

Université de Montréal

**Impacts de l'urbanisation sur la diversité spécifique et
fonctionnelle dans les forêts riveraines**

par

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Résumé

L'urbanisation représente une menace majeure pour la biodiversité. Ce mémoire de maîtrise vise à comprendre ses effets sur la composition fonctionnelle et l'homogénéisation biotique dans les forêts riveraines. Des inventaires floristiques ont été réalisés dans 57 forêts riveraines de la région de Montréal.

Afin d'étudier la variation de la composition fonctionnelle avec l'urbanisation, des moyennes pondérées de traits par communauté ont été calculées pour les arbres, arbustes et herbacées. Chaque forêt a été caractérisée par des variables relatives au paysage urbain environnant, aux conditions locales des forêts et aux processus spatiaux. Les conditions locales, notamment les inondations, exerçaient une pression de sélection dominante sur les traits. L'effet du paysage était indirect, agissant via l'altération des régimes hydrologiques. La dispersion le long des rivières était aussi un processus important dans la structuration des forêts riveraines.

Les changements dans la diversité β taxonomique et fonctionnelle des herbacées ont été étudiés entre trois niveaux d'urbanisation et d'inondation. Alors que l'urbanisation a favorisé une différenciation taxonomique, les inondations ont favorisé une homogénéisation taxonomique, sans influencer la diversité β fonctionnelle. L'urbanisation était l'élément déclencheur des changements de la diversité β , directement, en causant un gain en espèces exotiques et une diminution de la richesse totale dans les forêts très urbanisées, et, indirectement, en entraînant un important turnover d'espèces par l'altération des régimes hydrologiques.

Globalement, ces résultats suggèrent que la modification des processus naturels par les

activités anthropiques est le principal moteur de changements dans les communautés riveraines urbaines.

Mots-clés : Analyses spatiales (AEM et MEM), Communautés riveraines, Dispersion, Diversité alpha et beta, Espèces exotiques, Homogénéisation biotique, Inondation, Moyennes pondérées de traits par communauté (CWM), Traits fonctionnels, Urbanisation

Abstract

Urbanization is a major threat to biodiversity worldwide. This thesis aims at understanding its effects on plant functional composition and biotic homogenization in riparian forests. Floristic inventories were carried out in 57 riparian forests of the Montreal area.

To investigate changes in functional composition with urbanization, community weighted means were computed for trees, shrubs and herbs using eight functional traits. Each forest was characterized by variables related to the surrounding urban landscape, local forest conditions and spatial processes. The relative importance of these three subsets on the functional composition was quantified by variation partitioning using redundancy analyses. Local conditions, especially flood intensity, exerted an overriding selection pressure on riparian functional communities. The effect of the landscape was suspected to be indirect, acting on trait patterns likely through alteration of hydrological disturbances in riparian forests. In addition to environmental filtering, dispersal along rivers was also an important process structuring riparian forests.

Changes in taxonomic and functional β -diversity for herb species were studied between three urbanization and flood levels. While urbanization led to taxonomic differentiation, flood intensity fostered taxonomic homogenization, both without influence on functional β -diversity. Urbanization was the main trigger for all β -diversity changes, as it directly caused a gain in exotic species and a net species loss in highly urban forests, and indirectly fostered an important species turnover through alteration of the hydrological regime.

Overall, these results suggest that the alteration and interruption of natural landscape-scale processes by human activities are major mechanisms underlying changes in urban riparian

communities.

Keywords : Alpha and beta diversity, Biotic homogenization, Community weighted means of traits (CWM), Dispersal, Exotic species, Flood, Functional traits, Riparian plant communities, Spatial eigenvector analysis (AEM and MEM), Urbanization

Table des matières

Résumé.....	i
Abstract.....	iii
Liste des tableaux.....	viii
Liste des figures.....	ix
Liste des annexes.....	xi
Remerciements.....	xiii
Chapitre 1.....	1
Introduction.....	1
Les filtres écologiques dans les milieux urbains.....	2
Urbanisation et homogénéisation biotique.....	4
Historique de perturbations et héritage écologique dans les villes.....	6
Les forêts riveraines.....	7
Impact de l'urbanisation sur les forêts riveraines.....	10
Objectifs.....	12
Chapitre 2.....	14
Environmental filtering and spatial processes in urban riparian forests.....	14
Abstract.....	15
Introduction.....	17
Methodology.....	20
Study area.....	20
Site selection and sampling design.....	20

Vegetation sampling	22
Environmental data sampling	22
Data analysis	25
Results.....	29
Directional vs non-directional spatial patterns	29
Scales of spatial variation	31
Partitioning trait variation between environmental filtering and spatial processes	31
Discussion.....	35
The interplay between local, landscape and spatial filters.....	35
Shift of plant traits along an urban–rural gradient	37
Shift of plant traits along a human-induced successional gradient.....	38
Conclusion	39
References.....	41
Chapitre 3.....	47
Does urbanization lead to taxonomic and functional homogenization in riparian forests?	47
Abstract.....	48
Introduction.....	50
Methodology.....	53
Study area.....	53
Site selection and vegetation sampling.....	54
Urbanization and flooding intensity.....	56
Functional traits	57
Data analyses	57

Results.....	62
Discussion.....	68
Conclusion	75
References.....	77
Chapitre 4.....	84
Conclusion	84
Annexes du chapitre 2.....	i
Annexes du chapitre 3.....	xxii

Liste des tableaux

Chapitre 2

Table 2.1. Description of all explanatory variables characterizing the 57 riparian forests of the Greater Montreal region..... 23

Table 2.2. Description of the selected functional traits used in analyses..... 25

Chapitre 3

Table 3.1. Number of forest patches and class ranges for the different levels of urbanization and flood intensity..... 57

Table 3.2. Description of the selected functional traits used to measure functional β -diversity changes in urban riparian forests..... 58

Table 3.3. Results of permutational test of multivariate dispersion and permutational MANOVA between urbanization and flood levels for taxonomic and functional β -diversity of total, native and exotic species..... 63

Liste des figures

Chapitre 2

Figure 2.1. Location map of the 57 riparian forests sampled in the Greater Montreal region.....	21
Figure 2.2. Variation partitioning of trait composition explained by the subsets of selected AEM and MEM variables.....	30
Figure 2.3. Maps of selected AEM functions, reflecting patterns at different spatial scales, for tree, shrub and herb CWM data along des Mille Îles and des Prairies rivers	31
Figure 2.4. Variation partitioning and ordination diagrams of CWM explained by the subsets of local, landscape and spatial variables.....	35

Chapitre 3

Figure 3.1. Location map of the 57 riparian forests sampled in the Greater Montreal region.....	55
Figure 3.2. Taxonomic β -diversity. Influence of urbanization and flood levels on the multivariate dispersion of species composition in the forest patches for total, native and exotic species.....	64
Figure 3.3. Functional β -diversity. Influence of urbanization and flood levels on the multivariate dispersion of trait composition in the forest patches for total, native and exotic species.....	65

Figure 3.4. PCoA biplot of all forests based on total species functional composition matrix. Functional traits were projected on the PCoA ordination to show their contribution to β -diversity..... 67

Figure 3.5. Correlations between total species richness, exotic proportion, taxonomic β -diversity and functional β -diversity for the total species pool..... 69

Figure 3.6. Differences in taxonomic and functional β -diversity caused by exotic species between different urbanization and flood levels 70

Liste des annexes

Chapitre 2

Table S2.1. Number of patches selected for each range of the selection criterion: patch area, patch position, proportion of flooded forest area, and proportion of surrounding impervious surfaces.	ii
Table S2.2. Pearson correlation coefficients between all explanatory variables from the local and landscape subsets	iii
Table S2.3. Species functional trait matrix for trees, shrubs and herbs	iv
Table S2.4. Comparison of weights based on RDA models of CWM.....	xx
Table S2.5. Selected explanatory variables using the forward selection procedure	xxi
Figure S2.1. Connectivity diagram, based on the current direction, used to generate the AEM and the dbMEM eigenfunctions.....	xvii
Appendix S2.1. Steps to create the connectivity matrix	xvii

Chapitre 3

Table S3.1. Number of patches selected for each range of the selection criterion:

patch area, patch position, proportion of flooded forest area, and proportion of
surrounding impervious surfaces xxiii

