evaluated the potential role of environmental variables associated with changes in swamp community composition using a Redundancy Analysis (RDA) on Hellinger-transformed species IV (Legendre and Gallagher, 2001). Explanatory variables were subjected to a stepwise selection to identify the most parsimonious model explaining between-site differences. Both species and site scores were then displayed on an RDA biplot with significant environmental vectors to visualize species-environment relationships.

As we focussed here on differences in species richness or community composition between sites, all analyses were conducted at the site scale by calculating for each species its mean cover among plots surveyed in the same swamp. Analyses were performed on R v. 3.5.1 (R Core Team, 2019) using the *vegan* (Oksanen et al., 2016; non-hierarchical clustering, multivariate dispersion and variable transformation), *adespatial* (Dray et al., 2017; beta diversity partitioning), *nlme* (Pinheiro et al., 2018; linear mixed models), and *lsmeans* (Lenth, 2016; multiple comparisons) packages.

RESULTS

Overall, 278 plant taxa were identified in the 34 sampled swamps, corresponding to 110 native wetland, 119 native upland and 49 exotic taxa (Appendix S3). The most frequent species (present in > 90% of the swamps) were *Acer rubrum* and *Dryopteris carthusiana*, both native wetland species. The most frequent native upland species were *Athyrium filix-femina* (89% of sites), *Abies balsamea* (83%) and *Amelanchier arborea* (83%) while *Epipactis helleborine* (40%) and *Ranunculus repens* (29%) were the most frequent exotic species.

294 **Urbanization effect on swamp plant richness**

295 Urbanization effect on species richness differed between species groups (significant
 296 urbanization level x species group interaction: $F = 5.51$, $P = 0.0007$). While the richness of
 297 native wetland and native upland plants remained stable and similar to each other between
 298 urbanization levels, exotics richness increased with urbanization intensity, with four times
 299 more species in highly urbanized swamps compared to low urbanized ones (Figure 2).
 300 However, exotics were 27, 11 and 6 times less diversified than natives (both wetland and
 301 upland species summed together) at low, moderate and high levels of urbanization,
 302 respectively (Figure 2).

304 **Urbanization effect on swamp beta diversity**

305 Beta diversity differed between the three urbanization levels ($F = 20.7$; $P = 0.0001$),
 306 increasing from low to highly urbanized swamps (Figure 3). The highest site dispersion
 307 (indicated by ellipse size on Figure 3) and median distance to centroid (Figure 3) were
 308 indeed observed in highly urbanized swamps. Plant composition also differed significantly
 309 between urbanization levels, as the test comparing centroid locations was significant
 310 ($F = 4.3$; $P < 0.0001$; Figure 3). The even spacing between centroids between urbanization
 311 levels further suggests that mean species composition progressively changed with
 312 urbanization (Figure 3).

313 Different processes were involved in the response of plant species groups to
 314 urbanization levels. For the entire species pool (Table 1a) as well as for native wetland
 315 (Table 1b) and native upland plants (Table 1c), beta diversity increased from a low to a
 316 high level of urbanization primarily due to species replacement. The contribution of species
 317 replacement to beta diversity was especially important at a high level of urbanization for

both native wetland species and the entire species pool, and at a moderate level of urbanization for native upland ones. For exotic species, beta diversity was higher in moderately and highly urbanized swamps. However, richness difference was the main mechanism contributing to exotic beta diversity, especially at low urbanization, where it was four times more influential than species replacement (Table 1d).

Environmental conditions associated with urbanization levels

Distinct environmental conditions characterized swamps along a general gradient which also reflected urbanization levels, along the first RDA axis (explaining 15% of species composition variation over 25% of total variation explained; $p_{RDA1} = 0.001$; $p_{RDA2} = 0.164$; Figure 4). From low to highly urbanized swamps, bryophyte cover decreased, soils became less hydromorphic (smaller red mottles) and drainage increased. Low urbanized swamps were characterized by both native wetland (*Acer rubrum*, *Carex intumescens*, *Dryopteris carthusiana* and *Viburnum cassinoides*) and native upland (*Betula alleghaniensis*) species. In moderately and highly urbanized swamps, different native wetland (*Fraxinus pennsylvanica* and *Matteuccia struthiopteris*) and native upland (*Geum canadense*, *Rubus idaeus* and *Sanguinaria canadensis*) plants occurred. Finally, moderately and highly urbanized swamps were mostly distinguished by the presence of exotic or upland species such as *Acer negundo*, *Arctium* spp., *Lysimachia nummularia* and *Salix xfragilis*.

DISCUSSION

This study reveals that urbanization can foster biotic differentiation of swamp plant communities by promoting the co-occurrence of native and exotic species without leading to the dominance of the latter. Beta diversity indeed increased from low to highly urbanized

342 swamps due to species replacement of native wetland and upland plants in conjunction
343 with an increase in exotic richness (which, however, remained six times lower than native
344 richness in highly urbanized swamps). The inconsistent effect of urbanization on swamp
345 conditions, notably on soil water saturation, likely explains this differentiation pattern.

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347 **High resistance to exotics characterizes urban swamps**

348 Intensifying human disturbances in the landscape surrounding wetlands have often been
349 shown to induce plant species loss (Ehrenfeld, 2000; Faulkner, 2004; Kercher and Zedler,
350 2004; Moffatt et al., 2004; Houlahan et al., 2006; Lougheed et al., 2008; Noble and Hassall,
351 2015). In many cases, this lower species richness in urban wetlands has been attributed to
352 the dominance of exotic species (Lougheed et al., 2007; Larson et al., 2016), although the
353 role of exotics in extirpating natives is still controversial (Farnsworth and Ellis, 2001;
354 Lavoie et al., 2003). However, reduced plant richness in urban wetlands has also been
355 associated with the dominance of well-adapted species, regardless of their origin
356 (Houlahan and Findlay, 2004). Here, we found that the richness of native wetland and
357 native upland plants remained stable with urbanization intensity despite a fourfold increase
358 in exotic richness. Rather than excluding natives, exotics therefore have coexisted with
359 them in the highly urbanized swamps studied. Although previous studies have shown that
360 exotics can reach 50% cover in freshwater wetlands (Magge et al., 1999), the swamps
361 studied here were characterized by a relatively low exotic cover (less than 10% on average,
362 even in highly urbanized swamps), which most likely explains their non-detrimental effect
363 on native richness. The absence of an apparent impact of urbanization on native (wetland
364 and upland) species richness has also been reported for forested wetlands of New Jersey
365 (Ehrenfeld, 2005) and Northeastern Illinois (Chu and Molano-Flores, 2013), as well as in

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isolated wetlands of eastern Canada (Loiselle et al., 2020). Although the biotic differentiation observed here could relate to a differential role of non-invasive vs. invasive exotics, 10 of the 49 exotic species surveyed are considered invasive in the Quebec province (see <https://www.pub.enviroweb.gouv.qc.ca/SCC/Default.aspx>) which represents about 25% of the 43 plants listed as invasive, including some of the most problematic plants such as *Acer platanoides*, *Lythrum salicaria* or *Reynoutria japonica*. Further investigations should help to disentangle the relative contribution of these two exotic groups to biotic differentiation in response to urbanization.

Urbanization promotes swamp biotic differentiation

Species composition was more similar between low urbanized swamps than between highly urbanized ones, evidencing that urbanization intensity promotes biotic differentiation (increased beta diversity), rather than homogenization, of swamp plant communities. Although urbanization has been largely associated with biotic homogenization, this process has mostly been reported in large-scale studies investigating biodiversity changes between cities (McKinney, 2006; Qian and Ricklefs, 2006; La Sorte et al., 2007; Knapp and Wittig, 2012; Thomas, 2013). At a local scale (i.e., within cities), biotic differentiation along urbanization gradients has sometimes been evidenced (Kühn and Klotz, 2006; Aronson, et al., 2015; Bossu et al., 2014). In the New York metropolitan region, for example, the beta diversity of woody plant species in mesic forests was shown to increase with urbanization (Aronson et al., 2015). As well, similarity in plant composition among private gardens of the French Mediterranean decreased with the density of build-up areas (Bossu et al., 2014) and in Germany, urbanization intensity did not coincide with flora homogenization (Kühn and Klotz, 2006). Greater plant beta

diversity was also found in marshes located in developed landscapes of Michigan compared to marshes in forested landscapes (Lougheed et al., 2008), while urbanization was reported to promote higher plant diversity and turnover in riparian forests of eastern Canada (Brice et al., 2017).

Biotic differentiation of swamp vegetation along the studied urbanization gradient was associated with a differentiated response between species groups. Across all sites, native wetland and native upland plants primarily experienced species replacement (turnover), while changes in exotic beta diversity were mainly due to species enrichment. Furthermore, species replacement was more influential at high urbanization levels for native wetland species, while the enrichment of exotic species was higher at a low urbanization level. In fact, with intensifying urbanization, changes in native wetland species composition are amplified, but in an unpredictable way, contributing to an increase in beta diversity along the studied urbanization gradient. The higher stochasticity in the composition of native wetland plants with urbanization intensity most probably evidenced a higher variability in environmental conditions among highly urbanized swamps that allowed different species to establish from site to site. In addition, our results revealed that exotics contributed to differentiating exotic plant assemblages mainly at low urbanization levels. This finding concurs with previous studies showing that patchy colonization by exotic species promotes biotic differentiation of wetlands in disturbed landscapes (Lougheed et al., 2008) and of riparian forests at low urbanization levels (Brice et al., 2017). As McKinney (2004) has explained, such a differentiation process is likely when diverse exotic species occur over a given area, whereas homogenization is expected when a few exotics have a widespread distribution, although the historical degree of similarity among communities and the

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richness of the recipient communities can modulate this pattern (Olden and Poff, 2003). Exotics are even more likely to contribute in differentiating plant communities when the ratio exotic/native is low (McKinney, 2004). In our study, exotics only contributed from 5 to 19% of swamp species richness, and none seemed invasive in the studied systems. Still, they were clearly associated to highly urbanized swamps (Figure 4) and our results may only reflect the early stages of the successional trajectories of swamp plant communities after urbanization. An increase in exotic richness can initially promote differentiation, but be followed by a homogenization phase as exotics spread and eventually dominate less competitive species (Sax and Gaines, 2003). As previously shown, important time lags can occur in swamp ecosystems with delayed vegetation response to land use legacies such as former agricultural uses (Loiselle et al., 2020). Besides time lags in vegetation response to land-use changes, exotic introduction history can also influence vegetation shifts. In Europe for example, archaeophytes (i.e., exotics introduced before 1500) have been shown to contribute to the biotic homogenization of urban flora, while neophytes (i.e., recently introduced exotics) rather induce biotic differentiation (Lososová et al., 2012). Given that only neophytes are present in Quebec (Lavoie et al., 2012), the patchy colonization of exotics observed here that promotes biotic differentiation might partly result from recent plant introduction history and, hence, reflect early stages of exotic spread. Therefore, assessing plant diversity patterns along gradients of introduction history and landscape urbanization history is a promising research avenue to reveal such exotic colonization dynamics.

Anoxia stress release is associated with biotic differentiation

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3 436 The urbanization gradient studied here was clearly associated with smaller red mottles,
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5 437 higher drainage and decreasing cover of bryophytes, a species group highly sensitive to
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7 438 changes in light and hydrological regime (Ehrenfeld and Schneider, 1991; Nelson and
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9 439 Halpern, 2005; Goguen and Arp, 2017). Given that the studied swamps had a closed canopy
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11 440 (89% of shade on average), the observed decrease of bryophytes points to altered
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13 441 hydrological regimes as a major environmental change induced by urbanization. With
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15 442 urbanization, wetlands usually experience important changes in hydrological conditions
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17 443 due to the proliferation of impervious surfaces that modify surface water and groundwater
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19 444 flows (Azous and Horner, 1997). In general, urban wetlands are characterized by higher
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21 445 water level fluctuations, shorter periods of water retention, and decreased recharge from
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23 446 groundwater (in the case of groundwater-fed wetlands; Kentula et al., 2004; Barksdale et
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25 447 al., 2014), but these hydrological changes are often highly unpredictable (Ehrenfeld, 2003;
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27 448 Bhaskar et al., 2016). Depending on the specific local context, road development, grading
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29 449 alterations and the presence of rain collectors can disrupt flow patterns at the inlets or
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31 450 outlets of wetlands, thereby leading to increased flooding or drought (Ehrenfeld, 2000;
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33 451 Barksdale et al., 2014). By releasing or intensifying anoxia stress in particular, drier or
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35 452 wetter wetland conditions often create new ecological plant niches (MacDougall and
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37 453 Turkington, 2005; Mayfield et al., 2010), which may contribute to their high beta diversity.
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45 454 In addition to abiotic determinants, greater landscape heterogeneity in the surroundings
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47 455 of highly urbanized swamps (Appendix S1) may also have contributed to their higher beta
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49 456 diversity, due to a larger species pool. Gardens or roads are notably known to increase
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51 457 propagule pressure of exotic species (Gelbard and Belnap, 2003; Smith et al., 2006;
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53 458 Aronson et al., 2014; Li et al., 2014; Cubino et al., 2015) and thus could have played a key
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role in increasing swamp beta diversity in highly urbanized landscapes. Further investigation may be required to fully disentangle the relative contribution and potential interaction of environmental variability and species pool diversity in the biotic differentiation of swamp plant communities induced by urbanization.

