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RESEARCH ARTICLE

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Changes in spatial structures of plant communities lead to functional homogenization in an urban forest park

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Abstract

Aims: We investigated whether biotic homogenization of plant communities occurs over three decades in a small urban protected forest, and what the possible drivers are underlying the observed changes.

Location: A 96 ha temperate forest, Montréal, Canada.

Methods: We surveyed vegetation and explanatory variables (ecological conditions, disturbances, spatial structure) in 62 plant communities in 1980 and 2011. We collected plant attributes to identify functional groups (FGs). We evaluated changes in beta diversity using tests for homogeneity of multivariate dispersions. We used space–time interaction models to assess changes in FGs spatial structures. We used multivariate analyses to identify relationship between spatial patterns and explanatory variables, and variation partitioning analyses to identify the drivers involved in beta diversity changes.

Results: Beta diversity declined only in the herb–shrub communities. About 35% of their FGs had significantly changed their spatial distribution over time. Those that contracted their distribution were mainly composed of plants with wind-dispersed seeds or with low to intermediate vegetative propagation capabilities, while those that expanded were plants with fleshy fruits or extensive vegetative propagation capabilities. In 1980, communities were structured into small isolated clumps, while in 2011, clumps expanded and coalesced near disturbed areas. In 1980, the spatial assembly processes relied essentially on endogenous factors while in 2011 exogenous factors, such as disturbances, became more influential. Multivariate analyses suggested that edge effect, past agricultural disturbances, and beaver activities facilitated the decrease of beta diversity (homogenization process).

Conclusions: The homogenization of herb–shrub communities likely resulted from changes in their clumped spatial structure. FGs with the most adapted attributes to disperse under urban forest conditions were those that expanded spatially. Structural changes seem to have begun with an unpredictable stage governed by dispersal limitation processes, followed by a predictable stage mostly driven by land-use legacy and disturbances.

KEYWORDS

biotic homogenization, bird-dispersed plant, land-use changes, plant community, plant functional group, resampling study, spatial ecology, urban forest, vegetative propagation

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1 | INTRODUCTION

The composition and structure of plant communities in urban ecosystems are mostly determined by human-associated factors operating at multiple spatial and temporal scales, rather than by natural biotic and abiotic factors (Godefroid & Koedam, 2007; Knapp et al., 2008; Williams, Hahs, & Vesk, 2015). At the local scale, human factors acting on communities include management practices and horticultural interventions, whereas at the regional level habitat loss and fragmentation prevail (Swan, Johnson, & Nowak, 2016; Williams et al., 2008). Several studies also showed that past land uses, such as agriculture before urbanization, still influence current species distribution through the modification of soil properties and the disruption of natural disturbance regimes (Flinn & Vellend, 2005; Johnson, Tauzer, & Swan, 2015; Vellend et al., 2007). Land use changes affect the environmental conditions and the spatial configuration of habitats, as well as the regional pool of species, which in turn alter the plant community assembly processes such as environmental filtering and dispersal limitation. Altogether, the overriding influence of human factors on communities in urban ecosystems may result in biotic homogenization (McKinney, 2006; Olden & Poff, 2003).

Because plant attributes are an expression of the physiological responses to their environment, the use of a functional approach can help to understand the key drivers of homogenization (Lavorel, McIntyre, Landsberg, & Forbes, 1997; McCune & Vellend, 2013). However, despite the fact many studies showed that plant communities converge towards long-distance dispersed, thermophilous and disturbance-tolerant species in urban ecosystems (Brice, Pellerin, & Poulin, 2016; Flinn & Vellend, 2005; Knapp et al., 2008; Schleicher, Peppler-Lisbach, & Kleyer, 2011; Williams et al., 2015), to what extent this also results in functional homogenization remains to be substantiated. Furthermore, the drivers of homogenization are not well understood because long-term studies are lacking, especially in North America. Such studies are crucial because plant responses to disturbances, environmental changes or endogenous biological processes are often time-lagged (Jackson & Sax, 2010).

Several strategies can be used to identify long-term changes in plant communities, but recently, the comparison of historical and recent vegetation data has gained in popularity (Kapfer et al., 2017; Vellend, Brown, Kharouba, McCune, & Myers-Smith, 2013). Resampling studies in urban environments are abundant (e.g., DeCandido, Muir, & Gargiullo, 2004; Drayton & Primack, 1996; McCune & Vellend, 2013), but most are descriptive, generally consisting in comparison of past and recent species lists. However, to better understand the drivers of beta diversity changes and to disentangle the relative importance of different community assembly processes underlying the changes (e.g., environmental filtering or dispersal), analyses of abundance data (species and their attributes) and of the spatial patterns of changes are needed (Laliberté, Paquette, Legendre, & Bouchard, 2009; Legendre, De Cáceres, & Borcard, 2010; Legendre & Gauthier, 2014; Vellend et al., 2007). Resampling historical vegetation data can also provide information on which strategies should be adopted for the preservation of diversity or on the long-term efficiency of management and conservation practices (Beauvais, Pellerin, & Lavoie, 2016; DeCandido et al., 2004; Koch et al., 2017). For example, because extirpations overly affected the native flora of New York City compared to the exotic one, DeCandido et al. (2004) suggested, among others, to use native plants as key components of restoration or renewal projects and to propagate rare or uncommon native species in already protected areas. Similarly, Beauvais et al. (2016) showed that converting a suburban forest into a protected area helps preserve its native flora, despite natural and anthropogenic disturbances, when exotic species are adequately managed.

In this study, we documented the spatiotemporal changes that occurred over three decades in the plant functional group communities of a small urban protected forest. Our specific objectives were (a) to assess whether taxonomic and functional homogenization occurred, (b) to evaluate the changes in plant spatial patterns over time, and (c) to identify possible drivers, including community assembly processes, underlying the observed changes. We predicted (a) that the changes in plant attribute composition that occurred in the last 30 years induced a taxonomic and functional homogenization by the convergence of attributes associated with adaptation to urban forest environment and (b) that patterns of changes are spatially structured in response to disturbances.

2 | METHODS

2.1 | Study site

We conducted the study at Bois-de-Saraguay municipal park (hereafter BDS; 45°31′ N, 73°44′ W), a 96-ha protected area established in 1984 in Montréal (Figure 1). The BDS protects one of the few mature deciduous forests in the Montréal area, Canada's second most populous metropolitan region (~3.8 million inhabitants; www.statcan.gc.ca). On mesic soils, BDS is characterized by *Acer saccharum*, *Acer nigrum* and *Tilia americana* tree stands, whereas *Acer saccharinum* and *Fraxinus pennsylvanica* dominate poorly drained soils. About two-thirds of the area occupied by forest communities is mature, some trees reaching 165 years of age (Domon, Vincent, & Bouchard, 1990). The soils are silty clay loams with neutral to alkaline pH. The microtopography is characterized by a succession of mounds and depressions (elevation range: 9 m) influencing drainage, which was previously identified as the main driver of tree species distribution (Domon, Bouchard, Bergeron, & Gauvin, 1986). Mean annual temperature is 6°C and mean annual precipitation is about 1,000 mm, 21% of which falls as snow (www.climate.weather.gc.ca).