Table S3.2. Herb species functional traits and immigration status xxiv

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Chapitre 1

Introduction

L'urbanisation représente une menace majeure pour la biodiversité (Grimm et al., 2008). Dans les forêts urbaines, les conditions environnementales sont souvent radicalement modifiées par les activités anthropiques, menant ainsi à l'extinction locale d'espèces sensibles aux perturbations au profit d'espèces plus résistantes (McKinney, 2006). En effet, l'environnement urbain agit comme une succession de filtres écologiques qui exercent une forte pression de sélection sur les traits fonctionnels des espèces (Williams et al., 2008), de façon analogue à la sélection naturelle, ce qui altère les processus d'assemblage des communautés. L'altération des règles d'assemblage modifie les patrons de distribution des traits fonctionnels dans le paysage (Knapp et al., 2009; Vallet et al., 2010a; Duncan et al., 2011; McCune & Vellend, 2013; Williams et al., 2015) et peut également mener à une homogénéisation biotique des communautés due à une sélection artificielle biaisée vers un nombre restreint d'espèces ou de traits (McKinney, 2006; La Sorte et al., 2007, 2014; Aronson et al., 2014a). Par conséquent, la distribution des espèces dans les écosystèmes urbains est en général gouvernée par des facteurs anthropiques (e.g., Godefroid & Koedam, 2007; Knapp et al., 2008; Čepelová & Münzbergová, 2012), tandis que les facteurs biotiques et abiotiques naturels jouent un rôle secondaire. Toutefois, dans les forêts riveraines, l'intensité des perturbations naturelles pourrait davantage complexifier l'impact de l'urbanisation sur les communautés végétales. Les forêts riveraines sont soumises à de fréquentes inondations qui peuvent interagir avec les filtres anthropiques associés à l'urbanisation. De plus, comme les

inondations agissent directement sur la survie des individus, en particulier par l'anoxie (Blom & Voesenek, 1996; Parent et al., 2008), leurs effets pourraient outrepasser ceux des filtres urbains. Pourtant, l'importance relative des filtres urbains et naturels sur les communautés riveraines a été peu explorée jusqu'à récemment (e.g., Burton et al., 2009; Sung et al., 2011). Ce mémoire de maîtrise étudie donc les impacts de l'urbanisation sur les forêts riveraines et tente de démêler les effets des filtres urbains et naturels, d'une part sur la composition fonctionnelle (chapitre 2), et d'autre part, sur l'homogénéisation biotique (chapitre 3) des communautés végétales. Dans le présent chapitre, le concept des règles d'assemblage des communautés permet d'examiner comment l'urbanisation et les conditions riveraines, notamment les inondations, agissent sur les traits fonctionnels des plantes et, par conséquent, sur la distribution de la diversité.

Les filtres écologiques dans les milieux urbains

La perte et la fragmentation d'habitats, conséquences inhérentes de l'urbanisation, sont les principaux filtres écologiques déterminant les patrons de végétation dans les villes (Williams et al., 2008). Les milieux urbains sont des paysages très fragmentés où ne subsistent souvent que de petits vestiges de forêts, isolés les uns des autres par une matrice humanisée. Alors que la perte d'habitat cause l'extinction de nombreuses populations d'espèces, plus particulièrement les espèces spécialistes (McKinney & Lockwood, 1999; Sax & Gaines, 2003; Van der Veken et al., 2004), la fragmentation réduit la probabilité de colonisation des habitats isolés, favorisant entre autres les espèces ayant une grande capacité de dispersion, telles que celles ayant recours à l'anémochorie et la zoochorie (Moffatt et al., 2004; Knapp et al., 2009; Marini et al., 2012; Penone et al., 2012).

Cette fragmentation du paysage crée également des lisières dans les forêts, où les facteurs abiotiques sont altérés par la matrice environnante. Comparativement à l'aire centrale des forêts, les lisières sont soumises à des conditions environnementales hostiles pour les espèces forestières, notamment à des conditions de luminosité et de température plus élevées, une plus faible humidité du sol et des perturbations plus fréquentes (Murcia, 1995; Vallet et al., 2010b). Ces conditions favorisent ainsi l'établissement d'espèces annuelles, à croissance rapide et tolérantes aux perturbations (Godefroid & Koedam, 2003; Guirado et al., 2006; LaPaix & Freedman, 2010). Les lisières sont aussi vulnérables à l'introduction de plantes exotiques dans les forêts (Cadenasso & Pickett, 2001; Guirado et al., 2006), car, en plus de leur offrir des conditions environnementales propices, elles subissent une pression de propagules d'espèces ornementales provenant des jardins et des parcs aménagés dans leur voisinage (Williams et al., 2008; Kowarik, 2011). En outre, la plupart des forêts urbaines, étant soumises à un usage récréatif intense (Moffatt et al., 2004; Duguay et al., 2007), sont traversées par de multiples sentiers qui perturbent le sous-bois (Godefroid & Koedam, 2004) et facilitent la percolation des espèces de lisières dans l'aire centrale des forêts (Guirado et al., 2007; LaPaix et al., 2012).

L'urbanisation entraîne aussi une augmentation des surfaces imperméables au détriment du couvert végétal. Cette transformation du sol modifie les conditions environnementales dans les habitats résiduels, en particulier en altérant les conditions hydrologiques. Les surfaces imperméables sont aussi associées à la formation d'îlots de chaleur urbains, lesquels provoquent un stress thermique et hydrique qui favorise les espèces tolérantes à la sécheresse (Williams et al., 2015). Dans les régions froides, les îlots de chaleur urbains peuvent également prolonger la saison de croissance (Imhoff et al., 2000) et ainsi

favoriser l'établissement des espèces ayant des exigences thermophiles, comme de nombreuses plantes rudérales et exotiques introduites à partir de régions plus chaudes (Knapp et al., 2008, 2009; Čepelová & Münzbergová, 2012; Penone et al., 2012). De plus, les surfaces imperméables limitent l'infiltration des eaux pluviales dans le sol et la recharge de la nappe phréatique (Walsh et al., 2005; White & Greer, 2006), exerçant un stress hydrique supplémentaire sur la végétation (Groffman et al., 2003; Sung et al., 2011). Il en résulte aussi une augmentation du ruissellement de surface (Paul & Meyer, 2001; White & Greer, 2006) qui peut accumuler les polluants urbains et contaminer les habitats résiduels (Kaye et al., 2006) et ainsi favoriser les espèces ayant une préférence pour les sols alcalins et fertiles (Godefroid et al., 2007; Vallet et al., 2010b).

Urbanisation et homogénéisation biotique

L'urbanisation entraîne des changements non aléatoires dans la distribution des espèces, créant des patrons complexes de biodiversité à travers différentes échelles spatiales (Grimm et al., 2008; Williams et al., 2015). Bien que les perturbations humaines aient causé un déclin de la biodiversité mondiale en raison des extinctions, à l'échelle locale, l'introduction d'espèces exotiques semble généralement compenser la perte d'espèces indigènes et enrichir la diversité locale α (Sax & Gaines, 2003). De plus, indépendamment de la diversité α , l'extinction des espèces indigènes spécialisées couplée à l'invasion par des espèces exotiques cosmopolites peut mener à une homogénéisation de la composition des communautés (diminution de la diversité β ; McKinney & Lockwood, 1999; McKinney, 2006). Toutefois, ce processus par lequel les communautés deviennent de plus en plus similaires les unes par rapport aux autres dépend de nombreux facteurs, principalement de l'échelle (Olden & Poff,

2003), du type d'habitat (Qian & Guo, 2010; Gong et al., 2013) et du temps de résidence des espèces exotiques (Kühn & Klotz, 2006; Lososová et al., 2012). Par exemple, l'homogénéisation a surtout été observée entre différentes villes à l'échelle planétaire ou continentale (Baiser et al., 2012; Aronson et al., 2014a; La Sorte et al., 2014). Alors qu'à l'échelle locale, le long d'un gradient urbain à rural dans les régions métropolitaines, certaines études tendent à montrer que l'urbanisation peut provoquer une différenciation taxonomique plutôt que l'homogénéisation prédite (Kühn & Klotz, 2006; Aronson et al., 2014b; Bossu et al., 2014). D'ailleurs, bien que l'homogénéisation à l'échelle planétaire soit imputée à l'expansion des espèces exotiques, à l'échelle locale, celles-ci semblent généralement accroître la diversité β dans les écosystèmes perturbés par l'humain (Kühn & Klotz, 2006; Abadie et al., 2011; Lososová et al., 2012; Aronson et al., 2014b), tandis que les espèces indigènes semblent favoriser l'homogénéisation (McCune & Vellend, 2013; Johnson et al., 2014; Li & Waller, 2015).

Comme les espèces ne sont pas sélectionnées au hasard, mais selon leurs traits fonctionnels, une homogénéisation ou une différenciation taxonomique devrait se traduire en une homogénéisation ou une différenciation fonctionnelle (Olden et al., 2004). Cependant, les preuves empiriques d'une relation entre la diversité β taxonomique et fonctionnelle sont inconsistantes et contradictoires (Smart et al., 2006; Abadie et al., 2011; Naaf & Wulf, 2012; Sonnier et al., 2014), probablement parce que cette relation dépend notamment de la redondance des traits entre les espèces (Baiser & Lockwood, 2011), de même que de la composition en espèces et des conditions environnementales initiales (Fukami et al., 2005; Smart et al., 2006). Par exemple, l'absence d'homogénéisation fonctionnelle malgré une homogénéisation taxonomique dans le temps reflète un haut niveau de redondance

fonctionnelle entre les communautés, i.e. le remplacement des espèces par d'autres espèces ayant des traits similaires (Sonnier et al., 2014). Inversement, une diminution de la richesse locale suivie d'une différenciation taxonomique et d'une homogénéisation fonctionnelle indique que la perte d'espèces entraîne une convergence des traits, tout en maintenant la distinction historique des espèces entre les communautés (Smart et al., 2006). Par conséquent, il demeure incertain si une homogénéisation taxonomique implique réellement une homogénéisation fonctionnelle.