CONCLUSIONS

Biotic differentiation, rather than homogenization, characterized the response of swamp plant communities to urbanization. Several mechanisms appeared to be associated with this differentiation process. In particular, the unpredictable effect of urbanization on hydrological regimes may have promoted a greater variability of ecological niches among highly urbanized swamps, while the higher heterogeneity of highly urbanized landscapes may have enabled more diverse species to colonize these newly created niches. Although exotic richness increased with urbanization intensity, these species did not dominate natives, whose richness was stable along the urbanization gradient due to high species turnover. Low light availability likely limited the spread of exotics and prevented them from dominating plant communities, even in highly urbanized swamps. Field experiments involving the manipulation of key environmental filters (e.g., Bourgeois et al., 2016) could help to confirm such causal relationships. In addition, regardless of the ecological mechanisms involved, the increase in exotic richness with urbanization documented here merits long-term swamp monitoring in order to evaluate potential exotic spread and adapt ecosystem management accordingly. Evaluating the effect of urbanization more broadly, across the entire drainage area of wetlands, or establishing a conservation buffer around urban wetlands, could also help to prevent hydrological changes that could be detrimental to plant communities. Altogether, this study deepens our understanding of the multifaceted

effects of urbanization on biodiversity, a key step toward the design of sustainable cities and the conservation of urban wetlands that support essential ecosystem services.

ACKNOWLEDGEMENTS

The authors would like to thank Gilles Ayotte, Geneviève Leblanc, Geoffrey Hall, Luc Brouillet as well as research assistants for their help during study design, data collection and plant identification.

DATA AVAILABILITY STATEMENT

Plant community and environmental data are archived on Zenodo (<http://doi.org/10.5281/zenodo.4099194>).

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802 SUPPORTING INFORMATION

803 Additional supporting information may be found online in the Supporting Information
804 section.

806 **Appendix S1.** Landscape composition for each urbanization level.

807 **Appendix S2.** Principal coordinate analysis of landscape composition.

808 **Appendix S3.** Plant species inventoried and associated groups

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For Review Only

TABLE 1. Partition of beta diversity (BD) into species replacement (i.e., species turnover, %) and richness difference (i.e., changes in the number of species, %) for a) the total pool of species and b, c, d) each plant species group at different levels of urbanization (low, moderate, high).

Urbanization level	BD total	Replacement (%)	Richness difference (%)
a) All species			
Low	0.16	60.7	39.3
Moderate	0.24	70.4	29.6
High	0.28	79.7	20.3
b) Native wetland			
Low	0.18	55.5	44.5
Moderate	0.25	61.4	38.6
High	0.27	72.3	27.7
c) Native upland			
Low	0.15	63.3	36.7
Moderate	0.24	70.6	29.4
High	0.30	63.7	36.3
d) Exotic			
Low	0.30	17.9	82.1
Moderate	0.38	43.9	56.1
High	0.35	47.2	52.8

FIGURE 1. Map of the 34 swamps sampled in Quebec City, Quebec, Canada, along a gradient of urbanization level (low, moderate, high).

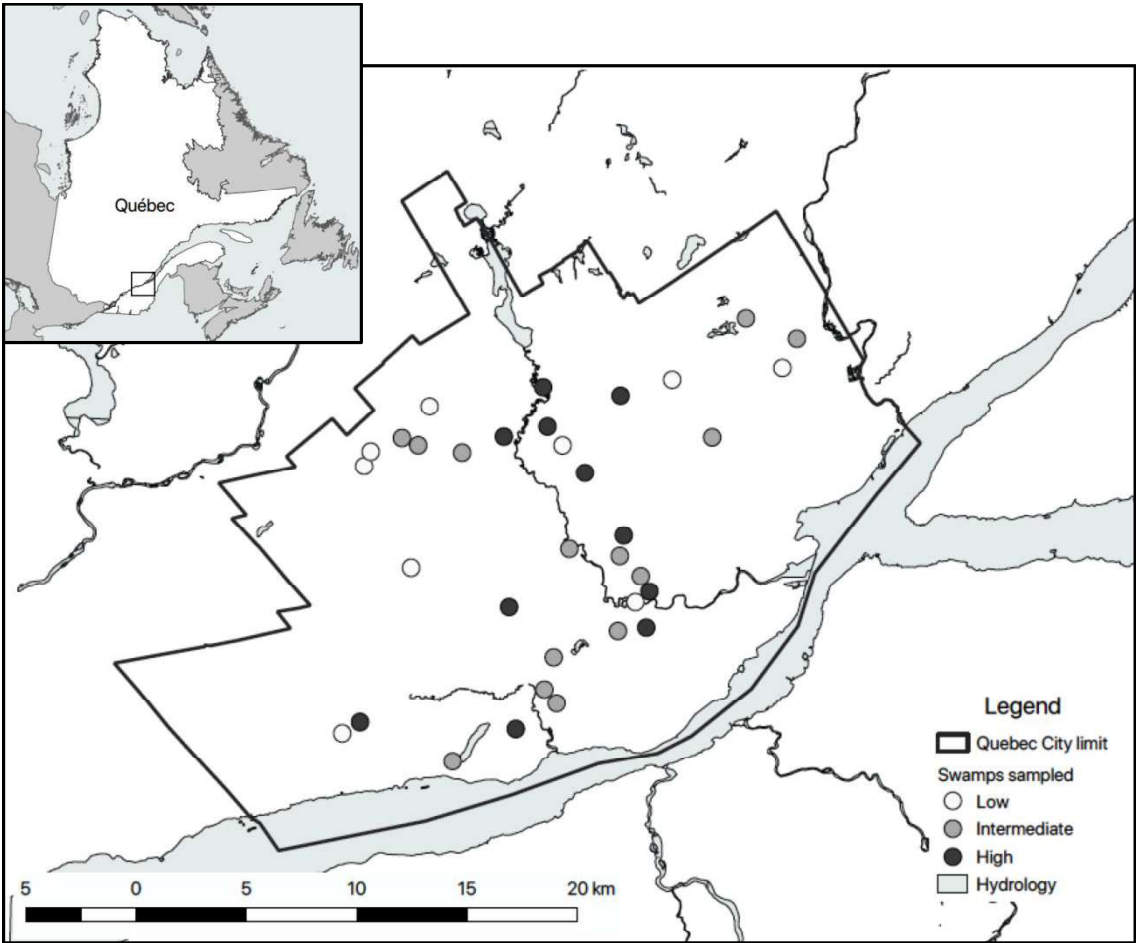


FIGURE 2. Differences in swamp species richness (mean \pm standard deviation) between urbanization levels and plant species groups. Uppercase letters indicate significant differences between levels of urbanization within a single plant group and lowercase letters differences between plant groups within a single level of urbanization, obtained by LSD.

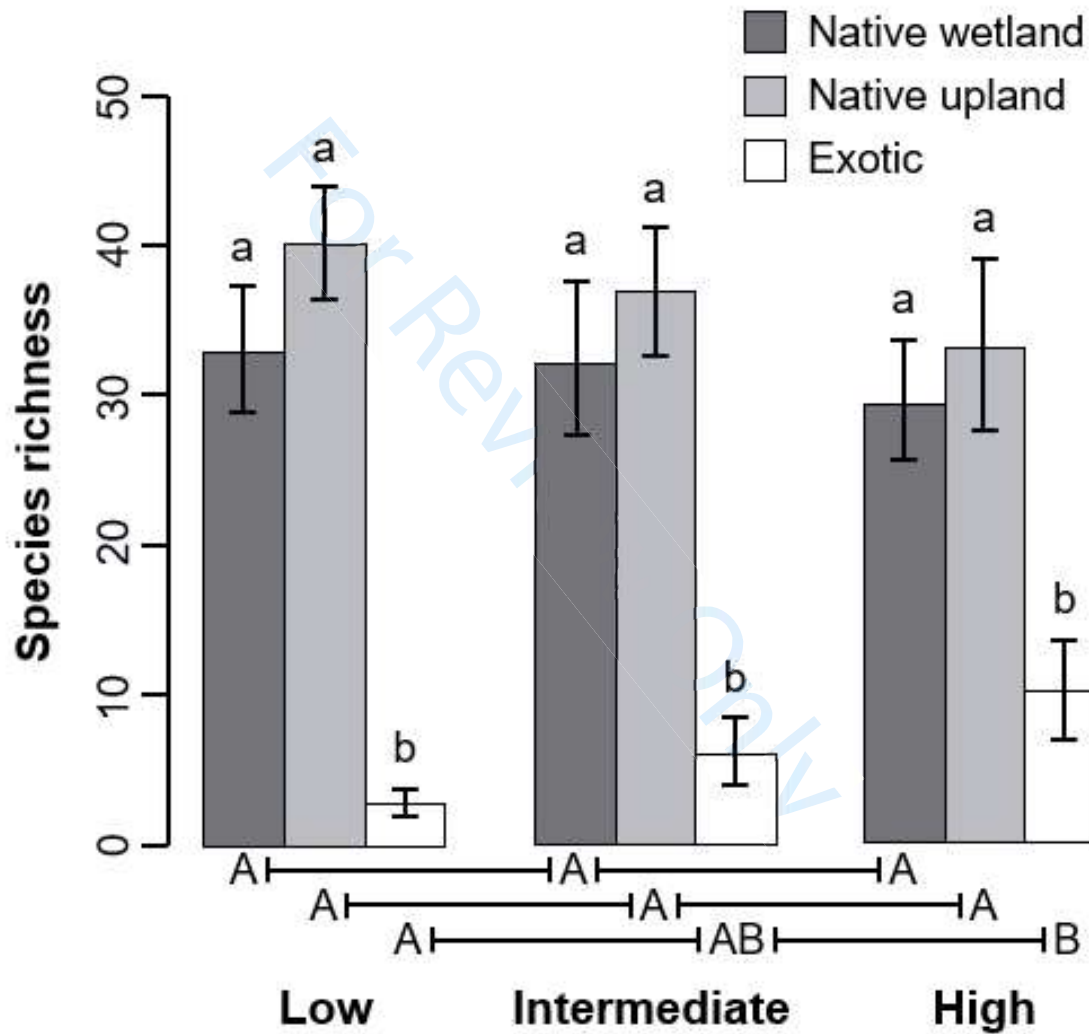


FIGURE 3. Response of swamp beta diversity to urbanization levels (calculated from land use composition in a 100 m radius buffer around each swamp; see Appendix S2). Taxonomic beta diversity was measured as the Euclidean distance of each site to their group centroid (based on Hellinger-transformed species importance value) as represented on the PCoA biplot with ellipses indicating standard deviation. Boxplots show the distribution of site-to-centroid distance (median and quartiles) for each urbanization level. Changes in dispersion around centroids reflect variations in beta diversity within urbanization level (boxplot), and changes of centroid position reflect variations in beta diversity between urbanization levels (biplot).