BDS surroundings remained nearly non-developed until the first homes were built in 1880 following the construction of a boulevard that crossed BDS in its northwestern part (Figure 1). A railroad, built in 1913, fragmented the forest in its southeastern part. In the 1920s, most agricultural activities practiced ceased, but the forest was still used as a source of firewood. The three main unpaved trails (~2–3 m wide) crossing the forest, still present today, were probably opened

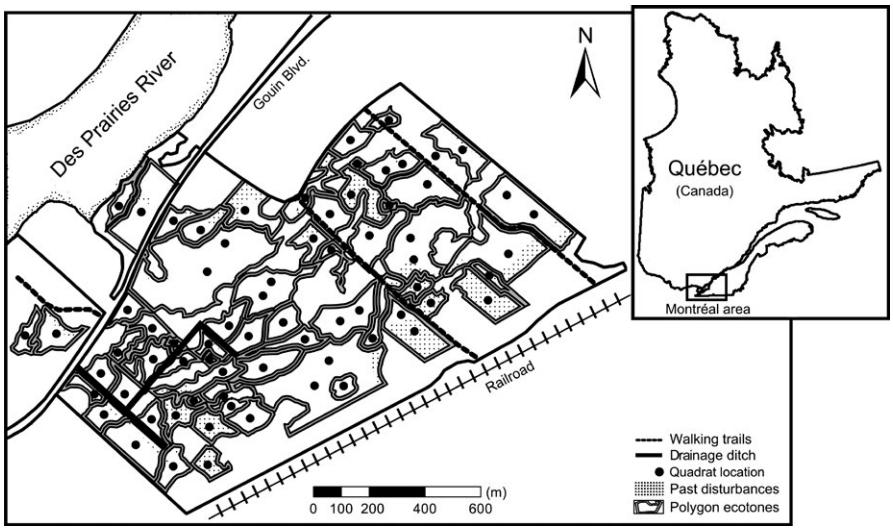

FIGURE 1 Location of the 62 quadrats and polygons used for vegetation sampling at Bois-de-Saraguay, Montréal, Canada

in the 1930s. In the late 1950s, a drainage ditch with two branches was dug in the southwestern part of the forest. BDS was completely embedded into an impervious urban matrix of single-family dwellings during the 1970s. By the early 1980s, the old fields and tree-cutting areas were almost entirely recolonized by trees, but a small marsh (0.4 ha) appeared in the central part of the BDS due to beaver activities (Domon et al., 1990).

2.2 | Original plant survey: 1980

In summer 1980, Domon and Bouchard (1981) conducted the first exhaustive plant survey of BDS. Before sampling, they divided the forest into 62 polygons (0.07–4.53 ha; mean: 0.8 ha), each representing a homogenous community of codominant tree species. In each polygon, they surveyed the vegetation in one rectangular quadrat, located in its central part, following a modified Whittaker's (1967) method. Depending on the size of the polygon, quadrats were 1,000 m^2 (8 polygons), 500 m^2 (48) or 125 m^2 (6). In each quadrat, the number and diameter at breast height (dbh) of all trees with dbh ≥10 cm were recorded per species to calculate their density-dominance index (Kershaw, 1973). They also evaluated the density of saplings (height: ≥1 m; dbh: <10 cm) of each tree species by counting all individuals. To evaluate the abundance of each herb and shrub species, they recorded their presence in 25 subquadrats of 1 m^2 spread along the longest median line of the quadrat. They also searched the entire quadrat for additional species.

2.3 | Resampling: 2011

Quadrats were not permanently marked, but a high-resolution hard copy of the map (1:2,400) outlying the precise location of each polygon was available. We digitized and georeferenced this map into ArcGIS (ESRI Co, Redlands, CA, USA). To take into account the possible source of spatial error inherent to the georeferencing of an old map, we delineated an inside buffer of 12.5 m (i.e., distance estimate necessary to avoid the overlap of two nearby quadrats) for each polygon before retrieving the geographic coordinates of its central point. During the summer of 2011, we relocated the 62 quadrats in the field using a GPS. In addition to geographic coordinates, we used all information available (general tree composition, topographic situation, soil drainage, presence of exposed stones and quadrat orientation) from the original survey for positioning the quadrats as precisely as possible. We added nine replicated quadrats in large or irregular polygons to test the similarity of their vegetation composition (efficiency of relocation). We sampled the vegetation using the same method and timeline as in 1980.

2.4 | Vegetation data

Before analyses, we standardized taxa at the species rank or supraspecific/infrageneric rank for a few doubtful cases. We used VASCAN nomenclature (Brouillet et al., 2017). Because quadrats were variable in size, we transformed vegetation data (i.e., tree density-dominance, sapling density or herb–shrub abundance) into relative abundances (expressed as percentages). Additionally, we performed a principal component analysis on vegetation data (Hellinger-transformed) to visually evaluate the ecological distances between the nine pairs of replicated quadrats sampled in 2011. Although distances were small (Appendix S1), indicating a reasonably uniform composition within the polygons, we used a cautious approach by merging the data of each pair of replicated quadrats.

2.5 | Plant functional group

We selected five plant attributes to identify functional groups (FGs): (a) seasonal life cycle, (b) shade tolerance, (c) vertical height, (d) lateral vegetative propagation, and (e) diaspore types (Table 1). These attributes can reveal changes in ecological processes structuring communities (e.g., plant succession, competition for light and space, dispersal). We gathered plant attribute values from the primary

TABLE 1 Plant attributes used to identify functional groups (Appendix S2 for details)

Attributes	Unit/Scale	Variable type	Strata
Seasonal life cycle	0: Long-lived; 1: Short-lived	Ordinal	Herb–shrub
Shade tolerance	1: Intolerant; 2: Mid-tolerant; 3: Tolerant	Ordinal	Tree, sapling
Vertical height	dm	Continuous	Tree, sapling, Herb–shrub
Lateral vegetative propagation	1: Compact; 2: Intermediate; 3: Extensive	Ordinal	Tree, sapling, Herb–shrub
Diaspore type	1: Adhesive; 2: Aerenchyma; 3: Cylindrical; 4: Dust-like; 5: Elaiosome; 6: Fleshy; 7: Globular; 8: Lenticular; 9: Pappus; 10: Polyangular; 11: Winged; 12: Heavy; 13: Woolly	Categorical	Tree, sapling, Herb–shrub

literature, online databases and through the examination of seed collections from the Université de Montréal Herbarium (see Appendix S2). Following the emergent group approach (sensu Lavorel et al., 1997), we numerically classified each taxon based on its attribute values. For each stratum, we combined data of the two sampling years and computed dissimilarity matrices using the Gower's coefficient (Legendre & Legendre, 2012). Each dissimilarity matrix was subjected to a cluster analysis using Ward's minimum variance method (Legendre & Legendre, 2012). We visually interpreted the three resulting dendrograms to identify plant FGs, ensuring that each FG consisted of plants having only one diaspore type. Using vegetation data, we calculated the relative abundances of all identified FGs in each quadrat, for each stratum and survey year, giving six additional response datasets (3 strata × 2 years).