Historique de perturbations et héritage écologique dans les villes

La réponse des écosystèmes à l'urbanisation est complexe, car l'historique de perturbations et d'utilisation du sol continue à influencer les écosystèmes, en laissant un héritage écologique qui persiste longtemps, parfois pour plusieurs décennies ou siècles (Foster et al., 2003; Kuussaari et al., 2009; Wulf & Kolk, 2014). L'influence de cet héritage du passé sur les composantes biotiques et abiotiques des écosystèmes dépend principalement du type de perturbations. Par exemple, l'héritage de l'agriculture persiste longtemps dans les caractéristiques des sols, lesquels ont généralement un pH et des concentrations en nutriments plus élevés ainsi qu'une plus faible teneur en matière organique que les sols forestiers (Flinn & Vellend, 2005). Ainsi, une perturbation majeure influence directement la composition des plantes qui viendront coloniser l'habitat une fois la perturbation terminée en léguant des conditions environnementales modifiées. À l'opposé, certaines perturbations, comme la fragmentation, présentent plutôt une réponse décalée dans le temps, car les espèces peuvent survivre à la perturbation, mais disparaître beaucoup plus tard. Cette dette d'extinction se produit en raison d'un décalage temporel entre la perturbation et la réponse des espèces

(Kuussaari et al., 2009; Ramalho et al., 2014). Ainsi, les petits vestiges de forêts peuvent parfois contenir une plus grande richesse que prédit par la relation aire-espèces, car de nombreuses espèces y sont établies depuis longtemps et leurs populations peuvent s'y maintenir localement par reproduction végétative ou par la dispersion sur de courtes distances (Vellend et al., 2006; De Sanctis et al., 2010; Wulf & Kolk, 2014). Les décalages temporels sont plus importants dans les fragments plus grands et plus connectés, et pour une perte d'habitat plus sévère, laquelle engendre une dette d'extinction plus grande. De plus, les espèces avec un cycle de vie long, comme les plantes vivaces ou ligneuses, ont une réponse plus lente aux perturbations que les espèces annuelles (Kuussaari et al., 2009).

Les forêts riveraines

Les forêts riveraines sont particulièrement fragiles aux transformations du paysage. Or, dans un contexte urbain, elles revêtent une grande importance pour la conservation (Kominoski et al., 2013) étant donné qu'elles soutiennent une grande diversité d'espèces végétales uniques qui assurent de multiples fonctions écosystémiques essentielles. Ces forêts jouent des rôles écologiques cruciaux pour le maintien de la qualité de l'eau et pour de nombreux processus hydrologiques, tels que la filtration des contaminants et des sédiments, la stabilisation des rives, l'atténuation de l'intensité des crues et la régulation thermique des cours d'eau (Tabacchi et al., 2000; Paul & Meyer, 2001; Décamps et al., 2004; Naiman et al., 2005). De plus, étant soumises à un régime de perturbations sévères, les forêts riveraines arborent des assemblages floristiques distincts des habitats terrestres adjacents et contribuent ainsi à augmenter la biodiversité régionale (Sabo et al., 2005).

Le régime de perturbations hydrologiques, soit les inondations, les sécheresses et les fluctuations de la nappe phréatique, gouverne la dynamique végétale et structure les patrons de distribution d'espèces dans les forêts riveraines (Tabacchi et al., 1998; Richardson et al., 2007). Les inondations, dont l'intensité et la fréquence varient selon la distance à la rive et la topographie, éliminent partiellement ou totalement la végétation en place, rendent disponibles les ressources (e.g., nutriments, lumière), déposent de nouveaux sédiments et créent des espaces vacants pour la colonisation (Jansson et al., 2005; Moggridge et al., 2009). Cette réinitialisation périodique de la succession végétale crée une mosaïque d'habitats hétérogènes, complexes et dynamiques favorisant la coexistence de nombreuses espèces (Tabacchi et al., 1998, 2005). Toutefois, la survie dans un milieu aussi dynamique requiert diverses stratégies de réponse aux perturbations et au stress (Violle et al., 2011) puisque les espèces riveraines sont confrontées de manière récurrente non seulement aux inondations, mais aussi à l'anoxie, l'érosion, l'abrasion et la sécheresse.

Dans les milieux riverains, l'anoxie au niveau de la rhizosphère quand le sol est inondé est certainement la contrainte la plus importante pour la survie et la croissance des plantes. Pour y faire face, les plantes ont développé différentes adaptations permettant la diffusion de l'oxygène à partir des parties aériennes de la plante vers les racines, notamment la production de tissus aérochymateux dans les racines et les tiges, ainsi que la croissance de racines adventives (Lytle & Poff, 2004; Parent et al., 2008). En réponse aux fluctuations extrêmes allant d'un surplus à un manque d'eau, certaines plantes peuvent persister dans le sol sous forme d'une banque de graines et attendre que les conditions deviennent favorables à leur germination et leur croissance (Gurnell et al., 2006; Moggridge et al., 2009). Outre le stress physiologique, les inondations exercent aussi des stress physiques sur les plantes par l'érosion,

qui rend le sol instable, ainsi que par l'action abrasive du courant et des débris transportés. Ces stress physiques peuvent favoriser des plantes ayant des branches flexibles, qui leur confèrent une protection contre les cassures, ou encore ayant la capacité de se reproduire végétativement à partir de fragments arrachés par le courant (Karrenberg et al., 2002; Lytle & Poff, 2004).

En plus de structurer les patrons de végétation par les perturbations hydrologiques, le cours d'eau représente un important vecteur de dispersion pour la colonisation des communautés végétales riveraines, particulièrement lors de la crue printanière où la plupart des propagules sont dispersées et déposées (Jansson et al., 2005; Moggridge et al., 2009). Ce processus de dispersion unidirectionnel suivant le courant structure les patrons de distribution de ces communautés (Levine, 2003), par exemple, en créant un gradient de richesse croissant d'amont en aval, autant en espèces indigènes qu'exotiques (Planty-Tabacchi et al., 1996; Tabacchi et al., 2005). Johansson et al. (1996) ont d'ailleurs trouvé une relation positive entre la flottabilité des propagules et la fréquence des espèces dans la végétation riveraine. L'hydrochorie, soit la dispersion par l'eau, peut aussi agir comme un mode de dispersion secondaire sur de très longues distances pour un grand nombre de propagules d'espèces non spécialisées, entre autres pour les espèces catégorisées comme principalement anémochores (Tabacchi et al., 2005; Seiwa et al., 2008; Säumel & Kowarik, 2010) et même zoochores (Hampe, 2004). En facilitant ainsi la dispersion, le cours d'eau maintient une grande connectivité entre les forêts riveraines, atténuant possiblement les effets délétères de la fragmentation du milieu terrestre. L'urbanisation pourrait toutefois perturber tous ces importants processus hydrologiques naturels.

Impact de l'urbanisation sur les forêts riveraines

Contrairement aux perturbations hydrologiques naturelles qui font partie intégrante des écosystèmes riverains, les perturbations anthropiques n'ont pas un effet revitalisant, mais plutôt un effet affaiblissant et détériorant (Naiman et al., 2005). Les conséquences des activités anthropiques sur les écosystèmes riverains sont complexes, car ces perturbations modifient et interagissent avec les processus naturels, et se répercutent à de multiples échelles spatio-temporelles (Naiman et al., 2005; Thorp et al., 2008). De plus, historiquement, les milieux riverains ont toujours été des foyers pour l'occupation humaine et l'agriculture (Groffman et al., 2003), laissant un héritage de perturbations disproportionnellement lourd à ces écosystèmes. Les pressions anthropiques sur les communautés riveraines découlent directement de la destruction des habitats riverains, mais aussi indirectement de la transformation du sol dans le bassin versant et de la modification des régimes hydrologiques par diverses constructions le long des rivières (e.g., les barrages et digues).

Les forêts riveraines en milieu urbain sont soumises aux mêmes pressions de sélection que les autres forêts (isolation, effet de lisière, îlots de chaleur, etc.). Cependant, étant étroitement associées aux conditions hydrologiques, les forêts riveraines sont particulièrement affectées par les transformations du sol découlant de l'urbanisation. Par exemple, les surfaces imperméables, en plus d'entraîner la création d'îlots de chaleur, l'abaissement de la nappe phréatique et la pollution des sols, engendrent une augmentation du débit et de l'amplitude des crues suite à l'augmentation du ruissellement de surface, ce qui endommage et érode les rives (Walsh et al., 2005; White & Greer, 2006). Ainsi, en général, les bassins versants urbains présentent des régimes hydrologiques plus contrastés, marqués par des crues plus intenses et

des débits de base plus faibles. De plus, diverses structures artificielles, typiques des milieux humanisés, telles que les systèmes de canalisation, les murs de soutènement, les barrages et les ponts, aggravent ces perturbations au régime hydrologique naturel (Paul & Meyer, 2001; Groffman et al., 2003; Walsh et al., 2005). Ces changements hydrologiques d'origine anthropique entraînent une homogénéisation des régimes d'inondations à l'échelle régionale (Poff et al., 2007), ce qui pourrait conduire à une homogénéisation taxonomique plus rapide dans les communautés riveraines que dans les milieux terrestres (Johnson et al., 2014). En outre, ces changements hydrologiques ont été reconnus comme le moteur principal des changements de végétation observés dans les forêts riveraines en favorisant les espèces terrestres tolérantes aux sécheresses (Groffman et al., 2003; Burton et al., 2009; Pennington et al., 2010; Sung et al., 2011) et en facilitant les invasions par les espèces exotiques (Stromberg et al., 2007; Mortenson & Weisberg, 2010; Catford et al., 2011). Les forêts riveraines sont d'ailleurs parmi les écosystèmes les plus vulnérables aux invasions biologiques (Hood & Naiman, 2000; Renöfält et al., 2005; Richardson et al., 2007), ce qui pourrait exacerber les processus d'homogénéisation biotique en milieu riverain par rapport au milieu terrestre. En effet, tandis que la matrice urbaine exerce une pression de propagules d'espèces exotiques constante (Williams et al., 2008; Kowarik, 2011), les rivières leur servent de corridors de dispersion vers les sites en aval, où, après une inondation, ces espèces peuvent profiter de l'absence de compétition et exploiter les ressources (Jansson et al., 2005; Sabo et al., 2005; Tabacchi et al., 2005).