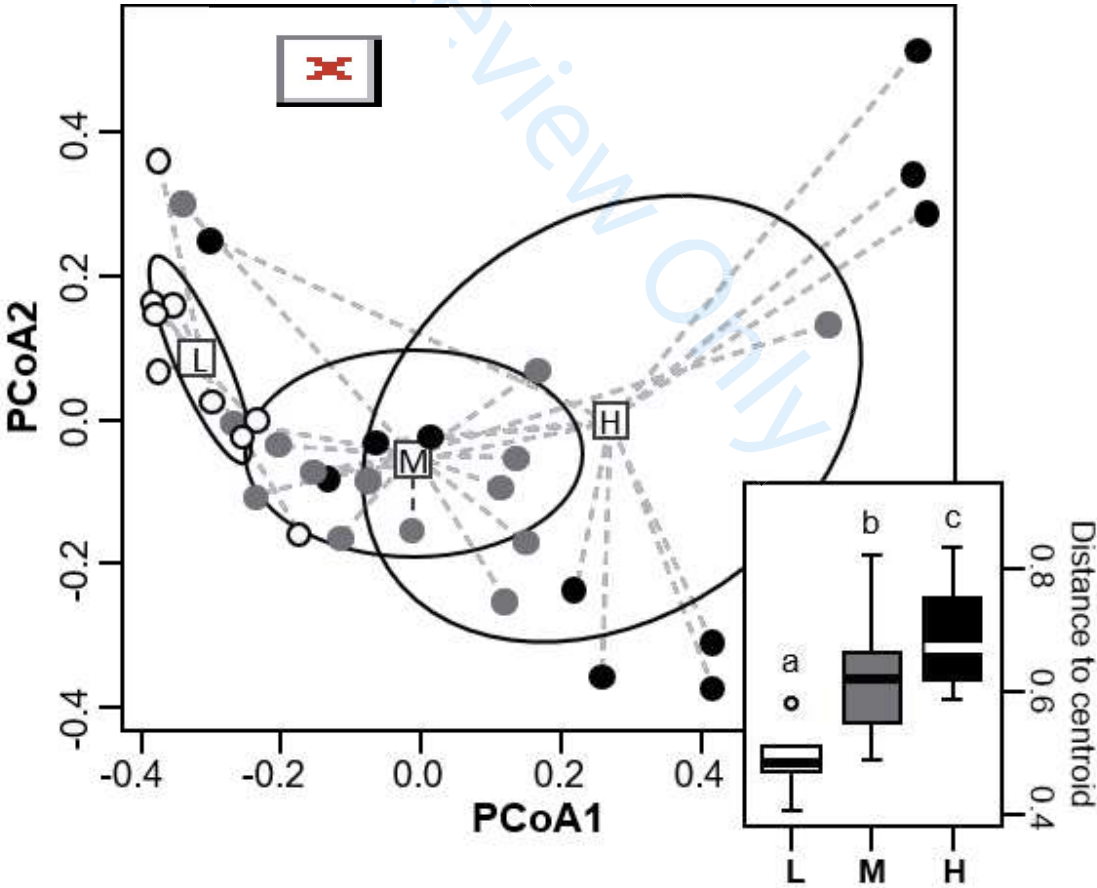
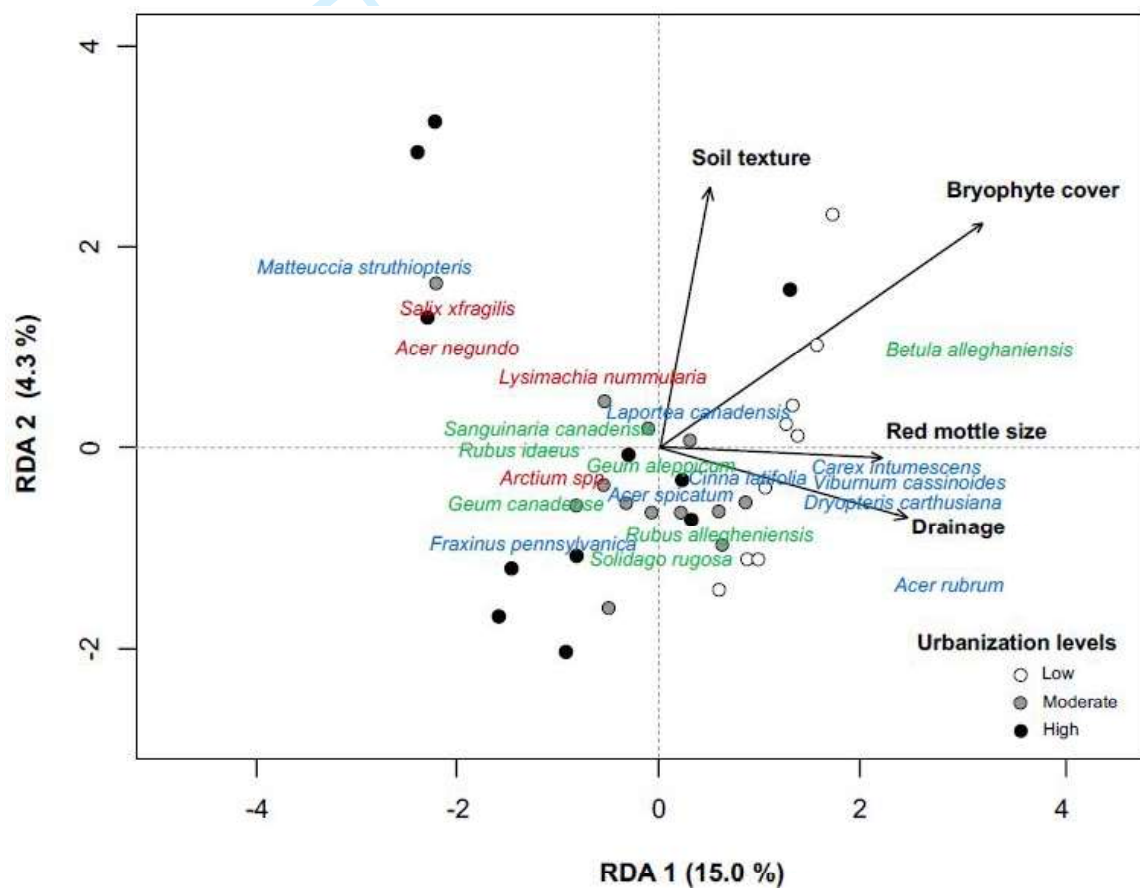


FIGURE 4. Effects of environmental variables (arrows) on the plant composition of swamps (dots), obtained by RDA. Only the four environmental variables (over nine measured) retained by stepwise selection are shown. XY coordinates of urbanization level centroids are (-0.92, 0.32) for high, (-0.05, -0.08) for intermediate, and (1.43, 0.04) for low urbanized swamps. The 20 species best fitted to the model are represented (blue: native wetland, green: native upland, red: exotic).



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Native plant turnover and limited exotic spread explain swamp biotic differentiation with urbanization

Short running title: Biotic differentiation of urban swamps

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Funding Information:
Organisme des Bassins Versants de la Capitale; Ville de Québec; Quebec Centre for Biodiversity
Science; Natural Sciences and Engineering Research Council of Canada (Discovery grants RGPIN-
2014-05367 to SP and RGPIN-2014-05663 to MP)

26 ABSTRACT

27 **Questions:** Does urbanization promote biotic differentiation or homogenization of swamp
28 plant communities? What is the contribution of natives and exotics to swamp response to
29 urbanization?

30 **Location:** Quebec City, Canada.

31 **Methods:** Plant communities of 34 swamps located in low, moderately or highly urbanized
32 landscapes were sampled, and species classified into three exclusive groups: native
33 wetland, native upland and exotic plants. Urbanization influence on the richness of each
34 plant group was assessed using mixed models. Between-site compositional similarities
35 were calculated to identify variations in beta diversity with urbanization level using tests
36 for homogeneity in multivariate dispersion. Beta diversity was further partitioned into
37 species replacement and richness difference for each plant group. Finally, the relationships
38 of ten environmental variables representing soil water saturation and microtopography with
39 plant assemblages were determined by Redundancy Analysis.

40 **Results:** Although the richness of exotics increased with urbanization intensity, revealing
41 increasing propagule pressure, it remained six to 27 times lower compared to natives,
42 whose richness remained stable with urbanization. On the other hand, beta diversity
43 increased with urbanization, with higher dissimilarities in species composition between
44 highly urbanized swamps than between low urbanized ones. This pattern resulted from
45 high species replacement among natives, while richness difference mainly contributed to
46 exotic beta diversity. Changes in plant assemblages were mostly associated with bryophyte
47 cover and soil drainage and red mottle size, suggesting that hydrological conditions likely
48 acted as a strong driver of swamp plant community response to urbanization.

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Conclusions: Swamp plant communities experienced biotic differentiation with increasing urbanization. This differentiation pattern likely was linked to the unpredictable effect of urbanization on hydrological regimes, which promoted high native turnover while limiting exotic spread. Long term monitoring is recommended to ensure that exotics do not outcompete natives through time. Designing sustainable cities requires a greater understanding of the multifaceted effect of urbanization on biodiversity.

KEYWORDS

Anoxia stress release; Assembly rules; Beta diversity; Biotic differentiation; Ecological constraints; Land use changes; Plant communities; Resistance to invasion; Species interactions; Swamps; Sustainable cities; Urbanization; Wetland conservation

INTRODUCTION

Land use transformation is a major driver of biodiversity change worldwide (Chapin et al., 2000; Thuiller, 2007). In human-altered landscapes, biological communities often experience biotic homogenization, i.e. a decrease in beta diversity (increased compositional similarity) across time or space (Olden et al., 2004, 2005; Gámez-Virúez et al., 2015; Gossner et al., 2016). Although changes in beta diversity can be related to both species replacement and richness difference (Legendre, 2014), reduced species richness has often been evidenced as a primary driver of biotic homogenization across a variety of taxonomic groups (Baeten et al., 2012; Baiser et al., 2012; Vellend et al., 2017; but see Hillebrand et al., 2018).

Urbanization, on the other hand, has been mostly associated with high species turnover among plant communities, and notably with a replacement of local plant specialists by generalists or exotics, leading to biotic homogenization (McKinney and Lockwood, 1999; Olden and Poff, 2003; McKinney, 2006; Olden and Rooney, 2006; La Sorte et al., 2014). Discrepancies in the relative contribution of exotics vs. native generalists to this homogenization process have nevertheless been reported, as previous studies have alternatively attributed declines in beta diversity to an increase of exotic species (Cadotte et al., 2017; Loiselle et al., 2020; Price et al. 2020) or to the spread of native species (Tabarelli et al., 2012; McCune and Vellend, 2013; Trentovani et al., 2013; Beauvais et al., 2016; Brice et al., 2017; Blouin et al., 2019). Furthermore, in some cases, urbanization has been shown to promote biotic differentiation (i.e., increased beta diversity; McKinney, 2008), depending on factors such as the size and composition of the initial species pool (Olden and Poff, 2003), the balance between native vs. non-native species and their residence time (Kühn and Klotz, 2006; Lososová et al., 2012, 2016) or the intensity and

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84 type of urbanization (Flynn et al., 2009; Allan et al., 2015; Newbold et al., 2015).
85 Urbanization is therefore a multifaceted process (Grimm et al., 2008) that can either
86 strengthen or release the ecological constraints shaping plant communities in urban
87 ecosystems (Pennington et al., 2010; Brice et al., 2017). Designing urban planning
88 guidelines and sustainable cities that reconcile human well-being and biodiversity
89 conservation hence requires a better understanding of plant community response to
90 urbanization.

91 Wetlands are receiving increasing attention due to the multiple ecosystem services they
92 provide (MEA, 2005; Maltby and Acreman, 2011), especially in urban areas where they
93 act as critical green infrastructures for flood control, water purification, aesthetics, cooling
94 effect and recreation (Taha, 1997; Bolund and Hunhammar, 1999; Lee and Scholz, 2006;
95 Sun et al., 2012; McLaughlin and Cohen, 2013). Empirical evidence shows that wetland
96 ecosystem services related to water quality are generally improved by higher plant
97 diversity, including increased nitrogen removal as well as reduced phosphorus loss and
98 methane efflux (Engelhardt and Ritchie, 2001; Bouchard et al., 2007; Brisson et al., 2020).
99 Yet, wetlands are generally highly vulnerable to invasion by exotics (Zedler and Kercher,
100 2004; Loiselle et al., 2020; Price et al., 2020) and wetland plants are more widely
101 distributed than upland ones (Santamaría, 2002; Ricklefs et al., 2008), which suggests that
102 these ecosystems are prone to biotic homogenization. Changes in ecological conditions due
103 to urbanization indeed generally promote the dispersal of exogenous species, either native
104 generalists or exotics, from surrounding heterogeneous urban lands to open wetlands
105 (Ehrenfeld and Schneider, 1991; Findlay and Bourdages, 2000; Ehrenfeld, 2008; Cutway
106 and Ehrenfeld, 2009). Wetland types might differ in their response to urbanization,

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3 107 however, based on their natural stress regimes. Some previous studies have indeed
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5 108 evidenced biotic differentiation of wetland communities following environmental changes
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8 109 (Ehrenfeld and Schneider, 1991; Favreau et al., 2019).
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10 110 Forested wetlands (i.e., wetlands characterized by the presence of trees) which include
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12 111 swamps or riparian forests for example are characterized by harsh ecological constraints
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14 112 that strongly filter the establishment of plant species (Battaglia et al., 2000; Lin et al.,
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16 113 2004). Compared to open wetlands or mesic forests, in forested wetlands, low light
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18 114 availability combines with periodic anaerobic soil conditions during the growing season to
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20 115 simultaneously shape plant assemblages (Conner et al., 1981; Mitsch and Gosselink, 2000;
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22 116 Colmer and Voeselek, 2009). Given these intense ecological constraints filtering out
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24 117 poorly adapted species, alterations of natural hydrological regimes by urban sprawl could
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26 118 promote the establishment of new species (Azous and Horner, 1997; Groffman et al., 2003;
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28 119 Kentula et al., 2004; Pennington et al., 2010), thereby leading to the biotic differentiation
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30 120 of forested wetlands. Such a pattern was previously evidenced in riparian forests, where
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32 121 urbanization has been associated with a decrease of flooding period and duration, a stress
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34 122 release process that led to a greater variation in species composition across sites (Brice et
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36 123 al., 2017). Despite recent investigations (Loiselle et al., 2020), swamp vegetation response
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38 124 to urbanization still remains to be explored to generalize the impact of urbanization on
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40 125 forested wetland flora.
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46 126 In this study, we examine how plant species richness and beta diversity of swamps vary
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48 127 with urbanization in the Quebec City metropolitan area, Canada. More precisely, we
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50 128 addressed the following questions: (i) Is urbanization associated with biotic
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52 129 homogenization or differentiation in swamp flora? (ii) How does urbanization affect
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species composition of swamps? (iii) What is the specific response of wetland and upland species as well as exotics to an urbanization gradient? Because we expected a variable intensity of stress release after urbanization, we hypothesized that it generates biotic differentiation. We predicted greater beta diversity and more divergent species composition among swamps surrounded by urbanized landscapes compared to less disturbed ones. We also anticipated that urbanization would foster upland and exotic species richness.