2.6 | Explanatory variables

2.6.1 | Ecological conditions

In each quadrat, we characterized soil drainage (*Drainage*) using six ordinal values ranging from 1: rapidly drained to 6: very poorly drained. We visually estimated the mean vegetation height (*VegHeight*: 5–10 m; 11–20 m; ≥21 m), the canopy closure (*CanClosure*: 5%–10%; 11%–25%; 26%–50%; 51%–75%; 76%–100%), and the surface stoniness (*Stoniness*: 0.1%–3%; 4%–15%; 16%–50%; 51%–100%). We estimated soil acidity (*pH*) using an interpolation map (kriging method) generated from 70 measurements made in previous studies (Bergeron & Pellerin, 2014; Domon et al., 1990). For each polygon, we evaluated the range between minimum and maximum values of slope (*Slope*) from a digital elevation model (DEM: XY = 8–23 m, Z = 1 m; Natural Resources Canada, 2017) and used it as an index of topographic heterogeneity. Based on the steepness and slope orientation data of the DEM, we computed total incoming solar radiation (*SolarRad*) using the ArcGIS *Area Solar Radiation* tool parameterized with the sun angle values of the growing season (April–September: 182 days) and altitude (45°31′N) of the BDS. We used this variable to ensure that if we found a significant effect of edges on vegetation composition, it was not simply an artefact of the structuring effect of slope orientation and elevation. Ecological conditions were measured both years, except for *Stoniness*, *pH*, *Slope* and *SolarRad* variables that were only measured in 2011. As we assumed these four variables to be stable over time, at least at the polygon resolution scale, we used values measured in 2011 for both survey years.

2.6.2 | Disturbance variables

In each quadrat, we noted the presence/absence of tree trunks gnawed or cut by beavers (*Beaver*) similarly as in 1980. We measured the distance of each quadrat to the forest edge (*ExtEdge*) and the nearest internal edge (*IntEdge*; i.e., trails and ditches), and subsequently converted these values into sign-inverted values to obtain measurements of proximity. Using georeferenced aerial photographs (1931, 1955, 1964, 1973, 1983, 1995, 2002 and 2009) and ArcGIS, we manually delineated all disturbed (i.e., cultivation or tree-cutting areas) and impervious (i.e., pavement or roofing areas) surfaces inside each polygon plus a buffer zone of 250 m for impervious surface (to take into account the land use change at the edge of the forest). These surfaces were then transformed in percentage of the area they covered. We developed a vegetation disturbance index (*VegDisturb*) and an impervious surface index (*Impervious*) for each survey year (1980 and 2011) by averaging the values obtained on the photographs taken prior to the survey, which allows consideration of long-term influences of disturbances or land use transformations.

2.6.3 | Spatial structure variables

We assessed past and present spatial structures of plant communities using the distance-based Moran's eigenvectors method (dbMEM; Dray, Legendre, & Peres-Neto, 2006). The dbMEM eigenvectors are used to model non-directional spatial patterns that could emerge from plant dispersal (e.g., clumping) or any other ecological processes leaving an autocorrelation signature in abundance data. We computed *dbMEM* eigenvectors using a connectivity matrix that summarized the connections between the studied quadrats. We used the longest distance (147 m) connecting two quadrats in a minimum spanning tree as a threshold (d) to truncate the Euclidean

distance matrix. The resulting first 23 eigenvectors had positive autocorrelation (*dbMEM*-1 to *dbMEM*-23), and the remaining 38 (*dbMEM*-24 to *dbMEM*-61) had negative autocorrelation.

2.7 | Data analyses

2.7.1 | Richness and beta diversity

We used paired *t*-tests to detect changes in the richness of taxa and FGs for each vegetation stratum. We analyzed differences in beta diversity using tests for homogeneity of multivariate dispersions (Anderson, Ellingsen, & McArdle, 2006). More precisely, we first used a site-by-site distance matrix for each vegetation stratum and response data (taxa and FG) calculated with the Bray–Curtis distance (McCune & Vellend, 2013) to compute the centroid of each group of sites (a group corresponds to a survey year). Then, we calculated the distance of each site to its associated group centroid. Finally, site distances to centroid were subjected to pairwise analysis of variance (ANOVA) with permutations to determine whether the dispersion of groups differed. The dispersion of these distances (within-group variance) was used as an estimate of beta diversity (the greater the within-group variance, the higher the beta diversity). To determine whether beta diversity changes were associated with a shift in composition (taxa or FG) between the two survey years, we also tested for differences in centroid locations using a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). Results indicated that no change in beta diversity occurred in tree and sapling communities for both taxa and FG data (Figure 2), and consequently, we performed subsequent analyses only on herb–shrub data.

2.7.2 | Spatial structure changes with time

To assess whether the spatial structure of the herb–shrub communities had significantly changed between the two surveys, we carried out space–time interaction (STI) tests using a two-way ANOVA crossed design with interaction under-fitted (Model 5 in Legendre et al., 2010). This model linked 1980–2011 response datasets with Helmert's contrasts to code the space and time as main factors (Legendre & Legendre, 2012), while the STI term was coded by multiplying spatial eigenvectors/2 by temporal eigenvectors/2. The spatial (31 out of 62; *d*: 147 m) and temporal (1 out of 2; *d*: 1) eigenvectors were derived from the principal coordinates of neighbor matrices method (PCNM; Borcard & Legendre, 2002). Using this coding scheme, we designed univariate models separately for each taxon and FG, after a log-transformation of their abundance values. Two multivariate models were also designed with the compositional data (Hellinger-transformed) of the taxa and FGs. Each response datasets transformed for the models had a significant spatial linear trend. To avoid bias in the detection of fine-scale spatial structures, each transformed dataset was detrended by retaining the residuals from a regression on the geographical coordinates of quadrats. Finally, the significance of the STI term of each model was subjected to an ANOVA-like permutation test by considering space as a random factor and time as a fixed factor (Laliberté et al., 2009).

2.7.3 | Relative roles of ecological, disturbance and spatial variables

To evaluate the influence of ecological, disturbance and spatial variables in herb–shrub communities of both years, we used only FG data which allow generalizations applicable to other forest ecosystems. More precisely, for each year, we constructed: (a) a non-spatial model to determine relationships between FGs and ecological and disturbance variables; (b) a spatial model to characterize the spatial structure of the community; and (c) a model with all explanatory datasets to evaluate their relative roles and to define the involvement of endogenous or exogenous assembly processes in shaping the community structure.