Comprendre et anticiper la réponse des forêts riveraines à l'urbanisation est essentiel afin de préserver leur intégrité écologique. Cependant, l'identification d'un filtre spécifique responsable des changements dans la répartition des espèces est difficile, car les effets de

multiples filtres sont souvent confondus et en interaction (Williams et al., 2008). La force des filtres liés à l'urbanisation et aux inondations et le rôle attendu de la rivière comme corridor de dispersion font des forêts riveraines urbaines un système modèle idéal pour étudier les effets indépendants et synergiques des filtres naturels et anthropiques sur la composition des communautés, et pour isoler les effets de ces filtres environnementaux de ceux des processus de dispersion. L'utilisation de traits fonctionnels permet de révéler les mécanismes clés sous-jacents à l'assemblage des communautés en comblant le fossé entre les changements de composition et les changements environnementaux (Lavorel & Garnier, 2002; Mayfield et al., 2010).

Objectifs

Dans ce contexte, l'objectif global de ma maîtrise est de comprendre les effets de l'urbanisation sur les patrons de diversité et de composition des forêts riveraines. La première étude (chapitre 2) examine les changements de composition fonctionnelle en réponse aux filtres anthropiques et hydrologiques ainsi qu'aux processus de dispersion et aborde les questions suivantes:

- (1) Quels sont les filtres environnementaux clés qui structurent la composition fonctionnelle des communautés riveraines dans les villes?
- (2) Quelle est l'importance relative des processus de dispersion par la rivière et par voie terrestre dans la distribution des traits, dans un contexte de forêts à la fois fragmentées par l'urbanisation et connectées via le réseau hydrologique?

La seconde étude (chapitre 3) explore les effets de l'urbanisation et des inondations sur l'homogénéisation taxonomique et fonctionnelle dans les forêts riveraines. Plus précisément, les questions suivantes sont abordées:

(1) L'urbanisation et les inondations entraînent-elles une tendance d'homogénéisation ou de différenciation des espèces et des traits dans les communautés forestières riveraines?

(2) Cette tendance est-elle associée à un changement de la composition en espèces ou en traits, de la richesse locale, ou de la dominance des espèces exotiques?

(3) Quelle est la relation entre diversité α et la diversité β fonctionnelle et taxonomique?

Chapitre 2

Environmental filtering and spatial processes in urban riparian forests

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Abstract

Questions This project aims to understand the effects of urbanization on plant functional composition in riparian forests, and addresses the following questions: What are the key environmental filters shaping riparian communities in cities? How important is dispersal by water currents in functional composition patterns relative to overland dispersal?

Location Montréal, Quebec, Canada

Methods Fifty-seven riparian forest patches were inventoried and community weighted means (CWM) were computed using eight functional traits. Forests were characterized by a subset of local variables describing their physical features, hydrological regime and historical disturbances, and a subset of landscape variables describing surrounding land use. To assess direction of spatial processes in structuring riparian communities, two subsets of spatial variables, Moran's eigenvector maps (MEM) and asymmetric eigenvector maps (AEM) were compared, and the best spatial model was used in subsequent analyses. The relative importance of these three subsets on tree, shrub and herb functional composition was quantified by variation partitioning using redundancy analyses.

Results Functional patterns in riparian forests resulted primarily from environmental filtering (local and landscape variables), but also from dispersal processes. Local conditions, especially flood intensity, exerted an overriding selection pressure on functional communities. However, urbanization seemed to act indirectly on trait patterns through the alteration of hydrological disturbances in riparian forests caused by ongoing and historical land transformation. Dispersal along rivers was also a structuring force in riparian forests, and was more important than overland dispersal.

Conclusions Alteration and interruption of natural landscape-scale processes by human activities are major mechanisms underlying changes in urban riparian communities. Furthermore, the influence of dispersal along rivers highlights the role of river connectivity for biodiversity in fragmented urban landscapes.

Keywords Asymmetric eigenvector maps (AEM); Community weighted means of traits (CWM); Dispersal spatial processes; Ecological filters; Flood; Moran's eigenvector maps (MEM); Plant functional traits; Riparian plant communities; Urbanization

Introduction

Urbanization is a driver of global change and a major threat to biodiversity worldwide (Grimm et al., 2008). In urban ecosystems, both human and natural filters influence the composition of communities through the selection of certain species with specific traits (Williams et al., 2015). Human filters acting on species distribution include habitat transformation and fragmentation, alteration of local conditions and horticultural human preferences (Williams et al., 2008). Urbanization changes the quality and spatial configuration of habitats as well as the regional pool of species, which in turn alter natural environmental filtering and dispersal-based processes of community assembly. Consequently, species distributions in urban ecosystems are generally prevailingly structured by anthropogenic (Godefroid & Koedam, 2007; Knapp et al., 2008), rather than by natural biotic and abiotic factors. In contrast, riparian forests are subject to frequent flooding, which may override the effects of the above mentioned anthropogenic filters associated with urbanization. Yet, the relative importance of both urban and natural filters on riparian communities has been overlooked until recently (e.g., Burton et al., 2009; Sung et al. 2011).

In riparian forests, floods constitute both a destructive and regenerating force that strongly structures plant communities (Naiman et al., 2005). Riparian species have developed numerous adaptations to waterlogging, fluctuating water levels and physical stress from currents. For example, the production of aerenchyma and growth of adventitious roots are traits that enable species to survive anoxia resulting from prolonged waterlogging (Lytle & Poff, 2004; Parent et al., 2008). In response to extreme fluctuations ranging from water excess to water shortage, some plants persist as soil seed bank and wait for favorable conditions

(Gurnell et al., 2006; Moggridge et al., 2009). Stress from floods and sediment erosion/deposition can favor plants with flexible branches or capable of vegetative reproduction from ripped off fragments (Karrenberg et al., 2002; Lytle & Poff, 2004). In addition to strongly influencing local conditions, rivers structure riparian communities by acting as an important upstream to downstream dispersal vector (Moggridge et al., 2009; Nilsson et al., 2010), especially for species with high seed buoyancy (Johansson et al., 1996). Urbanization can, however, disrupt these natural hydrological processes.

Dispersal is an important mechanism of community assembly that structures diversity and induces spatial patterns (Logue et al., 2011). While riparian forests are highly connected through the river network (Nilsson et al., 2010), urban forests are highly isolated by habitat fragmentation (Williams et al., 2008). These contrasting contexts impede the extension of traditional predictions about terrestrial remnants to riparian remnants in urban areas, but they provide an opportunity to study the importance of different dispersal processes in community assembly. Although dispersal is expected to mainly occur in a downstream direction (Nilsson et al., 2010), this directional process may not be as effective in a fragmented landscape, and urban riparian communities may also be influenced by other long-distance overland dispersal vectors, such as animal or human (e.g., Knapp et al., 2009). In addition, hydraulic structures on rivers (e.g., dams and dikes) disrupt upstream-downstream connectivity (Jansson et al., 2000; Merritt et al., 2010) as well as lateral connectivity, which can lead to a terrestrialization of riparian communities by allowing upland species to invade the formerly dynamic riparian habitat (Ward & Stanford, 1995). Spatial modeling methods (Dray et al., 2006) can be used to shed light on the pathways of dispersal processes in riparian plant communities and assess the importance of spatial processes relative to local and landscape factors.

This study aims to investigate the effects of urbanization on riparian forest communities. Identifying a specific filter as the cause of changes in species distribution is challenging, since the effects of multiple filters often interact and are therefore easily confounded (Williams et al., 2008). Given the strong structuring forces of urbanization and flooding, and the expected role of the river as a dispersal corridor, urban riparian forests are an ideal model system to study the independent and synergistic effects of natural and anthropogenic filters on community composition, and to further unravel the role of these environmental filters from that of dispersal processes. The use of functional traits can further reveal the key mechanisms underlying community assembly by bridging the gap between shifts in community composition and environmental changes (Lavorel & Garnier, 2002; Mayfield et al., 2010). Using a trait-based approach, we address the following questions: In the context of forests both fragmented by urbanization and connected through the hydrological network, how is functional trait composition spatially structured and how important is dispersal by river currents in compared to overland dispersal? What are the key filters (local conditions, landscape context or spatial processes) that shape the functional composition of riparian forest communities in cities? We hypothesize that (1) directional dispersal by river currents will be more important in structuring community trait composition than overland dispersal by other vectors given the importance of hydrochory in riparian habitats; (2) urbanization and hydrological disturbances will lead to opposing trait patterns, with urbanization favoring high dispersal ability and light demanding species, and hydrological disturbances favoring flood tolerance and waterborne dispersal; and (3) hydrological disturbances will exert the strongest selection pressure, as numerous biological adaptations are needed for plant establishment in floodplains.

Methodology

Study area

The study was conducted in riparian forests of the Greater Montreal region (Québec, Canada), principally along the shores of des Prairies and des Mille Iles rivers, as well as of the Lake of Two Mountains, a widening of the Ottawa River delta which split into distinct water masses that flow into both studied rivers (Fig. 2.1). These rivers flow from west to east and their flow is controlled by various dams, particularly during spring floods (CEHQ, 2014).