METHODS

Study area

The study was conducted in the Quebec City metropolitan area (46°48'52"N 71°12'28"W; hereafter referred to as Quebec City), the seventh most populous urban area in Canada (569 717 inhabitants; Statistics Canada, 2016). Across this 548 km² territory, 50% of land use consists of remnants of natural habitats, 39% of built-up areas and 11% of agricultural lands. Built-up areas, which have increased by 79% in the last 35 years (Nazarnia et al., 2016), correspond to residential (24%), industrial/commercial (5.5%), road networks and mining areas (5%), and vacant lots (4.5%; Cimon-Morin and Poulin, 2018). Yet, nearly 4 921 ha of wetlands (8% of the landscape) are still present across Quebec City metropolitan area, including 2 394 ha of swamps (Beaulieu et al., 2014)

Site selection

Sites were selected based on a map of Quebec City that situates wetlands larger than 0.3 ha according to seven classes identified by photointerpretation (bog, fen, forested peatland, marsh, swamp, wet meadow and shallow water). Among them, 102 swamps were retained according to the following criteria: 1) an area ranging from 1 to 6 ha, to avoid

biases due to size effect; 2) a distance of at least 300 meters between sites; 3) a balance between riparian and isolated swamps (i.e., not directly connected to a permanent watercourse); and 4) a surrounding landscape not dominated by agricultural fields. These 102 swamps were then visited, to exclude bush-dominated, degraded and misclassified swamps (such as forested peatlands). Thirty-four swamps met all criteria. For each swamp, we then characterized landscape composition in a 100 m buffer zone using nine land use categories (Appendix S1) obtained from photointerpretation in QGIS 3.0.0 (QGIS Development Team, 2018). In the surrounding of the sampled swamps, urbanization had mostly taken place from the 1960s to the 1980s (Raimbault, 2019). Land use composition was then used to group swamps according to three levels of landscape urbanization based on the optimum of a non-hierarchical k-means clustering (Legendre and Legendre, 2012). This clustering approach allowed us to account for different land-use classes simultaneously, and therefore better represent the complexity of urbanization process which is hardly synthesized by a single continuous landscape variable (Grimm et al., 2008). Nine low, 14 intermediate and 11 highly urbanized swamps were identified (i.e., swamps respectively located in surrounding landscapes with low, intermediate and high urbanization levels). These urbanization levels increased with decreasing cover of forests and wetlands in the landscape surrounding each site (87% cover at low urbanization level, 57% at intermediate urbanization level and 25% at high urbanization level), and with increasing cover of impervious surfaces including residential and commercial areas, industrial sites, highways and secondary roads (8% cover at low urbanization level, 23% at intermediate urbanization level and 50% at high urbanization level; Appendix S1-2).

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Vegetation surveys

Vascular plant communities in the 34 selected swamps were sampled during the summer of 2016 (end of June-beginning of September). Two to five sampling plots each measuring 400-m² (20 × 20 m) were established per swamp, depending on its size, in order to uniformize sampling intensity per swamp area, for a total of 92 plots (i.e., 25, 38 and 29 plots sampled in swamps respectively corresponding to low, intermediate and high urbanization level) . These plots were randomly positioned within each swamp while respecting a 30-meter distance between plots to limit spatial autocorrelation and a 25-meter distance from the edge to avoid edge effect (Alignier et al., 2014). In each plot, the cover of each plant species was visually estimated using seven classes: <1%, 1–5%, 6–10%, 11–25%, 26–50%, 51–75%, 76–100%. Nomenclature follows VASCAN (Brouillet et al., 2019). Plant cover was averaged at the site scale for analyses. A preliminary analysis detected no significant correlation between swamp area and species richness ($r = -0.06$; $P = 0.74$), nor between sampling area and species richness ($r = 0.18$; $P = 0.31$), indicating that the sampling method did not induce species-area bias.

Species groups

To better determine the impacts of urbanization level on plant communities, all inventoried species were classified into three mutually exclusive plant groups: native wetland, native upland and exotic plants (Appendix S3). We first distinguished between species based on their origin (native or exotic to the Quebec province) following VASCAN (Brouillet et al., 2019). Then, all native species were sorted based on their habitat preference (wetland or upland species) following Bazoge et al. (2014) and the PLANT

database (USDA, 2019). “Obligate” and “facultative wetland” were classified as wetland species (i.e., specialist plants preferentially occurring in wetlands), and “facultative,” “facultative upland” and “upland” as upland species (i.e., generalist plants equally occurring in wetland and terrestrial habitats as well as plants occurring preferentially in terrestrial habitats). Only two species, *Lythrum salicaria* and *Lysimachia nummularia*, were both exotics and wetland species, but neither was frequent (present in 15% and 9% of the sites, respectively) or abundant (<1% of cover in each site for both species) and they were thus classified as exotics exclusively.

Environmental variables

Ten environmental variables were evaluated in each plot. Soil texture and drainage were evaluated using a semi-quantitative scales ranging from 1 (sand) to 12 (clay) for texture and from 0 (excessive) to 6 (very bad) for drainage (Saucier, 1994). The size (1: < 5 mm; 2: 5-15 mm; 3: > 15 mm), depth (cm) and abundance (1: <2%; 2: 2-20%; 3: > 20%) of soil mottles as well as the thickness of humus or peat (cm) were quantified as proxies of water table depth and near-surface water saturation, given that humus degrades more rapidly in aerobic conditions (Zoltai and Vitt, 1995; Mitsch and Gosselink, 2015). No significant correlation between soil mottle abundance and sampling date was detected ($r = 0.25$; $P = 0.16$), suggesting that our sampling design did not induce biases in soil conditions, and evidencing that soil mottles are relatively stable through time as previously reported (Vepraskas and Craft, 2016). Similarly, no significant correlation was detected between soil type (organic vs. non-organic) and soil mottle abundance ($r = -0.27$; $P = 0.12$). Microtopographic variation was assessed using a four-class index based on the elevation

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223 difference between pits and mounds (0: flat, 1: <0.5 m, 2: 0.5-1 m, 3: more than 1 m of
224 amplitude). The cover of bryophytes (largely dominated by *Sphagnum* spp.), vernal pools
225 and bare ground surfaces was additionally estimated using the same classes as for plant
226 cover to approximate hydric conditions at soil surface (Goguen and Arp, 2017).

227
228 **Statistical analysis**

229 Changes in plant richness per site between levels of urbanization intensity were first
230 evaluated using a linear mixed model including urbanization levels (low, intermediate,
231 high) and species groups (native wetland, native upland, exotic) as fixed effects. As a
232 significant interaction between urbanization level and species group was detected, the
233 individual effect of each factor was tested for each level of the other factor using least
234 square means comparisons. Richness values were square root-transformed to meet residual
235 normality and variance homogeneity, and back-transformed for result presentation.

236 Second, changes in swamp beta diversity between levels of urbanization intensity were
237 investigated using tests of homogeneity for multivariate dispersions (Anderson et al., 2006)
238 to reveal biotic homogenization or differentiation processes. This method uses
239 permutations to compare groups of sites based on the average distance between sites and
240 their associated group centroid in an ordination space, as a measure of beta diversity. For
241 this, the cover of each species in the site-by-species matrix was first transformed into its
242 importance value (IV; Barbour et al., 1987), to account for differences in sampling effort
243 between sites (i.e., 2 to 5 plots sampled per swamp). The IV of a species corresponded
244 more precisely to the mean of its relative frequency (number of plots per swamp in which
245 the species occurred relative to the total number of occurrences of all species) and relative
246 dominance (cover of the species per swamp relative to the total cover of all species, using

the median of the cover classes). Species IV therefore allow to take into account differences in sampling intensity by rescaling species cover according to the number of plots surveyed per swamp through the use of species relative frequency. A site-by-site Euclidean distance matrix based on Hellinger transformation (Legendre and Gallagher, 2001) was then computed for calculating the centroids of low, moderately and highly urbanized swamps. Hellinger transformation (which corresponds to the square root of the cover/frequency of a species i at site j divided by the sum of species cover/frequency at site j) is advised prior to compute Euclidean distance-based ordinations such as PCA, PCoA or RDA as it accurately preserves Euclidean distances among sites (Legendre and Gallagher, 2001). Finally, the distances of each site to its associated group centroid were subjected to an ANOVA with 9,999 permutations to determine whether beta diversity differed within urbanization levels. To reveal differences in species composition between urbanization levels, we additionally compared the three centroid locations using a PERMANOVA (9,999 permutations; Anderson, 2001) interpreted from a PCoA biplot (Anderson and Walsh, 2013). Given that changes in beta diversity can relate to both species turnover and richness difference, these two mechanisms were further investigated for a thorough understanding of the drivers of biotic homogenization or differentiation. We partitioned beta diversity into these two components using Sørensen dissimilarity on presence-absence data (Legendre, 2014; Borcard et al., 2018) given we were interested in richness difference rather than abundance as a proxy of ecological niche diversity and competitive interactions potentially leading to species exclusion. For this, four partitionings were conducted for each urbanization level, one for the entire pool of species and one for each plant ecological group (native wetland, native upland, and exotic species).

Finally, we evaluated the potential role of environmental variables associated with changes in swamp community composition using a Redundancy Analysis (RDA) on Hellinger-transformed species IV (Legendre and Gallagher, 2001). Explanatory variables were subjected to a stepwise selection to identify the most parsimonious model explaining between-site differences. Both species and site scores were then displayed on an RDA biplot with significant environmental vectors to visualize species-environment relationships.

As we focussed here on differences in species richness or community composition between sites, all analyses were conducted at the site scale by calculating for each species its mean cover among plots surveyed in the same swamp. Analyses were performed on R v. 3.5.1 (R Core Team, 2019) using the *vegan* (Oksanen et al., 2016; non-hierarchical clustering, multivariate dispersion and variable transformation), *adespatial* (Dray et al., 2017; beta diversity partitioning), *nlme* (Pinheiro et al., 2018; linear mixed models), and *lsmeans* (Lenth, 2016; multiple comparisons) packages.

RESULTS

Overall, 278 plant taxa were identified in the 34 sampled swamps, corresponding to 110 native wetland, 119 native upland and 49 exotic taxa (Appendix S3). The most frequent species (present in > 90% of the swamps) were *Acer rubrum* and *Dryopteris carthusiana*, both native wetland species. The most frequent native upland species were *Athyrium filix-femina* (89% of sites), *Abies balsamea* (83%) and *Amelanchier arborea* (83%) while *Epipactis helleborine* (40%) and *Ranunculus repens* (29%) were the most frequent exotic species.

294 Urbanization effect on swamp plant richness

295 Urbanization effect on species richness differed between species groups (significant
 296 urbanization level x species group interaction: $F = 5.51$, $P = 0.0007$ ~~Table 4~~). While the
 297 richness of native wetland and native upland plants remained stable and similar to each
 298 other between urbanization levels, exotics richness increased with urbanization intensity,
 299 with four times more species in highly urbanized swamps compared to low urbanized ones
 300 (Figure 2). However, exotics were 27, 11 and 6 times less diversified than natives (both
 301 wetland and upland species summed together) at low, moderate and high levels of
 302 urbanization, respectively (Figure 2).

304 Urbanization effect on swamp beta diversity

305 Beta diversity differed between the three urbanization levels ($F = 20.7$; $P = 0.0001$),
 306 increasing from low to highly urbanized swamps (Figure 3). The highest site dispersion
 307 (indicated by ellipse size on Figure 3) and median distance to centroid (Figure 3) were
 308 indeed observed in highly urbanized swamps. Plant composition also differed significantly
 309 between urbanization levels, as the test comparing centroid locations was significant
 310 ($F = 4.3$; $P < 0.0001$; Figure 3). The even spacing between centroids between urbanization
 311 levels further suggests that mean species composition progressively changed with
 312 urbanization (Figure 3).

313 Different processes were involved in the response of plant species groups to
 314 urbanization levels. For the entire species pool (Table 12a) as well as for native wetland
 315 (Table 12b) and native upland plants (Table 12c), beta diversity increased from a low to a
 316 high level of urbanization primarily due to species replacement. The contribution of species
 317 replacement to beta diversity was especially important at a high level of urbanization for

both native wetland species and the entire species pool, and at a moderate level of urbanization for native upland ones. For exotic species, beta diversity was higher in moderately and highly urbanized swamps. However, richness difference was the main mechanism contributing to exotic beta diversity, especially at low urbanization, where it was four times more influential than species replacement (Table 12d).

Environmental conditions associated with urbanization levels

Distinct environmental conditions characterized swamps along a general gradient which also reflected urbanization levels, along the first RDA axis (explaining 15% of species composition variation over 25% of total variation explained; $p_{RDA1} = 0.001$; $p_{RDA2} = 0.164$; Figure 4). From low to highly urbanized swamps, bryophyte cover decreased, soils became less hydromorphic (smaller red mottles) and drainage increased. Low urbanized swamps were characterized by both native wetland (*Acer rubrum*, *Carex intumescens*, *Dryopteris carthusiana* and *Viburnum cassinoides*) and native upland (*Betula alleghaniensis*) species. In moderately and highly urbanized swamps, different native wetland (*Fraxinus pennsylvanica* and *Matteuccia struthiopteris*) and native upland (*Geum canadense*, *Rubus idaeus* and *Sanguinaria canadensis*) plants occurred. Finally, moderately and highly urbanized swamps were mostly distinguished by the presence of exotic or upland species such as *Acer negundo*, *Arctium* spp., *Lysimachia nummularia* and *Salix xfragilis*.

DISCUSSION

This study reveals that urbanization can foster biotic differentiation of swamp plant communities by promoting the co-occurrence of native and exotic species without leading to the dominance of the latter. Beta diversity indeed increased from low to highly urbanized

342 swamps due to species replacement of native wetland and upland plants in conjunction
343 with an increase in exotic richness (which, however, remained six times lower than native
344 richness in highly urbanized swamps). The inconsistent effect of urbanization on swamp
345 conditions, notably on soil water saturation, likely explains this differentiation pattern.