For these analyses, we used the detrended and Hellinger-transformed FG datasets from the STI analyses. We previously normalized ecological and disturbance variables into *z*-scores ($\mu = 0$ and $\sigma = 1$). We then performed a forward-selection procedure with double-stopping criteria (Blanchet, Legendre, & Borcard, 2008) to select explanatory variables that significantly explained the variation in the FG datasets. Variance inflation factors (VIFs) were computed for each forward-selection test, except for the selection of spatial variables as *dbMEM*s are orthogonal. Because all VIFs were <5, subsequent models were built only with the significant forward-selected variables (Legendre & Legendre, 2012).

For each year, we designed the non-spatial model using a partial redundancy analysis (*p*RDA; Legendre & Legendre, 2012) in

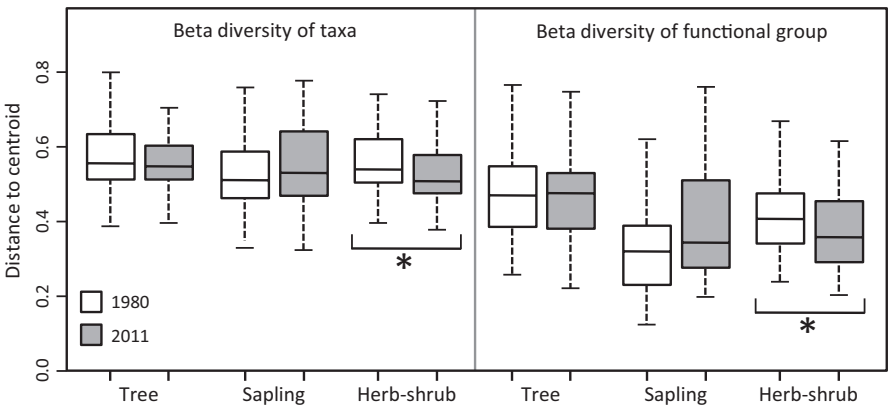

FIGURE 2 Beta diversity in 1980–2011 based on taxa (left) and functional group (right) for each vegetation stratum. Beta diversity was measured as the distance of sites to group centroid, here represented using boxplots (median and quartiles) of the sites-to-centroid distance. Significant differences in beta diversity ($p \leq 0.05$) are indicated with an asterisk

which the spatial autocorrelation of *dbMEM*s has been removed from the ecological and disturbance datasets. We then plotted the resulting unbiased scores in an ordination diagram to interpret ecological relationships. We rather modeled the *dbMEM* variables (either positive or negative) with redundancy analyses (RDA). We mapped the resulting scores of these spatial models to visualize the spatial structure of community. We also calculated a variation partitioning model through RDA to integrate all explanatory datasets. Thus, we divided the explained variation of the FG response data into seven fractions accounting for ecological, disturbance and spatial autocorrelation datasets and their shared effects. We used the fraction associated to true spatial autocorrelation to infer the endogenous assembly processes, while we inferred the exogenous processes from the induced spatial autocorrelation fractions. In addition to this model, we calculated a Moran's *I* coefficient test on each of the ecological and disturbance variables (d = 147 m) to determine which variable was likely to cause induced autocorrelation.

All analyses were carried out in the program *R* (version 3; *R* Core Team, Vienna, Austria), using the packages *FD* for the determination of FGs (Laliberté & Shipley, 2011), *PCNM* for the STI-tests and for the construction of *dbMEM*s (Legendre, Borcard, Blanchet, & Dray, 2013), *packfor* for the forward-selection tests (Dray, Legendre, & Blanchet, 2013), and *vegan* for homogeneity of dispersion tests, PERMANOVA of centroid locations, (*p*)RDA models and variation partitioning analyses (Oksanen et al., 2013). For all models, the percentages of explained variation were based on Ezekiel's R^2_a and the statistical hypotheses were tested under 10,000 permutations with pseudo-*F* ratios.

3 | RESULTS

3.1 | Richness and beta diversity

We recorded a total of 31 tree taxa in 1980 and 26 in 2011 (total = 31). Tree richness did not change over time (paired t = 0.98; two-tailed p = 0.3), with an average of six taxa per quadrat for both years. We identified 28 taxa of saplings in 1980 and 29 in 2011 (total = 30). Sapling richness per quadrat decreased from an average of eight to six taxa (paired t = 3.28; two-tailed p = 0.002). In 1980, 242 herb–shrub taxa were recorded and 202 in 2011 (total = 271). Herb–shrub richness per quadrat decreased from an average of 40 to 35 taxa (paired t = 1.93; two-tailed p = 0.05). Overall, we found 28 new taxa and failed to recover 68 others. About half of the new taxa (15) were exotics found in the central marsh. Most of the lost taxa were either wetland plants located in the floodplain (29) or exotics (18) found in young forest stands in 1980. However, in 2011 45 of the 68 lost plants were observed in non-forest habitats of the park (outside sampling quadrats).

For both years, we identified eight tree and sapling FGs (Appendix S3). Tree FG richness per quadrat slightly increased over time from an average of three to four (paired t = 1.92; two-tailed p = 0.05) while sapling FG richness per quadrat did not change (paired t = 0.33; two-tailed p = 0.7). We identified 26 herb–shrub FGs both years (Table 2). Herbs and small shrubs with fleshy fruits and extensive vegetative propagation were the most frequent type of FGs (*Ext.fles*) both years. The number of herb–shrub FGs per quadrat decreased from an average of 16 to 14 (paired t = 2.37; two-tailed p = 0.02).

As mentioned in the methods section, no change in beta diversity occurred in tree and sapling communities for both taxa and FG data (Figure 2). Herb–shrub beta diversity significantly decreased over time, for both taxa (F = 4.34, p = 0.04) and FGs (F = 4.37, p = 0.07; Figure 2). These decreases were associated with a shift in composition for both taxa (centroid location: F = 5.39, p = 0.0001) and FGs (centroid location: F = 4.17, p = 0.002).

3.2 | Spatial structure

According to STI-test results, 34 herb–shrub taxa out of 271 taxa significantly changed their spatial structures over time (Appendix S4). The most striking changes included the disappearance, or near disappearance, of 10 taxa associated in 1980 with cultivated areas (e.g., *Fragaria virginiana*, *Leucanthemum vulgare*, *Valeriana officinalis*; Appendix S5a–d), and the spatial expansion of some exotics, mainly *Alliaria petiolata* and *Rhamnus cathartica* (Appendix S5e–h). Also, 11 taxa either absent or sporadically present in 1980 colonized or moved toward the central sector in 2011 (e.g., *Carex pseudocyperus*, *Equisetum arvense*, *Impatiens capensis*, *Tussilago farfara*; Appendix S5i–l), while others, especially *Ribes cynosbati*, moved toward the external edges (Appendix S5m,n).