The study area is located within Canada's second most populous metropolitan region, with a population of about 3.8 million inhabitants (Statistics Canada, 2015). The region was largely agricultural prior to the 1960s, especially along the shores. Urban development then began slowly, and from this period onwards farmland was converted to residential use. Currently, the area is dominated by impervious surfaces (59% of the area of the sampled municipalities, of which 41% is residential), but rural areas are still present (19%), especially along the north shore of des Mille Iles river, the east end of Laval Island, and on Bizard Island, while on the Island of Montreal rural areas are limited to a small portion of the north-west shores (Fig. 2.1).

Site selection and sampling design

Forests were selected using satellite imagery (1:5 000) and field reconnaissance surveys, according to forest size (area >0.4 ha) and vegetation structure (tree cover >80% and no turf). A total of 95 forests met these criteria, and 57 of these were selected (Fig. 2.1; see Table S2.1 in Supporting Information) to represent a gradient of size, spatial position (from

west to east), flood intensity (little to mostly flooded) and surrounding impervious surfaces (low to high; for methods, see the Environmental data sampling section below).

Within each selected forests, sampling plots were positioned along transects perpendicular to the shoreline. Each forest contained 2 to 4 transects according to the length of its shore to keep sampling effort similar among forests, namely: 2 transects for sites between 50 and 300 m long; 3 transects for sites between 301 and 500 m; and 4 transects for sites > 500 m. Each transect contained 2 or 3 plots, depending on the forest width. The first plot was located at the shore tree line and the second plot was located 10 m from the first. In forests wider than 90 m, a third plot was located farther from the shore, at about 50 m from the second. A total of 438 plots (from 4 to 12 per site) was sampled in the 57 forests.

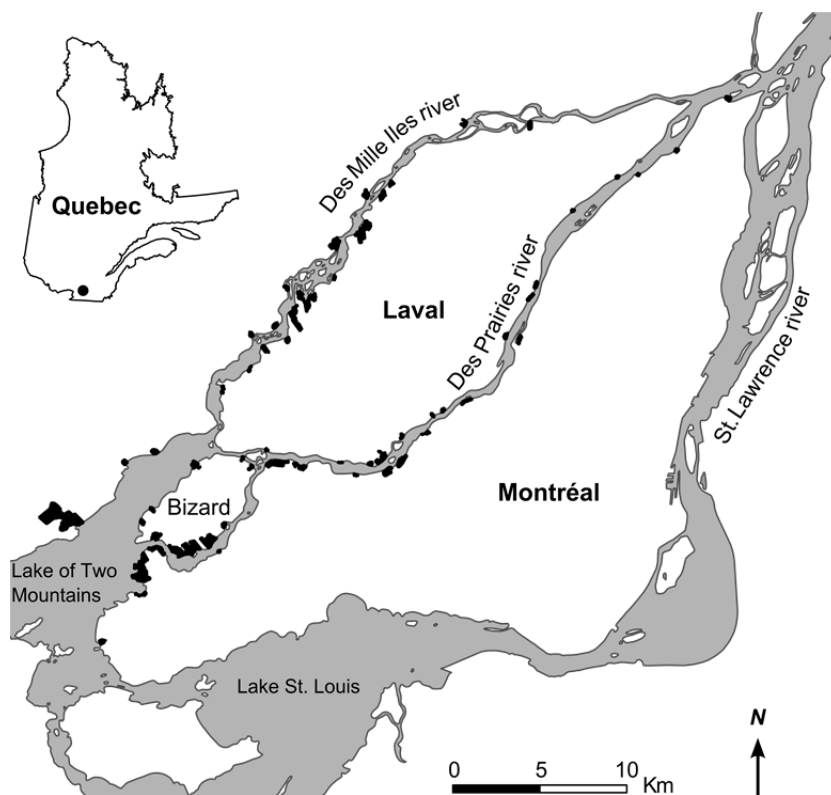


Figure 2.1. Location map of the 57 riparian forests (in black) sampled in the Greater Montreal region.

Vegetation sampling

Field sampling was carried out from mid-July to mid-August 2013. Within forest patches, all plant species were identified within 100 m² plots, 5 m × 20 m for the first plot (the length of the plot lying along the shoreline) and 10 m × 10 m for subsequent plots. Herbaceous and shrub species cover was assessed using seven classes: <1%, 1–5%, 6–25%, 26–50%, 51–75% and 76–100%. The diameter at breast height (DBH) of each tree was estimated using the mid-range of four classes (10–20 cm; 21–30 cm; 31–40 cm; 41–50 cm) and measured directly for individuals > 50 cm. DBH values were used to calculate the total tree basal area in each plot.

Environmental data sampling

Local variables

All variables (Table 2.1) were extracted from satellite images and maps of the region using ArcGIS 10.1 software (ESRI, 2012). Each forest patch perimeter was delineated, and the area and perimeter:area ratio were calculated. A digital elevation model (1 m resolution; MMC, 2009) was used to estimate mean altitude and slope of each forest. The intensity of flooding was evaluated according to the proportion of the forest that is usually inundated during spring, using flood hazard maps of the area (MMC & CEHQ, 2005), a digital elevation model (1 m resolution; MMC 2009) and based on field surveys during spring floods (3 classes from little to mostly flooded; see Table 2.1).

The recent history of the studied forests was characterized through interpretation of aerial photos (1950–2010). Forest age was estimated as the time since the last major

disturbance. Past land use was categorized as either agricultural or human use, which included residences (that no longer exist), and wasteland (industrial wastelands, borrow pits or embankments). An index of forest area changes was compiled by averaging the ratio of all previous forest areas for each decade (1950 to 2010) relative to the current area. In general, forests were historically smaller than today, since most were once harvested in whole or in part.

Table 2.1. Description of all explanatory variables characterizing the 57 riparian forests of the Greater Montreal region (see Table S2.2 for correlations between variables).

Code	Explanatory variables	Units
<i>Local conditions</i>		
area	Forest area	m ²
PAR	Perimeter: area ratio	ratio
flood	Seasonal flood intensity	1: flooded area ≤ 20% 2: flooded area]20, 50]% 3: flooded area > 50%
altitude	Forest mean altitude	m
slope	Forest mean slope	1: slope ≤ 2 ° 2: slope]2, 6] ° 3: slope > 6 °
age	Time since the last major disturbance	Years
histo.area	Mean proportion of historical area compared to current area	%
histo.agricult	Historical agricultural land use	0-1
histo.human	Historical human land use (residential or wasteland)	0-1
<i>Landscape context</i>		
isolation	Edge-to-edge distance to the nearest forest	m
HII	Human Influence Index	0 –72
bridge	Presence of a bridge in the vicinity	0-1
impervious	Proportion of impervious surfaces in a 500-m buffer zone	%
rural	Proportion of rural areas in a 500-m buffer zone	%
forest	Proportion of forest cover in a 500-m buffer zone	%
green	Proportion of vegetation in a 500-m buffer zone	%
NDVI	Mean NDVI value in a 500-m buffer zone	-1 –1
<i>Spatial process</i>		
XY	Geographic coordinates of forest centroid used for spatial eigenfunction analyses	UTM

Landscape variables

To assess the effect of the surrounding urban matrix on forests, the landscape was characterized in a 500 m buffer zone around each site (in accordance with Vallet et al., 2010) using land use maps (MMC, 2012). For each forest, we quantified the proportions of impervious surfaces (including transportation infrastructures and residential, commercial and industrial areas), green spaces (all vegetated areas including forests but excluding agricultural lands) and forests (areas dominated by trees). To assess vegetation density and quality near the studied forests, a Normalized Difference Vegetation Index (NDVI) was calculated using a satellite image (20 m resolution; Geobase, 2008). All pixel values (ranging from -1 to +1) in the buffer zone were average. Negative NDVI values indicate the absence or presence of sparse unhealthy vegetation, while positive values correspond to the presence of healthy vegetation. To include a more comprehensive measure of urbanization, we used the Human Influence Index (HII; WCS & CIESIN, 2005), which takes into account multiple human factors presumed to influence ecosystems (population density, roads, etc.). Using a map of the HII (1 km resolution), each forest was assigned the average index value of the pixels in the buffer zone. Finally, the edge-to-edge distance between each sampled forest and its nearest neighbor (> 0.5 ha) was measured to assess the degree of isolation.

Functional traits

Each species was characterized according to eight functional traits (Table 2.2; see Table S2.3 for raw data), which were selected to represent dispersal ability and tolerance to hydrological and anthropogenic disturbances. Some traits were selected to serve as surrogates of many others, e.g., the wetness coefficient substitutes several traits require to survive

waterlogging. Trait data were mainly extracted from the primary literature and published trait databases (Fitter & Peat, 1994; Kleyer et al. 2008; Michigan Flora 2011; Aubin et al. 2012).

Table 2.2. Description of the selected functional traits used in analyses.