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347 **High resistance to exotics characterizes urban swamps**

348 Intensifying human disturbances in the landscape surrounding wetlands have often been
349 shown to induce plant species loss (Ehrenfeld, 2000; Faulkner, 2004; Kercher and Zedler,
350 2004; Moffatt et al., 2004; Houlahan et al., 2006; Loughheed et al., 2008; Noble and Hassall,
351 2015). In many cases, this lower species richness in urban wetlands has been attributed to
352 the dominance of exotic species (Loughheed et al., 2007; Larson et al., 2016), although the
353 role of exotics in extirpating natives is still controversial (Farnsworth and Ellis, 2001;
354 Lavoie et al., 2003). However, reduced plant richness in urban wetlands has also been
355 associated with the dominance of well-adapted species, regardless of their origin
356 (Houlahan and Findlay, 2004). Here, we found that the richness of native wetland and
357 native upland plants remained stable with urbanization intensity despite a fourfold increase
358 in exotic richness. Rather than excluding natives, exotics therefore have coexisted with
359 them in the highly urbanized swamps studied. Although previous studies have shown that
360 exotics can reach 50% cover in freshwater wetlands (Magge et al., 1999), the swamps
361 studied here were characterized by a relatively low exotic cover (less than 10% on average,
362 even in highly urbanized swamps), which most likely explains their non-detrimental effect
363 on native richness. The absence of an apparent impact of urbanization on native (wetland
364 and upland) species richness has also been reported for forested wetlands of New Jersey
365 (Ehrenfeld, 2005) and Northeastern Illinois (Chu and Molano-Flores, 2013), as well as in

isolated wetlands of eastern Canada (Loiselle et al., 2020). Although the biotic differentiation observed here could relate to a differential role of non-invasive vs. invasive exotics, 10 of the 49 exotic species surveyed are considered invasive in the Quebec province (see <https://www.pub.enviroweb.gouv.qc.ca/SCC/Default.aspx>) which represents about 25% of the 43 plants listed as invasive-, including some of the most problematic plants such as *Acer platanoides*, *Lythrum salicaria* or *Reynoutria japonica*. Further investigations should help to disentangle the relative contribution of these two exotic groups to biotic differentiation in response to urbanization.

Urbanization promotes swamp biotic differentiation

Species composition was more similar between low urbanized swamps than between highly urbanized ones, evidencing that urbanization intensity promotes biotic differentiation (increased beta diversity), rather than homogenization, of swamp plant communities. Although urbanization has been largely associated with biotic homogenization, this process has mostly been reported in large-scale studies investigating biodiversity changes between cities (McKinney, 2006; Qian and Ricklefs, 2006; La Sorte et al., 2007; Knapp and Wittig, 2012; Thomas, 2013). At a local scale (i.e., within cities), biotic differentiation along urbanization gradients has sometimes been evidenced (Kühn and Klotz, 2006; Aronson, et al., 2015; Bossu et al., 2014). In the New York metropolitan region, for example, the beta diversity of woody plant species in mesic forests was shown to increase with urbanization (Aronson et al., 2015). As well, similarity in plant composition among private gardens of the French Mediterranean decreased with the density of build-up areas (Bossu et al., 2014) and in Germany, urbanization intensity did not coincide with flora homogenization (Kühn and Klotz, 2006). Greater plant beta

diversity was also found in marshes located in developed landscapes of Michigan compared to marshes in forested landscapes (Lougheed et al., 2008), while urbanization was reported to promote higher plant diversity and turnover in riparian forests of eastern Canada (Brice et al., 2017).

Biotic differentiation of swamp vegetation along the studied urbanization gradient was associated with a differentiated response between species groups. Across all sites, native wetland and native upland plants primarily experienced species replacement (turnover), while changes in exotic beta diversity were mainly due to species enrichment. Furthermore, species replacement was more influential at high urbanization levels for native wetland species, while the enrichment of exotic species was higher at a low urbanization level. In fact, with intensifying urbanization, changes in native wetland species composition are amplified, but in an unpredictable way, contributing to an increase in beta diversity along the studied urbanization gradient. The higher stochasticity in the composition of native wetland plants with urbanization intensity most probably evidenced a higher variability in environmental conditions among highly urbanized swamps that allowed different species to establish from site to site. In addition, our results revealed that exotics contributed to differentiating exotic plant assemblages mainly at low urbanization levels. This finding concurs with previous studies showing that patchy colonization by exotic species promotes biotic differentiation of wetlands in disturbed landscapes (Lougheed et al., 2008) and of riparian forests at low urbanization levels (Brice et al., 2017). As McKinney (2004) has explained, such a differentiation process is likely when diverse exotic species occur over a given area, whereas homogenization is expected when a few exotics have a widespread distribution, although the historical degree of similarity among communities and the

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3 413 richness of the recipient communities can modulate this pattern (Olden and Poff, 2003).
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5 414 Exotics are even more likely to contribute in differentiating plant communities when the
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7 415 ratio exotic/native is low (McKinney, 2004). In our study, exotics only contributed from 5
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9 416 to 19% of swamp species richness, and none seemed invasive in the studied systems. Still,
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11 417 they were clearly associated to highly urbanized swamps (Figure 4) and our results may
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13 418 only reflect the early stages of the successional trajectories of swamp plant communities
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15 419 after urbanization. An increase in exotic richness can initially promote differentiation, but
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17 420 be followed by a homogenization phase as exotics spread and eventually dominate less
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19 421 competitive species (Sax and Gaines, 2003). As previously shown, important time lags
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21 422 can occur in swamp ecosystems with delayed vegetation response to land use legacies such
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23 423 as former agricultural uses (Loiselle et al., 2020). Besides time lags in vegetation response
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25 424 to land-use changes, exotic introduction history can also influence vegetation shifts. In
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27 425 Europe for example, archaeophytes (i.e., exotics introduced before 1500) have been shown
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29 426 to contribute to the biotic homogenization of urban flora, while neophytes (i.e., recently
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31 427 introduced exotics) rather induce biotic differentiation (Lososová et al., 2012). Given that
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33 428 only neophytes are present in Quebec (Lavoie et al., 2012), the patchy colonization of
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35 429 exotics observed here that promotes biotic differentiation might partly result from recent
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37 430 plant introduction history and, hence, reflect early stages of exotic spread. Therefore,
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39 431 assessing plant diversity patterns along gradients of introduction history and landscape
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41 432 urbanization history is a promising research avenue to reveal such exotic colonization
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54 435 **Anoxia stress release is associated with biotic differentiation**
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3 436 The urbanization gradient studied here was clearly associated with smaller red mottles,
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5 437 higher drainage and decreasing cover of bryophytes, a species group highly sensitive to
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7 438 changes in light and hydrological regime (Ehrenfeld and Schneider, 1991; Nelson and
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9 439 Halpern, 2005; Goguen and Arp, 2017). Given that the studied swamps had a closed canopy
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11 440 (89% of shade on average), the observed decrease of bryophytes points to altered
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13 441 hydrological regimes as a major environmental change induced by urbanization. With
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15 442 urbanization, wetlands usually experience important changes in hydrological conditions
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17 443 due to the proliferation of impervious surfaces that modify surface water and groundwater
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19 444 flows (Azous and Horner, 1997). In general, urban wetlands are characterized by higher
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21 445 water level fluctuations, shorter periods of water retention, and decreased recharge from
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23 446 groundwater (in the case of groundwater-fed wetlands; Kentula et al., 2004; Barksdale et
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25 447 al., 2014), but these hydrological changes are often highly unpredictable (Ehrenfeld, 2003;
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27 448 Bhaskar et al., 2016). Depending on the specific local context, road development, grading
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29 449 alterations and the presence of rain collectors can disrupt flow patterns at the inlets or
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31 450 outlets of wetlands, thereby leading to increased flooding or drought (Ehrenfeld, 2000;
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33 451 Barksdale et al., 2014). By releasing or intensifying anoxia stress in particular, drier or
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35 452 wetter wetland conditions often create new ecological plant niches (MacDougall and
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37 453 Turkington, 2005; Mayfield et al., 2010), which may contribute to their high beta diversity.
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45 454 In addition to abiotic determinants, greater landscape heterogeneity in the surroundings
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47 455 of highly urbanized swamps (Appendix S1) may also have contributed to their higher beta
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49 456 diversity, due to a larger species pool. Gardens or roads are notably known to increase
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51 457 propagule pressure of exotic species (Gelbard and Belnap, 2003; Smith et al., 2006;
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53 458 Aronson et al., 2014; Li et al., 2014; Cubino et al., 2015) and thus could have played a key
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role in increasing swamp beta diversity in highly urbanized landscapes. Further investigation may be required to fully disentangle the relative contribution and potential interaction of environmental variability and species pool diversity in the biotic differentiation of swamp plant communities induced by urbanization.

CONCLUSIONS

Biotic differentiation, rather than homogenization, characterized the response of swamp plant communities to urbanization. Several mechanisms appeared to be associated with this differentiation process. In particular, the unpredictable effect of urbanization on hydrological regimes may have promoted a greater variability of ecological niches among highly urbanized swamps, while the higher heterogeneity of highly urbanized landscapes may have enabled more diverse species to colonize these newly created niches. Although exotic richness increased with urbanization intensity, these species did not dominate natives, whose richness was stable along the urbanization gradient due to high species turnover. Low light availability likely limited the spread of exotics and prevented them from dominating plant communities, even in highly urbanized swamps. Field experiments involving the manipulation of key environmental filters (e.g., Bourgeois et al., 2016) could help to confirm such causal relationships. In addition, regardless of the ecological mechanisms involved, the increase in exotic richness with urbanization documented here merits long-term swamp monitoring in order to evaluate potential exotic spread and adapt ecosystem management accordingly. Evaluating the effect of urbanization more broadly, across the entire drainage area of wetlands, or establishing a conservation buffer around urban wetlands, could also help to prevent hydrological changes that could be detrimental to plant communities. Altogether, this study deepens our understanding of the multifaceted

effects of urbanization on biodiversity, a key step toward the design of sustainable cities and the conservation of urban wetlands that support essential ecosystem services.

ACKNOWLEDGEMENTS

The authors would like to thank Gilles Ayotte, Geneviève Leblanc, Geoffrey Hall, Luc Brouillet as well as research assistants for their help during study design, data collection and plant identification.

DATA AVAILABILITY STATEMENT

Plant community and environmental data are archived on Zenodo (<http://doi.org/10.5281/zenodo.4099194>).

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802 SUPPORTING INFORMATION

803 Additional supporting information may be found online in the Supporting Information
804 section.

806 **Appendix S1.** Landscape composition for each urbanization level.

807 **Appendix S2.** Principal coordinate analysis of landscape composition.

808 **Appendix S3.** Plant species inventoried and associated groups

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TABLE 1. Effects of urbanization level (low, moderate, high) and plant species group (native wetland, native upland, exotic) on species richness obtained by a linear mixed model. Significant p-values are indicated in bold.

	<i>DF</i>	<i>F</i>	<i>p</i>
Urbanization level	2	0.32	0.7285
Species group	2	216.16	<0.0001
Urbanization level x Species group	4	5.51	0.0007

TABLE 12. Partition of beta diversity (BD) into species replacement (i.e., species turnover, %) and richness difference (i.e., changes in the number of species, %) for a) the total pool of species and b, c, d) each plant species group at different levels of urbanization (low, moderate, high).

Urbanization level	BD total	Replacement (%)	Richness difference (%)
a) All species			
Low	0.16	60.7	39.3
Moderate	0.24	70.4	29.6
High	0.28	79.7	20.3
b) Native wetland			
Low	0.18	55.5	44.5
Moderate	0.25	61.4	38.6
High	0.27	72.3	27.7
c) Native upland			
Low	0.15	63.3	36.7
Moderate	0.24	70.6	29.4
High	0.30	63.7	36.3
d) Exotic			
Low	0.30	17.9	82.1
Moderate	0.38	43.9	56.1
High	0.35	47.2	52.8

FIGURE 1. Map of the 34 swamps sampled in Quebec City, Quebec, Canada, along a gradient of urbanization level (low, moderate, high).

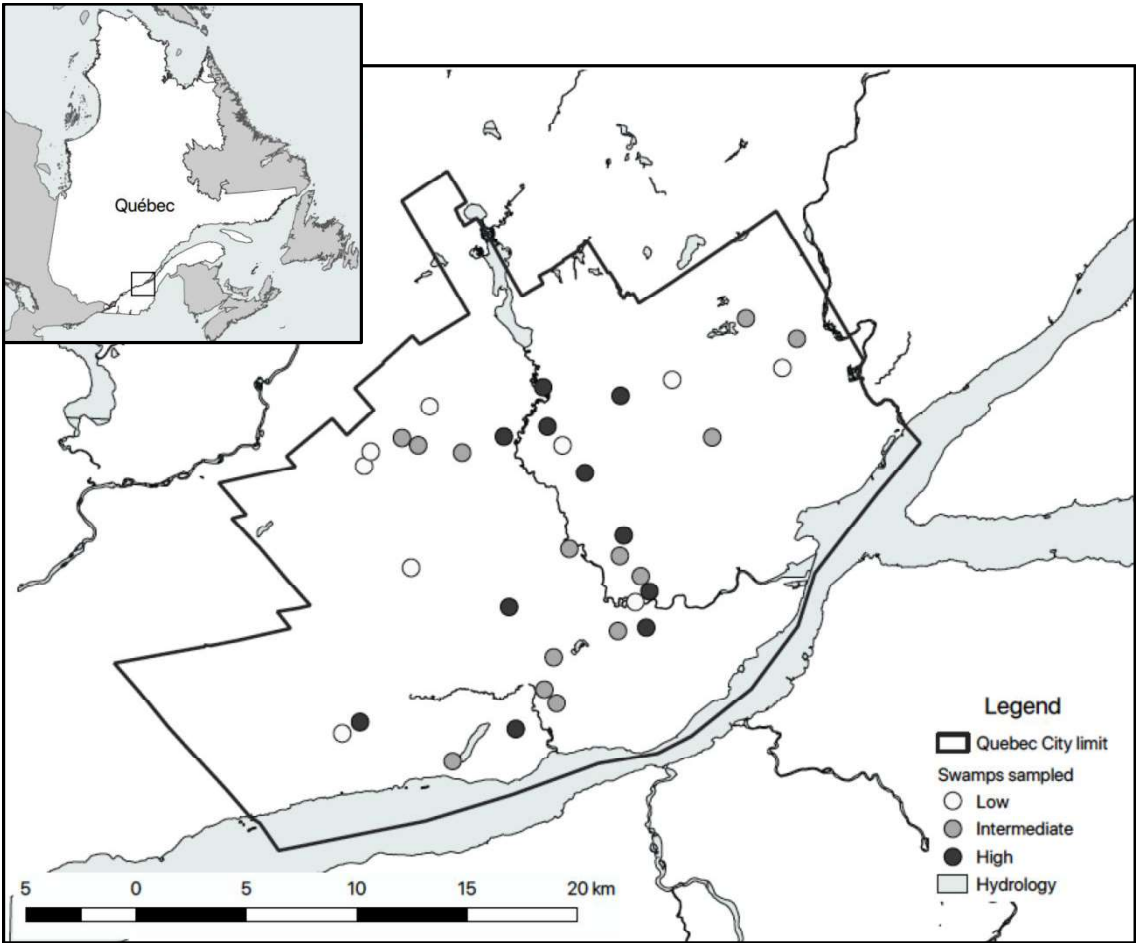


FIGURE 2. Differences in swamp species richness (mean \pm standard deviation) between urbanization levels and plant species groups. Uppercase letters indicate significant differences between levels of urbanization within a single plant group and lowercase letters differences between plant groups within a single level of urbanization, obtained by LSD.