The spatial structure of 9 of the 26 FGs changed significantly over time (Appendix S6). A contraction of the distribution occurred for *Com.poly*, *Com.papp*, *Int.papp*, *Int.wool* (Appendix S7a,b). They are mostly composed of plants with wind-dispersed seeds (pappus or woolly seeds) or with low to intermediate vegetative propagation capabilities. Inversely, the distribution of *Ext.aere*, *Ext.fles*, *Ext.fles.woody*, *Ann.lent* expanded (Appendix S7c,d). They are typically composed of plants with fleshy fruits or extensive vegetative propagation capabilities. The tall woody plant FG (*Ext.fles.woody*), that was abundant in a few quadrats in 1980, experienced extreme spatial expansion; its abundance increased in 70% of the quadrats (43 out of 62). Finally, relocation without changes in abundance was observed for *Ext.poly* (Appendix S7e,f). Multivariate STI-tests were significant for taxa (df = 30, F = 1.18, p = 0.023) and FGs (df = 30, F = 1.32, p = 0.016), indicating that changes detected at the level of individual taxon or FG were reflected in the whole community composition.

3.3 | Variables explaining FG composition

According to the forward-selection procedure, the FG composition of the herb–shrub communities in 1980 was significantly explained by the variables *Drainage*, *VegDisturb*, *Beaver* and *dbMEM*-3 (Table 3). These variables, except *dbMEM*-3, were still significant in 2011, along with seven new variables (*VegHeight*, *ExtEdge*, *IntEdge*, *dbMEM-4*, *dbMEM-5*, *dbMEM-8* and *dbMEM-13*). Among these, two

TABLE 2 Herb–shrub functional groups (FG) derived from the cluster analysis on plant attributes (in parentheses = the number of taxa composing the FG)

FG (nr. of taxa)	Mean height (dm)	Most frequent value (i.e., mode) of qualitative plant attributes	Proportion (%): 1980	Proportion (%): 2011
Ann.lent (13)	8.3	Short-lived; Compact; Lenticular	2.3	3.3
Ann.papp (9)	8.9	Short-lived; Compact; Pappus	0.6	0.5
Ann.adhe (5)	9.4	Short-lived; Compact; Adhesive	0.7	0.6
Int.elai.geo (10)	2.6	Long-lived; Intermediate; Elaiosome	9.9	11.8
Ext.fles (36)	15.8	Long-lived; Extensive; Fleshy	24.2	25.7
Int.fles (10)	41.1	Long-lived; Intermediate; Fleshy	5.0	6.8
Ext.fles.woody (7)	74.3	Long-lived; Extensive; Fleshy	5.4	9.5
Int.adhe (6)	6	Long-lived; Intermediate; Adhesive	5.0	3.3
Com.adhe (15)	7	Long-lived; Compact; Adhesive	1.9	1.3
Int.ribb (6)	5.3	Long-lived; Intermediate; Cylindrical	0.1	0.1
Int.dust (16)	6.2	Long-lived; Intermediate; Dustlike	4	6.7
Ext.dust (13)	8.6	Long-lived; Extensive; Dustlike	7.9	7.7
Int.papp (11)	7.9	Long-lived; Intermediate; Pappus	8.1	3.9
Ext.papp (7)	8.8	Long-lived; Extensive; Pappus	0.3	0.9
Com.papp (5)	9.9	Long-lived; Compact; Pappus	2.1	1.6
Ext.wing (10)	27.9	Long-lived; Extensive; Winged	0.4	0.3
Int.wool (6)	9.3	Long-lived; Intermediate; Woolly	0.4	0.1
Ext.wool (6)	26.8	Long-lived; Extensive; Woolly	0.2	0.5
Com.aere (6)	6.3	Long-lived; Compact; Aerenchyma	2.4	1.3
Int.aere (12)	6.8	Long-lived; Intermediate; Aerenchyma	0.9	1.1
Ext.aere (8)	11.1	Long-lived; Extensive; Aerenchyma	0.6	0.7
Int.lent (8)	6.9	Long-lived; Intermediate; Lenticular	1.7	0.6
Int.poly (10)	6.1	Long-lived; Intermediate; Polyangular	0.9	0.9
Com.poly (13)	7	Long-lived; Compact; Polyangular	2.1	1.9
Ext.poly (13)	8.5	Long-lived; Extensive; Polyangular	1.4	1.4
Ext.glob (10)	6.3	Long-lived; Extensive; Globular	11.5	7.4

The mean height of the taxa included in each FG is indicated. The proportion corresponds to the sum of the abundances in all quadrats for a given FG divided by the sum of the abundances of all FGs and presented in percentage.

were associated with disturbances (*ExtEdge* and *IntEdge*). All significant spatial variables were associated with positive autocorrelation. All these significant explanatory variables were used to subsequently build the non-spatial and spatial models as well as the integrative models that included all explanatory datasets.

3.4 | Influence of non-spatial variables on FG composition

According to the new models built to determine the influence of ecological and disturbance variables combined together, these variables explained a larger amount of variation in FG composition in 2011 (R^2_a = 24%, df = 6, F = 4.48, $p \leq 0.001$) than in 1980 (R^2_a = 19%, df = 3, F = 5.93, $p \leq 0.001$). Soil drainage was the main variable segregating the distribution of FGs through BDS for both years (axis 1; Figure 3). In both years, the second *p*RDA axis reflects the impact of beaver damage and the presence of vegetation disturbances, as well as edge effects and vegetation height in 2011. The main differences in FG distribution over time appear along the second *p*RDA axes. For instance, most FGs were negatively correlated to beaver damage in 1980 (Figure 3a), whereas this damage was positively correlated to some FGs in 2011 (Figure 3b), especially *Ext.wool* that was composed of plants having woolly appendages on their seeds and extensive vegetative propagation. In 1980, the FG composed of tall woody plants dispersing through fleshy fruits and extensive vegetative propagation (*Ext.fles.woody*) contributed little to the community composition while it was positively correlated to the proximity of edges in 2011.

Regardless of the survey year, the FGs contributing the most to the community composition were those dispersed by elaiosome seeds (*elai*) or through extensive vegetative propagation (*Ext*), and consisting of low-growing (*Int.elai.geo*), intermediate size (*Ext.glob*; *Ext.dust*) and tall-growing (*Ext.fles*) plants. Plants having propagules with high buoyancy (e.g., *Ann.lent*, *Int.aere*, *Ext.aere*) were also among the most influential FGs, especially through their positive relationships with poor drainage conditions.