Functional traits	Code	Units/Scale	Variable
Maximum height	height	cm	Quantitative
Life cycle (herbs only)	lifespan	0: annual 1: perennial	Nominal
Shade tolerance	shade	1: intolerant 2: mid-tolerant 3: tolerant	Ordinal
Wetness coefficient	wetness	1: upland (almost never in wetlands) 2: facultative upland (occasionally in wetlands) 3: facultative (equally likely in wetlands and uplands) 4: facultative wetland (usually in wetlands) 5: obligate wetland (almost always in wetlands)	Ordinal
Seed weight	seedWg	ln(mg)	Quantitative
Seed bank	seedBk	1: transient 2: short-term persistent 3: long-term persistent	Ordinal
Vegetative reproduction	veg	0: not possible 1: possible	Binary
Dispersal vector	endozoo bird epizoo hydro anemo anthropo other	endozoochore (internal animal dispersal) bird dispersal epizoochore (external animal dispersal) hydrochore (water dispersal) anemochore (wind dispersal) anthropochore (human dispersal) other (include unassisted, myrmechore, explosive)	Binary

Data analysis

Prior to analyses, species were separated into tree, shrub and herbaceous, to form three species-by-site matrices that were used individually. For each of the 57 forest patches, species importance values (IV), a measure of the relative dominance of a species in a community (Barbour, 1987), were computed. For trees, IVs were calculated as the mean of the relative

density (number of individuals per forest relative to the total number of individuals of all species), relative frequency (number of plots per forest in which a species occurred relative to the total number of occurrences of all species) and relative dominance (basal area coverage per forest relative to the total basal area of all species). For herbs and shrubs, IVs were calculated as the mean of the relative frequency and the relative dominance (cover of a species per forest relative to the total cover of all species).

Mean functional traits for community

To assess the effects of environmental filters on functional composition, community weighted means of traits (CWM) were used in subsequent analyses (e.g., Garnier et al., 2004, 2007; Lavorel et al., 2008). Compiled in a site-by-trait matrix, CWM were obtained by matrix multiplication of the species-by-site matrix and the standardized species-by-trait matrix (trait standardization ensures equal weight for all traits, regardless of their units). Traits with less than 10% of occurrence for a specific plant form were discarded; for example, bird dispersal was not used for herbs. For continuous traits, CWM was the average value of a trait for all species in the community, weighted by their relative abundance. For ordinal and binary traits, CWM was the relative abundance of species for each trait state.

Modeling spatial structure

To assess the relative importance of non-directional and directional spatial processes in trait distribution, we compared two eigenvector-based spatial methods: distance-based Moran's eigenvector maps (dbMEM; Dray et al., 2006) and asymmetric eigenvector maps (AEM; Blanchet et al., 2008a). MEM analyses are meant to model symmetric spatial structures, which could emerge from non-directional plant dispersal (e.g., aggregation). In contrast, AEM are

explicitly designed to model directional patterns, which are expected in riparian ecosystems. Contrary to AEM, MEM analyses were carried out on detrended response variables, i.e., the significant linear trend in the direction of the hypothesized spatial process was removed prior to MEM calculation (Borcard & Legendre, 2002).

AEM and MEM eigenfunctions were computed using a connectivity matrix which summarizes the connections between the studied forests. The connection diagram was created based on interpretation of satellite imagery showing flow direction (see Fig. S2.1). Rivers in the study area, as well as prevailing summer winds, flow from the southwest to the northeast. Each river was treated as independent from the other. Forests located on the north shore of the Lake of Two Mountains were linked to those of des Mille Iles river, while forests on the south shore to those of des Prairies river. To properly model the distinction between both rivers, the AEM method of Blanchet et al. (2008a, 2011) was adapted (see Appendix S2.1).

For MEM, the connectivity matrix was weighted using between-site overland distances. For AEM, distances corresponded to watercourse distances, and a measure of river fragmentation associated with the presence of bridges and dams was also considered. The weighting functions were: (1) no weight (binary connection); (2) a linear function of the distances ($f_1(d_{ij}) = 1 - (d_{ij}/\max(d_{ij}))$); (3) a concave-down function of the distances ($f_2(d_{ij}) = 1 - (d_{ij}/\max(d_{ij}))^2$); and (4) river fragmentation ($f = 1 - (0.2 \cdot \text{nb of dams} + 0.1 \cdot \text{nb of bridges})$). The weight or combination of weights leading to the highest explained variation in the functional composition data was retained for further analyses. The best sets of AEM variables were produced considering a concave-down function of distances and river fragmentation for trees, a linear function of distances and river fragmentation for herbs and only river fragmentation for shrubs (see Table S2.4).

Only spatial functions modeling positive spatial correlation were used (selected using Moran's I coefficients of spatial correlation). For each model, spatial variables were selected using a forward selection procedure (9999 permutations of residuals) based on two stopping criteria, the alpha significance level and the adjusted R^2 of the global model including all explanatory variables of each subset, as proposed by Blanchet et al. (2008b). AEM and MEM models were then compared through variation partitioning to assess the directional and non-directional components of variation. Since AEM always yield a larger explained variation (see Results), they were used to model spatial processes in the subsequent analyses.

Partitioning environmental and spatial variation

The relative and unique importance of landscape context, local conditions and spatial processes in the variation of plant trait distribution was assessed by partitioning the variation explained by each subset using redundancy analyses (RDA; Borcard et al., 1992). First, to linearize the relationship between explanatory and response variables in the RDA models, explanatory variables were transformed when necessary (Table S2.5), after which they were standardized. Then, to obtain parsimonious RDA models for each of the three explanatory subsets, only variables selected using a forward selection procedure (9999 permutations of residuals) based on the two stopping criteria of Blanchet et al. (2008b) were retained (Table S2.4). Finally, variation partitioning analyses were computed from the parsimonious RDA for the three plant forms, and the significance of each unique fraction was obtained by 9999 permutations. In the analysis on shrubs, two forests were excluded, as their trait composition was highly divergent from that of other forests due to the concomitant dominance of an uncommon wetland species and the absence of an invasive species.

All statistical analyses were performed in the R environment (version 3.0.1; R Core Team, 2013). Canonical analyses, variation partitioning, and tests of significance of the fractions were computed using the “vegan” package. AEM eigenfunctions were created using the “AEM” package, while MEM were constructed using the “PCNM” package. Forward selection was computed using the “packfor” package.

Results

Directional vs non-directional spatial patterns

For tree and herb strata, only directional patterns were detected, explaining respectively 24% and 37% of the variation in functional composition (Fig. 2.2). For shrubs, both directional and non-directional significant patterns were found, explaining respectively 26% and 10% of the variation. However, the pure fraction of directional patterns prevailed (19%), while the non-directional patterns were nearly all confounded with the directional patterns.

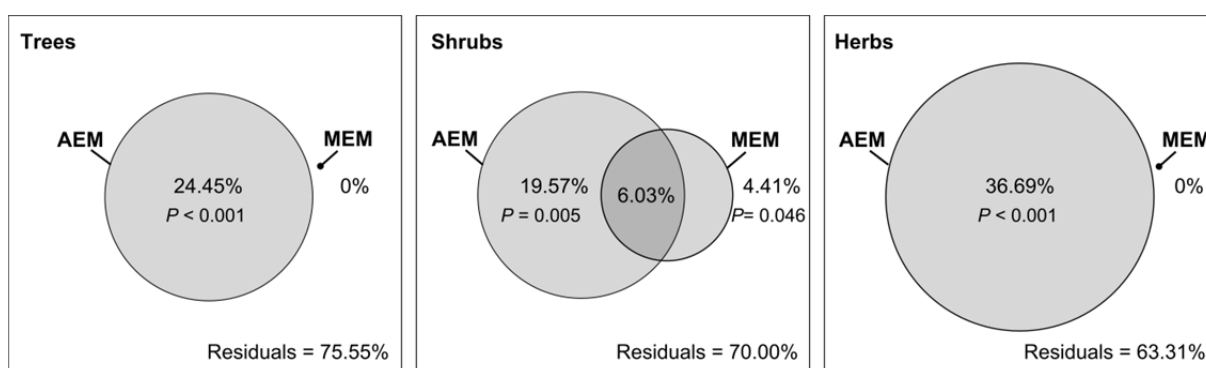


Figure 2.2. Variation partitioning of trait composition (CWM) explained by the subsets of selected AEM and MEM variables. Percentages in the partitioning are R^2_{adj} and P-values that were obtained through permutation tests ($n=9999$) of individual fractions.