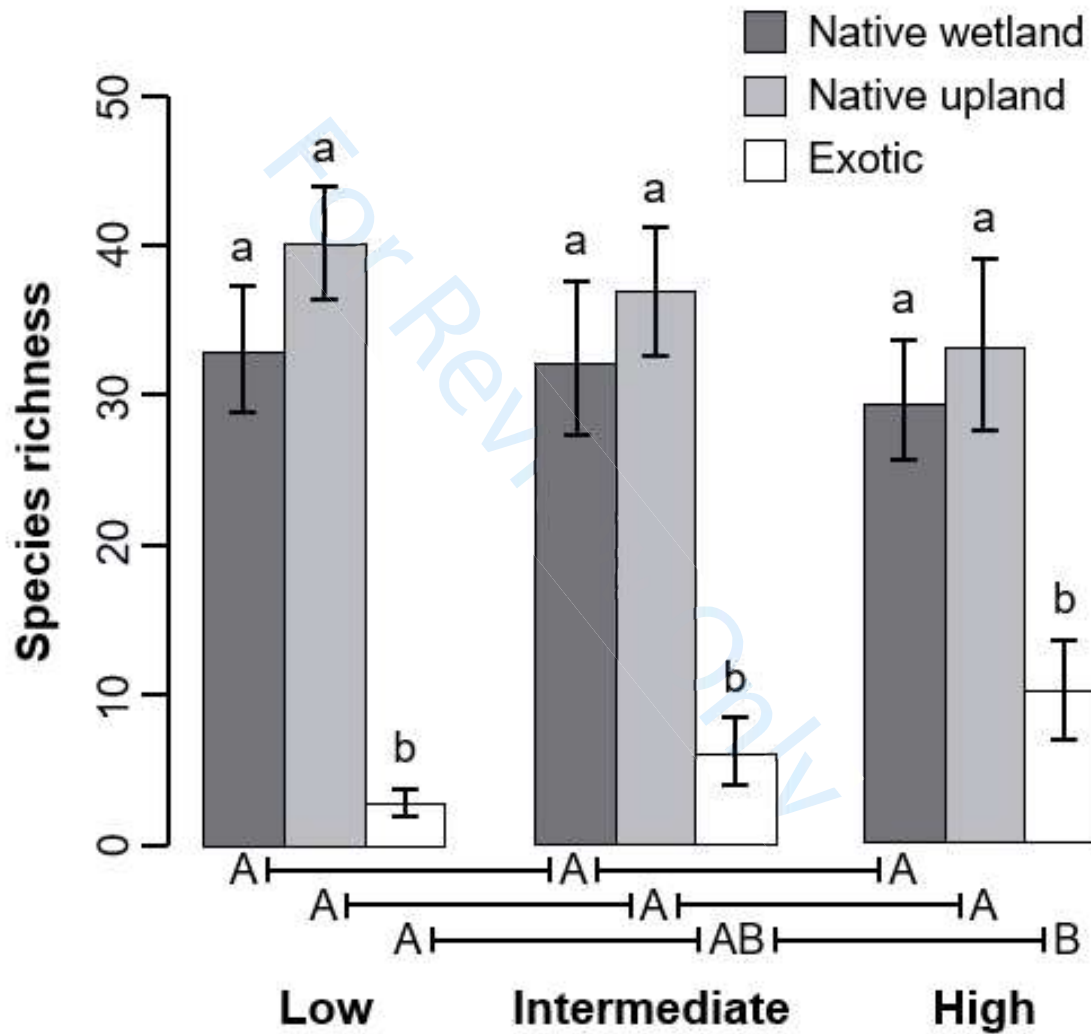


FIGURE 3. Response of swamp beta diversity to urbanization levels (calculated from land use composition in a 100 m radius buffer around each swamp; see Appendix S2). Taxonomic beta diversity was measured as the Euclidean distance of each site to their group centroid (based on Hellinger-transformed species importance value) as represented on the PCoA biplot with ellipses indicating standard deviation. Boxplots show the distribution of site-to-centroid distance (median and quartiles) for each urbanization level. Changes in dispersion around centroids reflect variations in beta diversity within urbanization level (boxplot), and changes of centroid position reflect variations in beta diversity between urbanization levels (biplot).

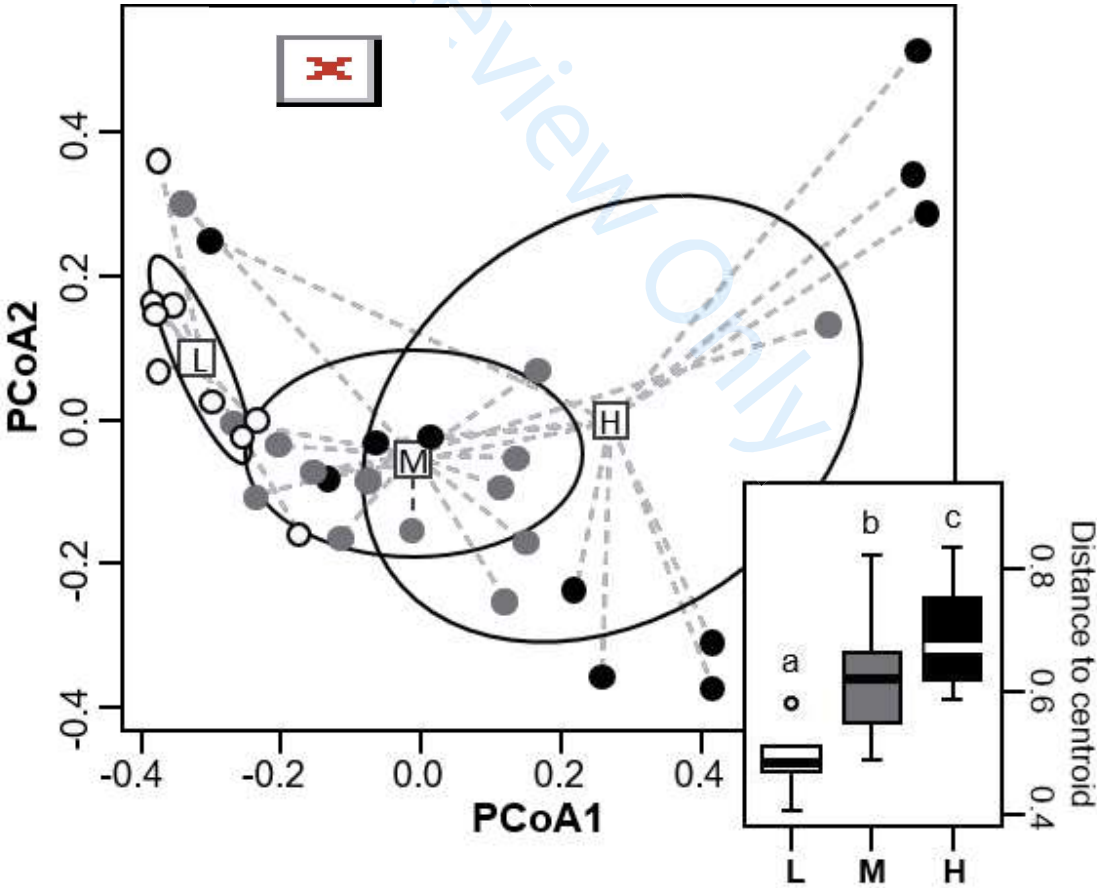
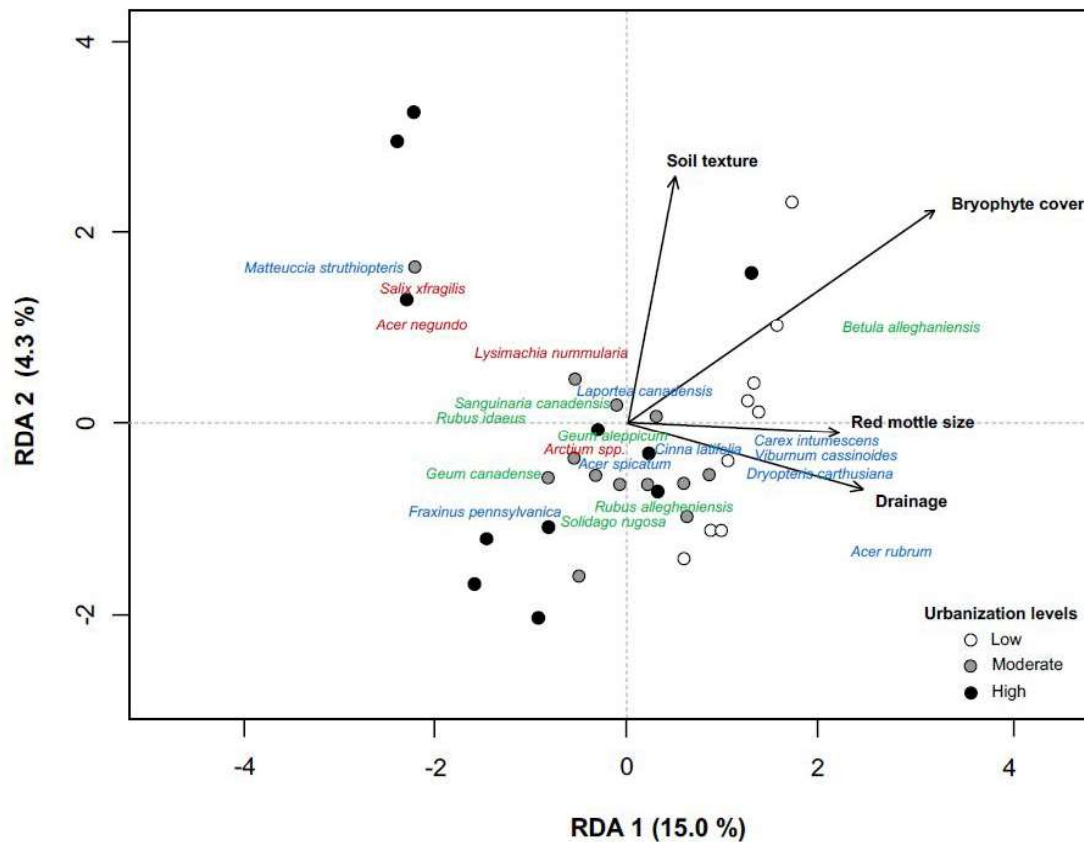
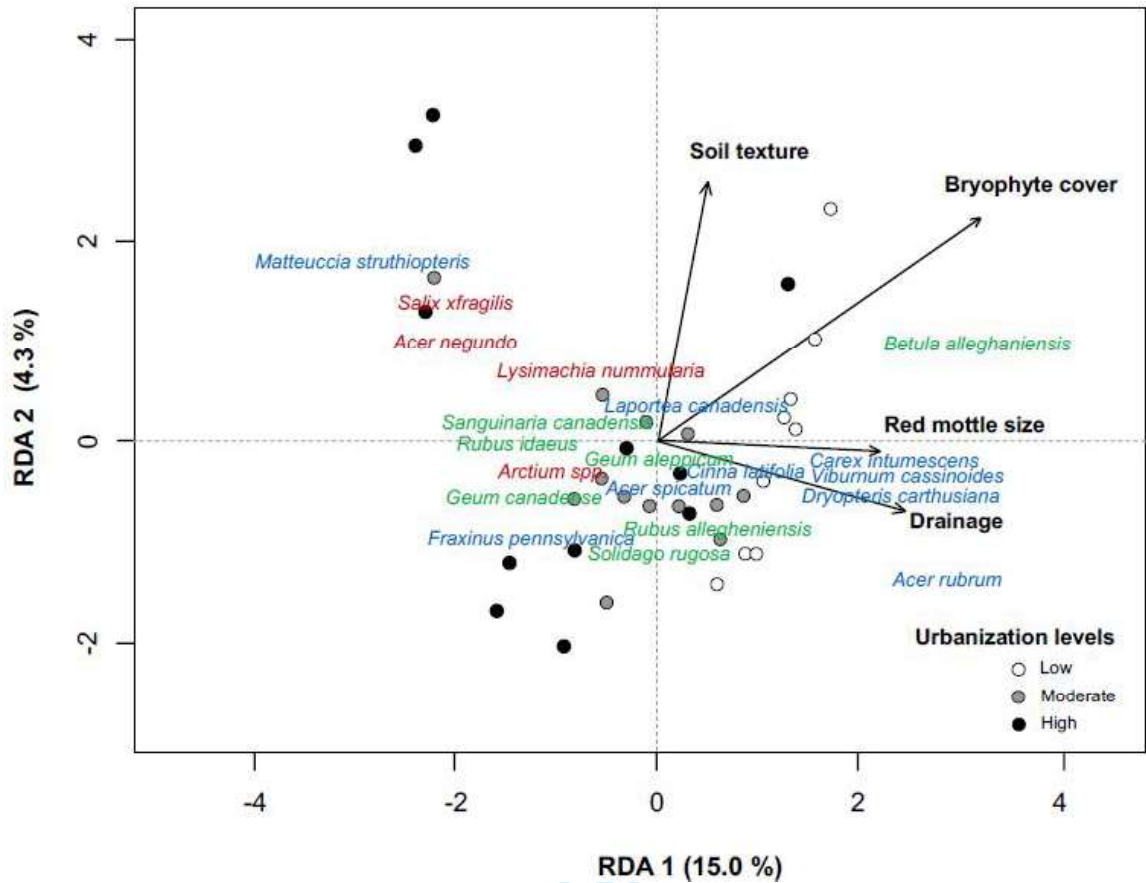


FIGURE 4. Effects of environmental variables (arrows) on the plant composition of swamps (dots), obtained by RDA. Only the four environmental variables (over nine measured) retained by stepwise selection are shown. XY coordinates of urbanization level centroids are (-0.92, 0.32) for high, (-0.05, -0.08) for intermediate, and (1.43, 0.04) for low urbanized swamps. The 20 species best fitted to the model are represented (blue: native wetland, green: native upland, red: exotic).