TABLE 3 Significant variables ($p \leq 0.05$) selected with forward-selection tests between the functional group composition of herb–shrub communities and each of the explanatory datasets

	Ecological	Disturbances	Positive spatial autocorrelation	Negative spatial autocorrelation
1980	R^2_a = 12.1%	R^2_a = 8.4%	R^2_a = 1.6%	R^2_a = 0%
	Drainage	VegDisturb	dbMEM-3	
		Beaver		
2011	R^2_a = 21.5%	R^2_a = 11.7%	R^2_a = 8.5%	R^2_a = 0%
	Drainage	VegDisturb	dbMEM-4	
	VegHeight	Beaver	dbMEM-5	
		ExtEdge	dbMEM-8	
		IntEdge	dbMEM-13	

The R^2 (in percentages) used as the second stopping criteria are also given. Models with all datasets combined together were significant in 1980 (R^2_a = 23.8%, df = 4, F = 5.77, p = 0.009) and 2011 (R^2_a = 30.7%, df = 4, F = 3.71, p = 0.009).

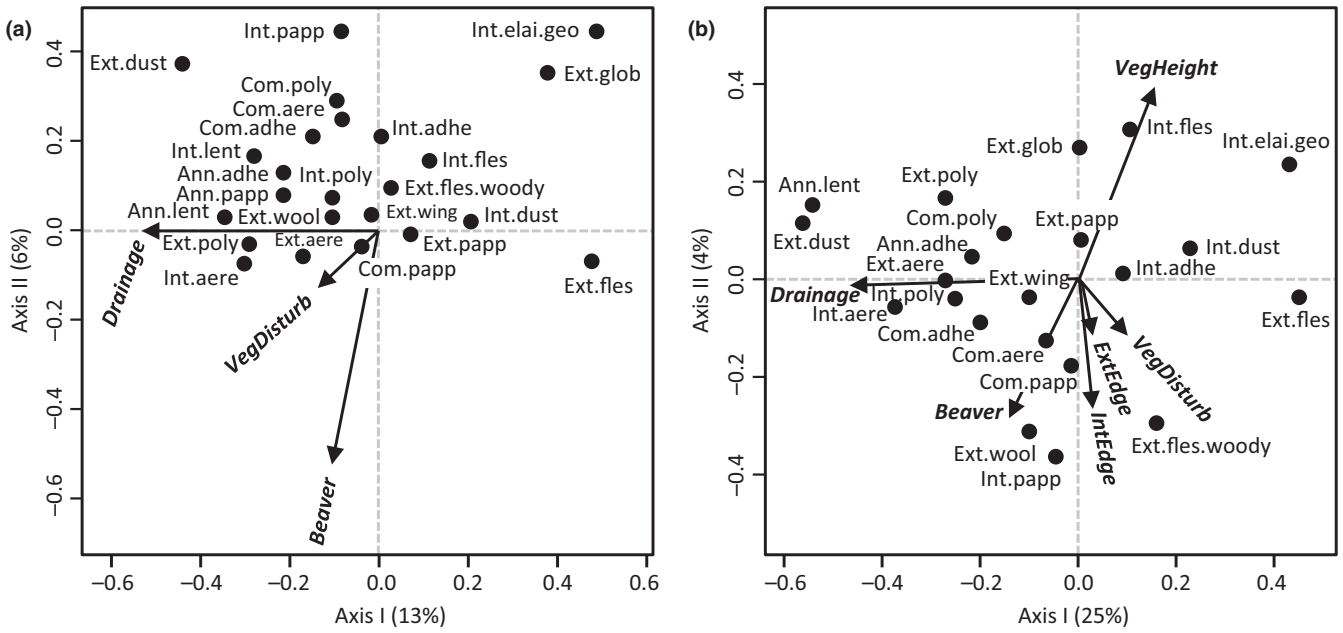

FIGURE 3 Ordination diagrams showing the functional group (FG) composition of the herb–shrub communities in 1980 (a) and 2011 (b) explained by ecological and disturbance variables with spatial effects removed. Axes I and II were significant ($p \leq 0.05$), and their contributions to the variance are indicated in brackets. See Table 2 for FG abbreviations

3.5 | Influence of spatial variables on FG composition

According to the new models built to characterize the spatial structure of the community, spatial variables explained a larger proportion of variation in 2011 (R^2_a = 9%, df = 4, F = 2.58, p = 0.005) than in 1980 (R^2_a = 2%, df = 1, F = 2.20, p = 0.036), meaning that the FG composition of nearby communities have become more similar than expected by chance (i.e., more spatially structured). For both surveys, the spatial structure of FG composition was characterized by the presence of clumped patterns (filled squares; Figure 4), but their location differed over the years. In 1980, clumps were observed in the north and the south (Figure 4a), while in 2011, they were mostly located near the drainage ditches (Figure 4b) and in the central sector (Figure 4c).

3.6 | Relative influence of explanatory datasets on FG composition

According to the new models using all datasets together, in both years ecological conditions alone were the main variables shaping the herb–shrub communities (Figure 5). In contrast, the effect of disturbances alone was stronger in 1980 than in 2011 (37.4 vs 9.6%). The influence of the true spatial autocorrelation was similar in 1980 and 2011 (11.2 vs 12.1%), meaning that some endogenous processes, such as dispersal, have remained stable. However, while only true spatial autocorrelation influenced the spatial structure (i.e., clumped patterns) of communities in 1980, most of the spatial autocorrelation found in 2011 was induced by ecological and disturbance variables (18.4%) with 11.4% specifically attributable to disturbances (*VegDisturb*, *Beaver*, *ExtEdge* and *IntEdge*; all having significant positive Moran's I coefficients).

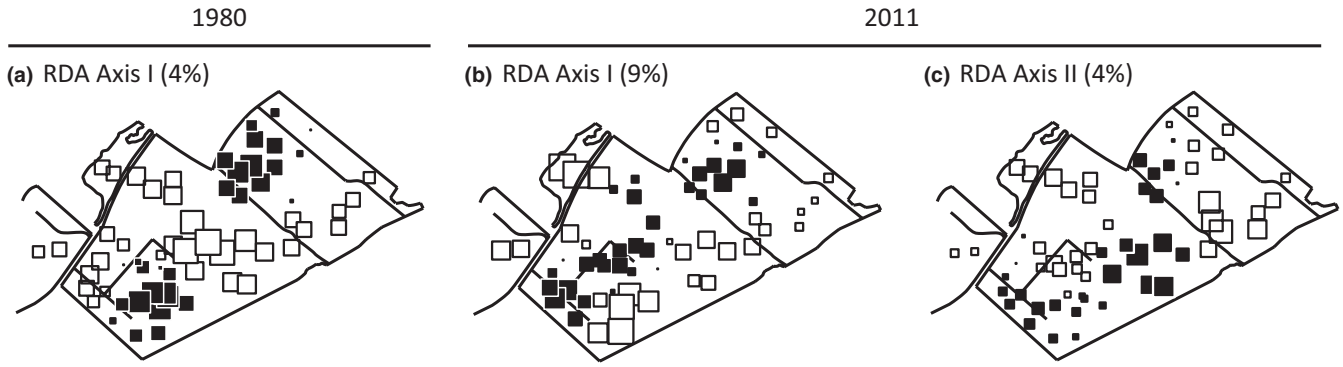

FIGURE 4 Maps showing the spatial structures of functional group composition of herb–shrub communities in 1980 (a) and 2011 (b, c). Squares are the fitted community scores of the redundancy analyses based on forward-selected *dbMEM* variables (Table 3). Only significant axes are plotted ($p \leq 0.05$), and their contributions to the variance are indicated in brackets. The size of the square is proportional to the score plotted. The filled squares are positive scores; empty squares are negative scores