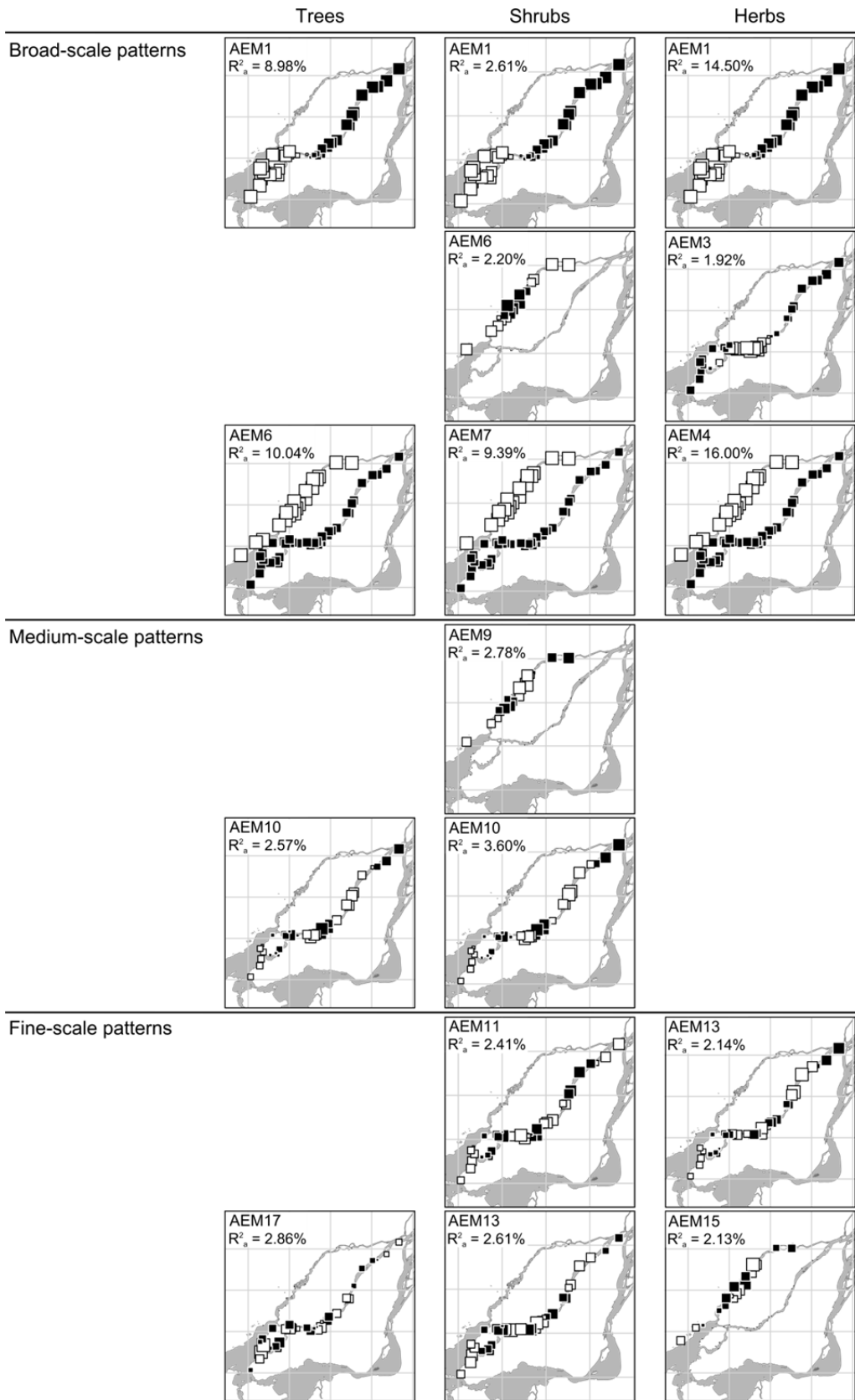


Figure 2.3. Maps of selected AEM functions, reflecting patterns at different spatial scales, for tree, shrub and herb CWM data along des Mille Iles (north) and des Prairies (south) rivers. The first functions model large-scale spatial structures, while the following functions model increasingly fine structures. Maps are organized to show similar patterns on each row. Square size is proportional to value; positive values are in black and negative values in white. The explanatory power of each function (R^2_{adj}) shows the relative importance of an individual scale pattern for the spatial variability of CWM.

Scales of spatial variation

Spatial structures were observed at broad, medium (except for herbs) and fine scales, the broad patterns usually being most important, as shown by their globally larger adjusted R^2 (Fig. 2.3). The AEM6 (trees), AEM7 (shrubs) and AEM4 (herbs) functions all represented the distinction between the two rivers, and were the spatial patterns most correlated with plant trait variation. The first AEM function (AEM1) of the three plant strata models represented a strong gradient along des Prairies river, while the AEM6 of the shrub model represented a broad-scale gradient along des Mille Iles river. While spatial patterns, from broad to fine-scale, were exclusively found along des Prairies river for trees, they contributed equally to shrub trait variation along both rivers. For herbs, trait variations were identified primarily along des Prairies river (AEM1, 3 and 13), while fine-scale patterns were minor along des Mille Iles river (AEM15).

Partitioning trait variation between environmental filtering and spatial processes

Local, landscape and spatial variables together explained about 40% of changes in the functional composition of trees and shrubs and about 51% of herbs (Fig. 2.4 a–c). Trait

composition was primarily structured by local conditions (trees: 34%; shrubs: 23%; herbs: 41%), and mostly by seasonal flood intensity (flood), as this variable alone had the highest explanatory power among all variables (trees: 22%; shrubs: 12%; herbs: 28%; Table S2.5). Most of the variance explained by the local subset was shared with landscape, and particularly with spatial variables. The fraction shared by the three subsets had a strikingly high adjusted R^2 compared with individual fractions, suggesting that local and landscape subsets together presented a strong spatial structure. Hence, although landscape context alone was less important in structuring functional composition, its influence was exerted through change in local conditions, especially for herbs. Still, the significance of the pure directional spatial fraction indicates that a directional process, other than the inherent spatial structure of the environment, acts on trait distribution. These pure spatial patterns were as important as local conditions (about 8%) in structuring shrub trait composition.

The first RDA axis of each plant form represents a flooding intensity gradient paralleled by an urban-to-rural gradient (Fig. 2.4 d-f). Forests associated with rural areas (right side of the plots) were associated with high vegetation cover (represented by forest, green or NDVI variables) and were subject to more severe flooding than urban forests. On the other end of the gradient (left side of the plots), urban forests were characterized by steep slopes, a high perimeter:area ratio (PAR), as well as a large proportion of impervious surfaces and a frequent occurrence of bridges in their vicinity. Along this gradient ranging from flooded rural forests to drier urban forests, AEM1 (modeling a linear gradient along des Prairies river for all plant groups) and AEM 6, 7 and 4 variables (modeling the distinction between both rivers for trees, shrubs and herbs respectively) were opposed to flooding intensity indicating that floods are more intense on des Mille Iles river and westward of des Prairies river.

As expected, flood intensity favored hydrochorous (hydro) wetland species (wetness) for all plant forms. In highly flooded forests located in rural areas, trees were taller (height) and mostly bird-dispersed, but also animal- (endozoo) and human-dispersed (anthropo). On the contrary, shrubs were taller and principally animal- or human-dispersed in drier urban forests. Dry forests in urban settings were dominated by annual herbs bearing wind-dispersed (anemo) or heavy seeds (seedWg), which were, as for shrubs, principally animal- (endozoo and epizoo) and human-dispersed. On the other hand, vegetative reproduction (veg) was favored in flooded rural forests.

Secondary to the urban-flooding gradient, a successional gradient also appeared in the three ordinations. Following the historical variables related to human activities (histo.human, which describes historically disturbed forests, and histo.area, which describes historically large forests), this gradient ranged from recently disturbed to old 'pristine' forests. This gradient contributed to the variance in the second axis and appeared perpendicular to the flood gradient (parallel to the second axis) for trees, crosswise for shrubs and almost parallel for herbs (almost parallel to the first axis). This decreasing distinctiveness of the successional gradient among the three life forms was also depicted by the decreasing variance explained by the second axis. Along this gradient, young, recently disturbed forests were dominated by human-dispersed (anthropo) trees, shrubs and herbs, wind-dispersed trees, and shrubs with a long-lived seed bank (seedBk). In contrast, old 'pristine' forests were dominated by shade-tolerant (shade) trees, shrubs and herbs, heavy-seeded (seedWg), animal-dispersed (endozoo) and long-lived seed banking trees, and perennial (lifespan) herbs.

Figure 4. Variation partitioning (a, b, c) and ordination diagrams (d, e, f) of CWM explained by the subsets of local, landscape and spatial variables. Percentages in the partitioning are R^2_{adj} and circle sizes are their approximation. P-values were obtained by permutation tests of individual fractions. Grey vectors are the explanatory variables; round end vectors are for local variables; arrow end vectors are for landscape variables; vectors without an end mark are for spatial variables (AEM vectors were named by the numbers corresponding to those of Figure 3). Response variables (black crosses) should be interpreted as vectors. See Table 2 for trait codes. The square terms of polynomial transformed variables model the non-linear (quadratic) relationship between the response and explanatory variables.

Discussion

The interplay between local, landscape and spatial filters

In this study, we showed that under severe natural disturbance regimes, the effect of natural filters outweighed the negative effects of urban filters, since seasonal flood intensity was the most important variable in explaining plant trait community composition (Fig. 2.4 d–f, Table S2.5). Nonetheless, the antagonism between flood and urbanization variables in the ordinations, coupled with the important shared fraction between the local, landscape and spatial subsets, indicated that urbanization also played a significant role by indirectly influencing traits through alteration of the hydrological regime. Urbanization also likely fostered a successional gradient in more mesic riparian forests, since species traits, notably for trees, differed between young disturbed and old ‘pristine’ forests. This result suggests that as flood intensity decreases, its filtering effect is relaxed and other filters associated with succession induced by human disturbances become more important in community assembly.

The effect of urbanization on riparian communities thus appeared to be twofold: a principal effect through hydrological alterations and a secondary effect through initiation of succession.

Although environmental filtering, driven directly by local conditions and indirectly by landscape modification, was predominant in riparian community assembly, dispersal processes through the river network still influenced community structure, as inferred by the pure spatial fraction. Water dispersal by river (AEM) was more important than overland dispersal (MEM) in explaining the assembly of plant communities. The importance of river connectivity was also illustrated by the fact that river fragmentation by dams and bridges was included in all AEM models. These structures act as barriers to the movement of propagules of the upstream species pool, impair seed deposition on river shores and severely alter hydrologic conditions, which may affect potential composition of downstream communities (Jansson et al., 2000; Merritt & Wohl, 2006; Merritt et al., 2010).