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APPENDIX S1. Land use categories used to classify each swamp by urbanization level, and mean cover for each level of urbanization (calculated in a 100m radius buffer around each swamp).

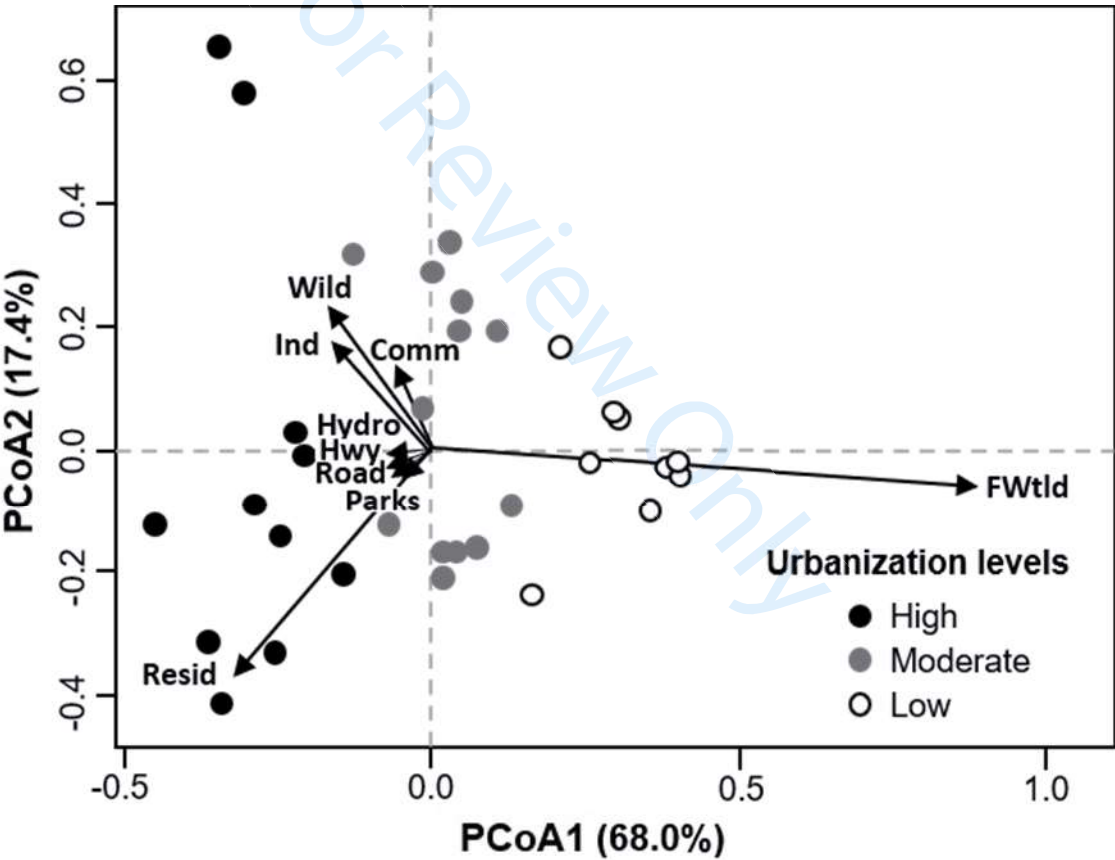
Classes of land use	Mean cover \pm sd (%)		
	Low	Intermediate	High
Forests/Wetlands	87.3 \pm 8.8	57.2 \pm 7.7	25.1 \pm 9.1
Residential areas	3.3 \pm 6.1	11.2 \pm 10	25.8 \pm 15.5
Wildlands¹	4.3 \pm 6.2	16 \pm 10.5	16.5 \pm 9.1
Commercial areas	2.3 \pm 5.1	4.8 \pm 5.8	4.8 \pm 7
Industrial sites	0.4 \pm 1.2	0.8 \pm 2.9	10.1 \pm 15.6
Highway	0.8 \pm 1.5	3.3 \pm 4.4	4.2 \pm 5.2
Secondary roads²	0.7 \pm 1.2	2.5 \pm 2.7	5 \pm 3.5
Parks and turfs³	0.4 \pm 0.9	1.8 \pm 1.9	5 \pm 5.4
Watercourses and lakes	0.6 \pm 1.2	2.4 \pm 3.4	3.5 \pm 5.9

¹ Vacant lots and wastelands

² Secondary road network

³ Lawns and maintained parks, no understory vegetation

APPENDIX S2. Principal coordinate analysis of land use composition in a 100m buffer around each of the 34 selected swamps. Sites were grouped according to three levels of urbanization based on non-hierarchical clustering k-means. Arrows represent land use categories evaluated from photointerpretation (FWtld: forests and wetlands; Resid: residential areas; Wild: wildlands; Comm: commercial areas; Ind : industrial sites; Hwy: highways and lakes; Road: secondary roads; Parks: parks and turfs; Hydro: water courses).



APPENDIX S3. Plant species inventoried in the 34 sampled swamps in Quebec City, Canada, and associated species group. Asterisks (*) identified the two exotic species classified as wetland plants, all other exotics being classified as upland plants. ¹ superscripts indicate species listed as invasive by the Government of Quebec (invasive species list available from : <https://www.pub.enviroweb.gouv.qc.ca/SCC/Default.aspx>) Species are sorted by trees, shrubs, and herbs and forbs.

Code	Latin name	Plant group
TREES		
ABI.BAL	<i>Abies balsamea</i>	Native upland
ACE.NEG	<i>Acer negundo</i>	Exotic ¹
ACE.PLA	<i>Acer platanoides</i>	Exotic ¹
ACE.RUB	<i>Acer rubrum</i>	Native wetland
ACE.SAC	<i>Acer saccharum</i>	Native upland
ACE.SAI	<i>Acer saccharinum</i>	Native wetland
BET.ALL	<i>Betula alleghaniensis</i>	Native upland
BET.PAP	<i>Betula papyrifera</i>	Native upland
BET.POP	<i>Betula populifolia</i>	Native upland
FAG.GRA	<i>Fagus grandifolia</i>	Native upland
FRA.AME	<i>Fraxinus americana</i>	Native upland
FRA.NIG	<i>Fraxinus nigra</i>	Native wetland
FRA.PEN	<i>Fraxinus pennsylvanica</i>	Native wetland
JUG.CIN	<i>Juglans cinerea</i>	Native upland
LAR.LAR	<i>Larix laricina</i>	Native wetland
PIC.GLA	<i>Picea glauca</i>	Native upland
PIC.MAR	<i>Picea mariana</i>	Native wetland
PIC.RUB	<i>Picea rubens</i>	Native upland
PIN.STR	<i>Pinus strobus</i>	Native upland
POP.BAL	<i>Populus balsamifera</i>	Native wetland
POP.GRA	<i>Populus grandidentata</i>	Native upland
POP.TRE	<i>Populus tremuloides</i>	Native upland
QUE.MAC	<i>Quercus macrocarpa</i>	Native upland
QUE.RUB	<i>Quercus rubra</i>	Native upland

SAL.FRA	<i>Salix x fragilis</i>	Exotic
THU.OCC	<i>Thuja occidentalis</i>	Native wetland
TIL.AME	<i>Tilia americana</i>	Native upland
TIL.COR	<i>Tilia cordata</i>	Exotic
TSU.CAN	<i>Tsuga canadensis</i>	Native upland
ULM.AME	<i>Ulmus americana</i>	Native wetland

SHRUBS

ACE.PEN	<i>Acer pennsylvanicum</i>	Native upland
ACE.SPI	<i>Acer spicatum</i>	Native upland
ALN.INC	<i>Alnus incana</i> subsp. <i>rugosa</i>	Native wetland
AME.ARB	<i>Amelanchier arborea</i>	Native upland
AME.BAT	<i>Amelanchier bartramiana</i>	Native upland
AME.LAE	<i>Amelanchier laevis</i>	Native upland
AME.SPI	<i>Amelanchier spicata</i>	Native upland
AMEL.SP	<i>Amelanchier</i> sp.	Native upland
ARO.MEL	<i>Aronia melanocarpa</i>	Native wetland
COR.ALT	<i>Cornus alternifolia</i>	Native upland
COR.CAN	<i>Cornus canadensis</i>	Native upland
COR.COR	<i>Corylus cornuta</i>	Native upland
COR.STO	<i>Cornus sericea</i>	Native wetland
CRAT.SP	<i>Crataegus</i> sp.	Native upland
DIE.LON	<i>Diervilla lonicera</i>	Native upland
DIR.PAL	<i>Dirca palustris</i>	Native upland
HYD.SP	<i>Hydrangea</i> sp.	Exotic
ILE.MUC	<i>Ilex mucronata</i>	Native wetland
ILE.VER	<i>Ilex verticillata</i>	Native wetland
KAL.ANG	<i>Kalmia angustifolia</i>	Native upland
LON.CAN	<i>Lonicera canadensis</i>	Native upland
LON.OBL	<i>Lonicera oblongifolia</i>	Native wetland
LON.TAT	<i>Lonicera tatarica</i>	Exotic
PHY.OPU	<i>Physocarpus opulifolius</i>	Native wetland
PRU.PEN	<i>Prunus pensylvanica</i>	Native upland
PRU.VIR	<i>Prunus virginiana</i>	Native upland
RHO.GRO	<i>Rhododendron groenlandicum</i>	Native wetland
RHU.TYP	<i>Rhus typhina</i>	Native upland
RIB.GLA	<i>Ribes glandulosum</i>	Native wetland

RIB.TRI	<i>Ribes triste</i>	Native wetland
RIBES.SP	<i>Ribes</i> sp.	Native upland
ROSA.SP	<i>Rosa</i> sp.	Native upland
RUB.ALL	<i>Rubus alleghaniensis</i>	Native upland
RUB.IDA	<i>Rubus idaeus</i>	Native upland
RUB.PUB	<i>Rubus pubescens</i>	Native wetland
SAL.BEB	<i>Salix bebbiana</i>	Native wetland
SAL.DIS	<i>Salix discolor</i>	Native wetland
SALIX.SP	<i>Salix</i> sp.	Native upland
SAM.CAN	<i>Sambucus canadensis</i>	Native wetland
SAM.RAC	<i>Sambucus racemosa</i> subsp. <i>pubens</i>	Native upland
SOR.AME	<i>Sorbus americana</i>	Native upland
SOR.OCU	<i>Sorbus aucuparia</i>	Exotic
SPI.LAT	<i>Spirea alba</i> var. <i>latifolia</i>	Native wetland
TAX.CAN	<i>Taxus canadensis</i>	Native upland
VAC.ANG	<i>Vaccinium angustifolium</i>	Native upland
VAC.MYR	<i>Vaccinium myrtilloides</i>	Native wetland
VIB.CAS	<i>Viburnum nudum</i> var. <i>cassinoides</i>	Native wetland
VIB.LAN	<i>Viburnum lantanoides</i>	Native upland
VIB.TRI	<i>Viburnum opulus</i> subsp. <i>trilobum</i> var. <i>amerincanum</i>	Native wetland

HERBS AND FORBS

ATH.FIL	<i>Athyrium filix-femina</i>	Native upland
ACT.PAC	<i>Actaea pachypoda</i>	Native upland
ACT.RUB	<i>Actaea rubra</i>	Native upland
AEG.POD	<i>Aegopodium podagraria</i>	Exotic ¹
AGR.CAP	<i>Agrostis capillaris</i>	Exotic
AGR.GRY	<i>Agrimonia gryposepala</i>	Native upland
AGR.PER	<i>Agrostis perennans</i>	Native upland
AGR.STR	<i>Agrimonia striata</i>	Native upland
ALL.PET	<i>Alliaria petiolata</i>	Exotic ¹
AMP.BRA	<i>Amphicarpa bracteata</i>	Native upland
ANE.CAN	<i>Anemonastrum canadense</i>	Native wetland
ANT.SYL	<i>Anthriscus sylvestris</i>	Exotic ¹
APO.AND	<i>Apocynum androsaemifolium</i>	Native upland
ARA.NUD	<i>Aralia nudicaulis</i>	Native upland