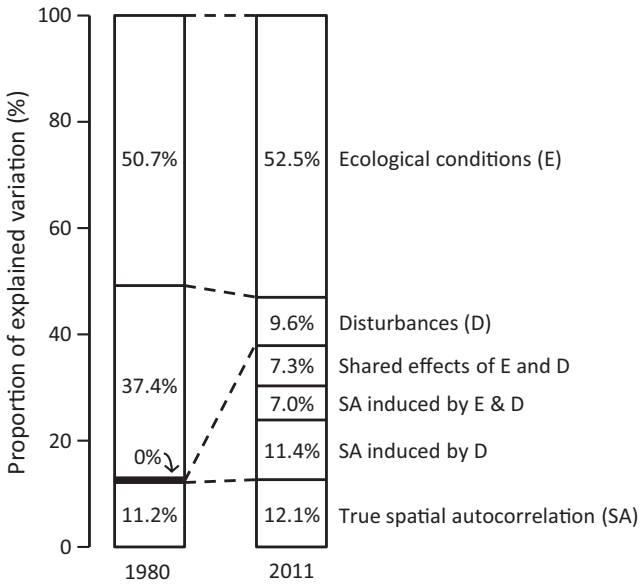

FIGURE 5 Relative influence of ecological conditions, disturbances and spatial variables on the functional group composition of the herb–shrub communities in 1980 and 2011. Unexplained variation is not shown. The boxes of the stacked column chart show the variation of each fraction divided by the total explained variation (calculated with R^2_a) resulting from a redundancy analysis of all forward-selected variables (Table 3). Effects of ecological conditions alone, disturbances alone, and true spatial autocorrelation were all significant ($p \leq 0.01$); other fractions were untestable

4 | DISCUSSION

In this study, we predicted that floristic homogenization occurred in a small protected urban forest. As expected, our results showed a decline of beta diversity over three decades in the taxonomic and functional aspects of the flora, but only in the herb–shrub communities. This homogenization was mirrored by a decrease in the gamma (all quadrats pooled) and alpha (quadrat level) diversity. It was also associated with a temporal shift in composition for both taxa and FGs.

4.1 | Mechanisms of beta diversity changes

Spatial species turnover and richness changes are the two primary mechanisms that can alter beta diversity (Legendre & Gauthier, 2014; Legendre et al., 2010; Olden & Poff, 2003). Although we found a decrease of the herb–shrub species richness, the decline of beta diversity observed was most likely induced by spatial processes associated with the expansion and coalescence of clumps near disturbed areas. Moreover, we found no changes in beta diversity for the tree and sapling communities, whereas they too have undergone some changes of richness but no change in their spatial structure. In fact, most of the studied tree stands were already mature in 1980 and the trees were probably already uniformly distributed; a spatial structure typical of late successional temperate forests that confer spatial stability in the absence of massive disturbances or mortality (Dray et al., 2012; Rozas, 2006; Schleicher et al., 2011). The herb–shrub communities were rather organized, in 1980, into small clumps functionally similar and relatively isolated from each other, and then expanded spatially and eventually coalesced in larger clumps (Figure 4).

Increase in clumping usually engendered an increase in beta diversity (Burkle, Myers, & Belote, 2016). However, this has mostly been observed at very small spatial scales (few meters) when, for instance, micro-disturbances release resources that allow the establishment of clumps of new plant populations in the existing communities (Seabloom, Bjørnstad, Bolker, & Reichman, 2005). It can also occur when a disturbance transforms a relatively uniform structure of vegetation into a clumped structure during the recolonization stage (Myers, Chase, Crandall, & Jiménez, 2015). In contrast, a clumped vegetation structure that turns over time into a more uniform pattern, or into larger clumps, tends to lower beta diversity. Such a phenomenon has been shown, for example, when a forest is converted to agriculture fields, subsequently abandoned, and naturally recolonized by homogeneous grass communities (Flinn & Vellend, 2005; Vellend et al., 2007). It is, therefore, possible that the coalescence of clumps observed at the BDS has induced the homogenization and that these larger clumps are only a transitional stage just before the community structure becomes uniform again in the future. Consequently, our

results support the view of biotic homogenization as a sequential and reorganizational spatial process in which a particular series of functionally similar taxa colonizes new communities, and reorganizes them by becoming dominant (Smith, Knapp, & Collins, 2009).

4.2 | Spatial reorganization of plant attributes

According to our results, the distribution of FGs formed by plants with wind-dispersed seeds and low to intermediate lateral propagation attributes has contracted over the years. These attributes are mostly related to pioneer colonizers (Moora, Öpik, Zobel, & Zobel, 2009; Ozinga, Bekker, Schaminee, & van Groenendael, 2004; Schleicher et al., 2011), that are usually poor competitors under closed canopy because, among others, their seeds are unable to germinate in the absence of light (Ozinga et al., 2004). Their decline was, therefore, likely favored by the increase of shade associated with the aging of trees. Inversely, FGs that significantly expanded their distributions consisted of plants with fleshy fruits, usually dispersed by birds, or with extensive lateral propagation attributes. Plants dispersed by birds are particularly well adapted for closed forests because their fruits can penetrate vegetation through the air, which increases the chances of reaching a suitable microsite (Ozinga et al., 2004; Schleicher et al., 2011). Also, fleshy fruits often fall and germinate near the parent plants, and with plants having extensive lateral propagation, they can form clumps that develop progressively by colonizing free microsites at short distances, which represents a competitive advantage when closed vegetation blocks the influx of long-distance migrants (Moora et al., 2009; Vittoz & Engler, 2007; Williams et al., 2015).

Spatial competition induced by the closed canopy of temperate forests usually creates a compartmentalization of growth space based on the maximum growth height of species (Hermy & Verheyen, 2007; Schamp & Aarssen, 2009). At BDS, herb–shrub communities were dominated both years by four FGs having average heights sufficiently different to occupy distinct levels of the stratum (*Int.elai.geo* = 2.6 dm, *Ext.glob* = 6.3 dm, *Ext.dust* = 8.6 dm, *Ext.fles* = 15.8 dm). This vertical compartmentalization may have caused a selective pressure on plant attributes over time and might explain that the FG of tall woody plants (*Ext.fles.woody*; average height: 74.3 dm) has undergone the most drastic spatial and demographic expansion across communities, becoming the third most abundant FG in 2011. This FG includes bird-dispersed shrubs or lianas such as *Rhamnus cathartica* and *Parthenocissus quinquefolia*, both considered problematic or overabundant plants in North American urban forests (Bergeron & Pellerin, 2014; Brice et al., 2014; Moffatt & McLachlan, 2004). Their tall sizes allow them to occupy the upper part of the herb–shrub stratum, which creates shading that eliminates vulnerable competitors (Godefroid & Koedam, 2007; Moffatt & McLachlan, 2004; Schamp & Aarssen, 2009).

4.3 | Drivers of floristic homogenization

At the time scale covered in this study, environmental filtering is usually the main community assembly process in operation in temperate forests (Gilbert & Lechowicz, 2004; Laliberté et al., 2009). According to our results (Figure 5), the influence of ecological conditions on the FG composition was indeed the most important both years, but this influence was relatively stable over time. Vegetation changes, therefore, rather seem to have occurred through the operating mode (endogenous/exogenous) of spatial processes. In 1980, these spatial processes were solely associated to true spatial autocorrelation variables. When all important explanatory variables are integrated into the spatial model – which is the case here according to Domon et al. (1986) – true autocorrelation is usually the signature of endogenous processes, such as dispersal limitations (Dray et al., 2012; Hubbell, 2001). Between 1980 and 2011, the clumped patterns have expanded, and although endogenous processes were still in operation (true spatial autocorrelation = 12%), much of the variation explaining the spatial structure of FG composition was autocorrelation induced by the patchiness of disturbances alone or in combination with ecological conditions (11.4% + 7% = 18.4%; Figure 5). This autocorrelation arising from exogenous factors is not caused by dispersal limitations, but rather an environmental filtering process (Dray et al., 2012; Gilbert & Lechowicz, 2004; Whittaker, 1967). Spatial structure changes have therefore likely begun in the studied forest with an unpredictable stage governed by dispersal limitations, followed by a predictable stage in which the spatial expansion of some FGs was mostly driven by past disturbances.

The openness of the vegetation and canopy created by the presence of forest edges can act as dispersal corridors for plants (De Blois, Domon, & Bouchard, 2002). According to our results, the proximity of edges has not only induced the clumped spatial structure of FG composition in 2011 but was also strongly correlated with the abundance of the tall woody plant FG. The ability of tall woody plants to spread laterally and occupy the upper part of the herb–shrub stratum probably makes them the most adapted FG to colonize new communities along the linear opening area of forest edges, and eventually to change the overall spatial structure of plant communities.

Changes in the spatial structure of communities were also induced by other types of land use transformation. Most areas with a high index of vegetation disturbance (*VegDisturb*) were agricultural fields in the early 20th century. Agriculture destroys soil structures and micro-landforms, thus limiting the reforestation of several specialist plants (Flinn & Vellend, 2005; Hermy & Verheyen, 2007). Reduced environmental heterogeneity in these disturbed areas has probably favored the establishment of generalist plants over time (Vellend et al., 2007).

Beaver activity was the most recent significant disturbance at BDS. Although herbivory is a homogenization driver (Rooney, Wiegmann, Rogers, & Waller, 2004), the composition modifications observed in the central portion of the forest were more likely induced by the hydric conditions resulting from beaver dams (Rosell, Bozsér, Collen, & Parker, 2005). For instance, the marsh was invaded in 2011 by plants with woolly seeds (e.g., *Phragmites australis*, *Typha* spp.), but this invasion remained localized. On the other hand, soil drainage can be altered well beyond areas permanently flooded by

beaver dams, which can induce peripheral changes in forest composition (Rosell et al., 2005). Indeed, two FGs with buoyant diaspores (*Ext.aere*, *Ann.lent*), a dispersal strategy using water as vector (Vittoz & Engler, 2007), became even more correlated to poorly drained soils in 2011 and have significantly expanded their distribution over time. However, neither of these FGs became dominant and, therefore, beaver damage was at most a weak driver of biotic homogenization.

5 | CONCLUSION

Overall, our study found significant changes in the plant diversity of a small protected urban forest over three decades. The main changes observed are a taxonomic and functional homogenization in the herb–shrub communities. These communities are now spatially structured (clumped), a testimony of land-use changes and site disturbances. The taxa involved in this process were mostly tall plants with fleshy fruits or lateral spreading. In northeastern North America, such species included the problematic shade-tolerant shrub *Rhamnus cathartica* and *Lonicera tatarica* as well as lianas such *Parthenocissus quinquefolia*, *Toxicodendron radicans* and *Vincetoxicum* spp. (Bergeron & Pellerin, 2014; Brice, Bergeron, & Pellerin, 2014; Moffatt & McLachlan, 2004; Rogers, Rooney, Olson, & Waller, 2008). From a management perspective, these results support the need to rapidly revegetate disturbed areas (e.g., logged area, trail sides). This is especially critical in new open areas located near communities dominated by plant of functional groups known to induce homogenization, because the degree of habitat openness and the distance between open areas and putative source populations are important predictors of invasiveness in urban forests (Alson & Richardson, 2006). Using a mixture of native taxa of different sizes at planting time and different sizes at maturity could help to revegetate the herb–shrub stratum, quickly and entirely. Some low and creeping taxa could also be sown or planted tightly to avoid leaving free microsites on the ground (Schuster, Wragg, & Reich, 2018). Sectors already reforested may be more problematic to manage, and increased monitoring of vegetation evolution and eradication of some taxa, especially the exotic ones, might be required. *Rhamnus cathartica* is especially of concern. This shrub species may locally be responsible for an invasional meltdown (sensu Simberloff & Von Holle, 1999), considering this highly invasive exotic species also increases the impacts of others, such as earthworms or starlings (Heimpel et al., 2010). At Bois-de-Saraguay, the cover of common *R. cathartica* is increasing in the polygons where seedlings were detected in 1980 (R^2_a = 63.5%, df = 1, F = 100.7, p < 0.0001; unpublished data), which highlights the necessity of controlling this species as soon as possible. Finally, our study showed that some environmental drivers facilitate the floristic homogenization of communities, but that this process can be initiated stochastically. The inclusion of neutral spatial processes (Hubbell, 2001; Schleicher et al., 2011) in future studies on homogenizing ecosystems could help to develop better intervention strategies.

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DATA ACCESSIBILITY

Data available upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Ecological distances between quadrats and replicates

Appendix S2. Plant attributes, sources and methods

Appendix S3. Functional groups derived from cluster analysis

Appendix S4. Effect of the space–time interaction of each taxon

Appendix S5. Examples of taxa spatial distribution changes

Appendix S6. Effect of the space–time interaction of functional groups

Appendix S7. Examples of functional group spatial distribution changes

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