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3	ARC.MIN	<i>Arctium minus</i>	Exotic
4	ARI.TRI	<i>Arisema triphyllum</i>	Native wetland
5	ART.VUL	<i>Artemisia vulgaris</i>	Exotic
6	BID.CER	<i>Bidens cernua</i>	Native wetland
7	BID.FRO	<i>Bidens frondosa</i>	Native wetland
8	BRA.ARI	<i>Brachyelytrum aristosum</i>	Native upland
9	CAL.CAN	<i>Calamagrostis canadensis</i>	Native wetland
10	CAL.PAL	<i>Caltha palustris</i>	Native wetland
11	CAL.SEP	<i>Calystegia sepium</i>	Native upland
12	CAN.SAT	<i>Cannabis sativa</i>	Exotic
13	CAR.PEN	<i>Cardamine pensylvanica</i>	Native wetland
14	CAR.ALO	<i>Carex alopecoidea</i>	Native wetland
15	CAR.ARC	<i>Carex arctata</i>	Native upland
16	CAR.BEB	<i>Carex bebbii</i>	Native wetland
17	CAR.BRO	<i>Carex bromoides</i>	Native wetland
18	CAR.BRU	<i>Carex brunnescens</i>	Native wetland
19	CAR.CAN	<i>Carex canescens</i>	Native wetland
20	CAR.CAS	<i>Carex castanea</i>	Native wetland
21	CAR.CRA	<i>Carex crawfordii</i>	Native wetland
22	CAR.DEB	<i>Carex debilis</i>	Native wetland
23	CAR.DEW	<i>Carex deweyana</i>	Native upland
24	CAR.DIS	<i>Carex disperma</i>	Native wetland
25	CAR.ECH	<i>Carex echinata</i>	Native wetland
26	CAR.FLA	<i>Carex flava</i>	Native wetland
27	CAR.GRA	<i>Carex gracillima</i>	Native upland
28	CAR.GYN	<i>Carex gynandra</i>	Native wetland
29	CAR.HAY	<i>Carex haydenii</i>	Native wetland
30	CAR.INT	<i>Carex interior</i>	Native wetland
31	CAR.LEB	<i>Carex leptalea</i>	Native wetland
32	CAR.LEO	<i>Carex leptonervia</i>	Native upland
33	CAR.LUR	<i>Carex lurida</i>	Native wetland
34	CAR.NOV	<i>Carex novae-angliae</i>	Native upland
35	CAR.PAL	<i>Carex pallescens</i>	Native upland
36	CAR.PLA	<i>Carex plantaginea</i>	Native upland
37	CAR.PRA	<i>Carex prasina</i>	Native wetland
38	CAR.PRO	<i>Carex projecta</i>	Native wetland
39	CAR.SCA	<i>Carex scabrata</i>	Native wetland
40	CAR.STI	<i>Carex stipata</i>	Native wetland
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CAR.STR	<i>Carex stricta</i>	Native wetland
CAR.TEN	<i>Carex tenera</i>	Native upland
CAR.TRI	<i>Carex trisperma</i>	Native wetland
CAR.WIE	<i>Carex wiegandii</i>	Native wetland
CHE.GLA	<i>Chelone glabra</i>	Native wetland
CHE.MAJ	<i>Chelidonium majus</i>	Exotic
CHR.AME	<i>Chrysosplenium americanum</i>	Native wetland
CIN.LAT	<i>Cinna latifolia</i>	Native wetland
CIR.ALP	<i>Circaea alpina</i>	Native wetland
CIR.LUT	<i>Circaea canadensis</i>	Native upland
CLE.VIR	<i>Clematis virginiana</i>	Native upland
CLI.BOR	<i>Clintonia borealis</i>	Native upland
CON.MAJ	<i>Convallaria majalis</i>	Exotic
COP.TRI	<i>Coptis trifolia</i>	Native wetland
CYP.ACA	<i>Cypripedium acaule</i>	Native wetland
DAC.GLO	<i>Dactylis glomerata</i>	Exotic
DEN.OBS	<i>Dendrolycopodium obscurum</i>	Native upland
DOE.UMB	<i>Doellingeria umbellata</i>	Native wetland
DRY.CCI	<i>Dryopteris intermedia</i>	Native wetland
DRY.CRI	<i>Dryopteris cristata</i>	Native wetland
ECH.LOB	<i>Echinocystis lobata</i>	Native wetland
ELE.ACI	<i>Eleocharis acicularis</i>	Native wetland
ELY.VIR	<i>Elymus virginicus</i>	Native wetland
EPI.CIL	<i>Epilobium ciliatum</i>	Native wetland
EPI.COL	<i>Epilobium coloratum</i>	Native wetland
EPI.HEL	<i>Epipactis helleborine</i>	Exotic
EQU.ARV	<i>Equisetum arvense</i>	Native upland
EQU.SYL	<i>Equisetum sylvaticum</i>	Native wetland
ERI.PHI	<i>Erigeron philadelphicus</i>	Native wetland
EUT.GRA	<i>Euthamia graminifolia</i>	Native upland
EUT.MAC	<i>Eutrochium maculatum</i>	Native wetland
FAL.CIL	<i>Fallopia cilinodis</i>	Native upland
FES.RUB	<i>Festuca rubra</i>	Native upland
FRA.VIR	<i>Fragaria virginiana</i>	Native upland
GAL.SP	<i>Galium</i> sp.	Native wetland
GAU.HIS	<i>Gaultheria hispidula</i>	Native wetland
GEU.ALE	<i>Geum aleppicum</i>	Native upland
GEU.CAN	<i>Geum canadense</i>	Native upland

GEU.LAN	<i>Geum laciniatum</i>	Native wetland
GEU.MAC	<i>Geum macrophyllum</i>	Native wetland
GEU.RIV	<i>Geum rivale</i>	Native wetland
GEU.URB	<i>Geum urbanum</i>	Exotic
GLY.CAN	<i>Glyceria canadensis</i>	Native wetland
GLY.SMX	<i>Glyceria striata</i>	Native wetland
GOO.REP	<i>Goodyera repens</i>	Native upland
GYM.DRY	<i>Gymnocarpium dryopteris</i>	Native upland
HEM.FUL	<i>Hemerocallis fulva</i>	Exotic
HES.MAT	<i>Hesperis matronalis</i>	Exotic
HIE.VUL	<i>Hieracium vulgatum</i>	Native upland
HOS.PLA	<i>Hosta plantaginea</i>	Exotic
HUP.LUC	<i>Huperzia lucidula</i>	Native upland
HYL.TEL	<i>Hylotelephium telephium</i>	Exotic
IMP.CAP	<i>Impatiens capensis</i>	Native wetland
IRI.VER	<i>Iris versicolor</i>	Native wetland
JUN.EFF	<i>Juncus effusus</i>	Native wetland
LAC.SER	<i>Lactuca serriola</i>	Exotic
LAP.CAN	<i>Laportea canadensis</i>	Native wetland
LEU.VUL	<i>Leucanthemum vulgare</i>	Exotic
LIN.BOR	<i>Linnaea borealis</i>	Native upland
LYC.AME	<i>Lycopus americanus</i>	Native wetland
LYC.ANO	<i>Lycopodium annotinum</i>	Native upland
LYC.UNI	<i>Lycopus uniflorus</i>	Native upland
LYS.BOR	<i>Lysimachia borealis</i>	Native upland
LYS.CIL	<i>Lysimachia ciliata</i>	Native wetland
LYS.NUM	<i>Lysimachia nummularia</i>	Exotic *
LYS.TER	<i>Lysimachia terrestris</i>	Native wetland
LYS.VUL	<i>Lysimachia vulgaris</i>	Exotic
LYT.SAL	<i>Lythrum salicaria</i>	Exotic *, ¹
MAI.CAN	<i>Maianthemum canadense</i>	Native upland
MAI.RAC	<i>Maianthemum racemosum</i>	Native upland
MAI.STE	<i>Maianthemum stellatum</i>	Native wetland
MAT.STR	<i>Matteucia struthiopteris</i>	Native wetland
MED.LUP	<i>Medicago lupulina</i>	Exotic
MED.VIR	<i>Medelola virginiana</i>	Native upland
MEN.CAN	<i>Mentha canadensis</i>	Native wetland
MES.UNI	<i>Moneses uniflora</i>	Native upland

MIL.SP	<i>Milium sp.</i>	Native upland
MIM.RIV	<i>Mimulus ringens</i>	Native wetland
MIT.NUD	<i>Mitella nuda</i>	Native wetland
MIT.REP	<i>Mitchella repens</i>	Native upland
MYO.LAX	<i>Myosotis laxa</i>	Native wetland
NAB.SP	<i>Nabalus sp.</i>	Native upland
OCL.ACU	<i>Oclemena acuminata</i>	Native upland
ONO.SEN	<i>Onoclea sensibilis</i>	Native wetland
ORC.SP	<i>Orchidaceae sp.</i>	Native upland
ORT.SEC	<i>Orthilia secunda</i>	Native upland
OSM.CIN	<i>Osmundastrum cinnamomeum</i>	Native wetland
OSM.CLA	<i>Osmunda claytoniana</i>	Native upland
OSM.REG	<i>Osmunda regalis</i>	Native wetland
OXA.MON	<i>Oxalis montana</i>	Native upland
OXA.STR	<i>Oxalis stricta</i>	Exotic
PAC.PAU	<i>Packera paupercula</i>	Native upland
PAR.QUI	<i>Parthenocissus quinquefolia</i>	Exotic
PAS.SAT	<i>Pastinaca sativa</i>	Exotic ¹
PHE.CON	<i>Phegopteris connectilis</i>	Native upland
PIL.AUR	<i>Pilosella aurantiaca</i>	Exotic
PLA.GRA	<i>Platanthera grandiflora</i>	Native wetland
PLA.MAJ	<i>Plantago major</i>	Exotic
POA.COM	<i>Poa compressa</i>	Exotic
POA.PAL	<i>Poa palustris</i>	Native wetland
POA.TRI	<i>Poa trivialis</i>	Exotic
POT.SP	<i>Potentilla sp.</i>	Native upland
PRU.VUL	<i>Prunella vulgaris</i>	Native upland
PTE.AQU	<i>Pteridium aquilinum</i>	Native upland
PYR.ELL	<i>Pyrola elliptica</i>	Native upland
RAN.ABO	<i>Ranunculus abortivus</i>	Native upland
RAN.ACR	<i>Ranunculus acris</i>	Exotic
RAN.REP	<i>Ranunculus repens</i>	Exotic
REY.JAP	<i>Reynoutria japonica</i>	Exotic ¹
RUB.REP	<i>Rubus repens</i>	Native upland
RUM.BRI	<i>Rumex britannica</i>	Native wetland
RUM.OBT	<i>Rumex obtusifolius</i>	Exotic
SBA.CAN	<i>Sanguisorba canadensis</i>	Native wetland
SCH.PUR	<i>Schizachne purpurascens</i>	Native upland

SCI.ATR	<i>Scirpus atrocinctus</i>	Native wetland
SCU.LAT	<i>Scutellaria lateriflora</i>	Native wetland
SMI.HER	<i>Smilax herbaceae</i>	Native upland
SNG.CAN	<i>Sanguinaria canadensis</i>	Native upland
SOL.DUL	<i>Solanum dulcamara</i>	Exotic
SOL.FLE	<i>Solidago flexicaulis</i>	Native upland
SOL.MAC	<i>Solidago macrophylla</i>	Native upland
SOL.RUG	<i>Solidago rugosa</i>	Native upland
STR.AMP	<i>Streptopus amplexifolius</i>	Native upland
STR.LAN	<i>Streptopus lanceolatus</i>	Native upland
SYM.COR	<i>Symphyotrichum cordifolium</i>	Native upland
SYM.FOE	<i>Symplocarpus foetidus</i>	Native wetland
SYM.LAN	<i>Symphyotrichum lanceolatum</i>	Native wetland
SYM.LAT	<i>Symphyotrichum lateriflorum</i>	Native upland
SYM.OFF	<i>Symphytum officinale</i>	Exotic ¹
SYM.PUN	<i>Symphyotrichum puniceum</i>	Native wetland
TAR.OFF	<i>Taraxacum officinale</i>	Exotic
THA.PUB	<i>Thalictrum pubescens</i>	Native wetland
THE.NOV	<i>Thelypteris noveboracensis</i>	Native upland
TOX.RAD	<i>Toxicodendron radicans</i>	Native upland
TRI.COR	<i>Triarella cordifolia</i>	Native upland
TUS.FAR	<i>Tussilago farfara</i>	Exotic
TYP.LAT	<i>Typha latifolia</i>	Native wetland
URT.URE	<i>Utica urens</i>	Exotic
VAL.OFF	<i>Valeriana officinale</i>	Exotic ¹
VER.AME	<i>Veronica americana</i>	Native wetland
VER.OFF	<i>Veronica officinalis</i>	Exotic
VER.VIR	<i>Veratrum viride</i>	Native wetland
VIC.CRA	<i>Vicia cracca</i>	Exotic
VIC.SEP	<i>Vicia sepium</i>	Exotic
VIOLA.SP	<i>Viola sp.</i>	Native upland
VIT.RIP	<i>Vitis riparia</i>	Native upland



92x106mm (220 x 220 DPI)

SUMMARY

Disentangling the multifaceted effect of urbanization on biodiversity is required for designing sustainable cities. Although urbanization often induces biotic homogenization, we revealed that increasing landscape urbanization level is associated with biotic differentiation of swamp plant communities. The unpredictable effect of urbanization on hydrological regimes indeed promoted high native species turnover while limiting exotic spread.

For Review Only