Plants dispersed predominantly through the river network, but the significant pure spatial fraction indicated that they were still subjected to dispersal limitation processes (Fig. 2.4 a,b,c; Peres-Neto & Legendre, 2010). This latter fraction was higher for herbs than for trees, likely because herbs are generally weaker dispersers than trees, due to their low seed releasing height (Garnier et al., 2013). In contrast to trees and herbs, shrubs were not limited by distance (no function of distance was included in their AEM model) and were influenced by non-directional spatial processes, modeled by MEM. While these results suggest good dispersal potential, shrubs nonetheless had a relatively high pure spatial fraction likely induced by other unstudied processes. For instance, as a consequence of human preference, ornamental shrubs with fleshy fruits are overrepresented in urban floras (Burton et al., 2009; Knapp et al., 2009; Huang et al., 2013). This could have created an asymmetrical spatial pattern, similar to

the one expected to arise from river dispersal, included in the pure spatial fraction. Also, the prevalence of human- and animal-dispersal, especially by birds, which have long-distance potential (Knapp et al., 2009), could contribute to the ability of shrubs to establish in isolated forests through overland dispersal.

Shift of plant traits along an urban–rural gradient

As expected, the main trait pattern found was a shift in species distribution from wetland water-dispersed species dominant in rural flooded forests to upland species in drier urban ones. This large-scale shift has been previously attributed either to flow regulation that lessens the river influence on riparian habitats (Aguiar & Ferreira, 2005; Stromberg et al., 2007; Catford et al., 2011) causing a terrestrialization process (Ward & Stanford 1995), or to regional alteration of the flood regimes that induces a low water table in urban areas (White & Greer, 2006; Burton et al., 2009; Sung et al., 2011) reported as hydrologic drought by Groffman et al. (2003). In light of our results, we suggest that urbanization, and not flow regulation alone, leads to a general trend toward terrestrialization. This process was noticeable mainly at the landscape-scale, but was also observed at a more local-scale, since upland shrubs and lianas (the latter represented by the height and endozoochory traits) were more abundant in forests adjacent to a bridge than in other forests. The rock fill of adjacent banks during bridge construction, inherent to the process of urbanization, likely disconnected the river from the forest (Blanton & Marcus, 2009) facilitating this local terrestrialization.

Shift of plant traits along a human-induced successional gradient

Our results also indicated the presence of a successional gradient induced by historical human activities, since species traits, especially shade-tolerance, differed between young disturbed and old pristine forest patches. Such trait patterns are observed with other types of disturbances (Garnier et al. 2004; Raavel et al., 2012) as the relative importance of ecological filters changes predictably during succession (Schleicher et al., 2011; Raavel et al., 2012; Purschke et al., 2013). In the studied sites, dispersal processes seemed to prevail in early-successional forests (historically small and human-disturbed forests), as indicated by the abundance of highly mobile tree species (dispersed by wind and humans). In contrast, late-successional communities, represented by historically large forests located in a vegetated matrix, the competition filter was likely more important and favored shade-tolerant tree species that disperse locally (e.g., large nuts).

The successional gradient was more pronounced for trees than for shrubs, and almost indistinguishable for herbs, suggesting that historical disturbances leave an ecological footprint (disturbance legacy; Flinn & Vellend, 2005; LaPaix & Freedman, 2010; Johnson et al., 2014) on species functional composition that likely fades over time proportionally to species longevity. Response to environmental changes depends on turnover rate (Kuussaari et al., 2009); long-lived species take longer to recover from past disturbances compared to short-lived ones. Due to their high turnover rate, herbs show not only faster, but also stronger responses to urban disturbances than woody species (Burton et al., 2009; Huang et al., 2013; Ramalho et al., 2014), which can persist long after their habitat has been degraded.

In the study area, most of the disturbed forest patches were industrial wastelands, borrow pits or embankments a few years ago. We suggest that their composition, characterized

by a high representation of anthropochores, could be the result of a source-sink process driven by *in situ* and *ex situ* plantation of cultivated species. In cities, cultivated plants are overrepresented in the species pool (Williams et al., 2008) and act as a massive source of propagules that wield a high pressure on nearby vacant habitats, which could be viewed as sinks. This source-sink process mirrors findings in other studies, which reported that the types of surrounding habitats exert a strong influence on species composition during succession in human-disturbed habitats (Prach et al., 2001; Westermann et al., 2011). This hypothesis is further reinforced by the shrub trait patterns identified here, where the observed successional gradient was exclusively related to a single species, *Rhamnus cathartica*, a tall invasive shrub from Eurasia which dominated the mid-story of most of the studied forests (68%). Brought to North America as ornamental and agricultural hedgerows (Knight et al., 2007), *R. cathartica* may have spread from these human-planted sources and invaded the studied sites when they were still largely open and non-forested, while its wide habitat tolerance (Knight et al., 2007) may have contributed to its success over time.

Conclusion

Local conditions, especially flood intensity, exerted an overriding selection pressure on riparian communities. The effect of the landscape was indirect, acting on trait patterns through alteration of hydrological disturbances in riparian forests. In addition to environmental filtering, dispersal along rivers was also an important process structuring riparian forests. Hence, urbanization seems to alter riparian community composition through changes in community assembly rules, primarily through changes to both natural and dispersal processes. While disturbances are an inherent feature of riparian ecosystems, human-induced

disturbances have long lasting consequences, longer than natural disturbances, and impair natural ecological processes. Management strategies in urban areas should therefore aim at restoring or preserving the natural processes critical for maintaining the functional composition of floodplain vegetation and limit terrestrialization. For instance, a simple first step is to avoid and remove any constructions or modifications that disconnect the riparian habitat from the river (e.g., dikes, embankments) along riverbanks. Identification of functional trait shifts can be useful for identifying forests that have high conservation value, or degraded forests in need of ecological restoration (Mayfield et al., 2006). Finally, because of the importance of water dispersal, maintaining upstream-downstream connectivity may be effective for preserving biodiversity in urban riparian forests. As dams and bridges are a necessary evil and thus cannot be avoided, managers should focus on maintaining as much as possible a continuous strip of vegetation along rivers.

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Chapitre 3

Does urbanization lead to taxonomic and functional homogenization in riparian forests?

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Abstract

Aim Biotic homogenization, a decrease in β -diversity among formerly distinct communities, has been recognized as an important form of biotic impoverishment resulting from urbanization. Exotic invasion and native extinction, together with alteration of habitats and natural processes, drive homogenization in cities. This study aims to investigate the effects of urbanization and flood on taxonomic and functional homogenization in riparian forests.

Location Montréal, Quebec, Canada

Methods Floristic inventories were carried out in 57 riparian forests in 2013. Changes in taxonomic and functional β -diversity (homogenization or differentiation) among herbaceous species were studied between three urbanization levels and three flood levels. We used multivariate dispersion as a measure of β -diversity, computed on a species composition matrix for taxonomic β -diversity and on a community weighted mean matrix for functional β -diversity.

Results Contrary to expectations, urbanization led to taxonomic differentiation, while flood intensity led to taxonomic homogenization. Despite a high correlation between taxonomic and functional β -diversity changes, there was no functional homogenization or differentiation among disturbance levels, implying that functional homogenization cannot be inferred from taxonomic homogenization. Changes in taxonomic β -diversity were driven by different changes in community structure. Taxonomic β -diversity was highly negatively correlated with total species richness and associated with a shift in species composition. Furthermore, exotic introduction in riparian forests was partly responsible for overall taxonomic differentiation.

Main conclusions Urbanization was likely the main trigger of all biodiversity changes, as it caused a gain in exotic species and a net species loss in forests that were highly urbanized, and promoted an important species turnover between flood levels, through alteration of the hydrological regime. Future studies on biotic homogenization at local scales should focus more on the role of land use changes than on exotic species to improve our understanding of biodiversity responses to human disturbances.

Keywords : Alpha and beta diversity, Community weighted means of traits (CWM), Plant functional traits, Exotic species, Flood, Riparian plant communities, Taxonomic and functional homogenization, Urbanization

Introduction

Land-use change is recognized as a major cause of biotic homogenization (McKinney & Lockwood, 1999; Baiser et al., 2012). This form of biodiversity loss is characterized by an increasing similarity in composition among communities (decrease β -diversity) and mainly resulted from the simultaneous extinction of specialist native species and gain in exotic species (McKinney & Lockwood, 1999). Among all land use changes, urbanization is known as the strongest homogenizing force (McKinney, 2006; La Sorte et al., 2014) because it radically alters natural environmental filtering. Cities are indeed strikingly uniform ecosystems, as well as epicenters of exotic introduction, thus driving non-random species extinction and invasion (McKinney & Lockwood, 1999).

Although the biotic homogenization concept predicts appealingly simple changes of biodiversity in cities, numerous outcomes are possible. Species invasions and extinctions can increase or decrease β -diversity through different mechanisms involving changes in local α -diversity or shifts in species composition due to non-random species replacement (Olden & Poff, 2003). These mechanisms depend on the spatial extent of the study and are likely responsible for the apparent scale-dependence of biotic homogenization. For instance, at a global scale, the increasing number of cosmopolitan species, due to exotic species introduction, coupled with native species extinction leads to an overall increase in community similarity (McKinney, 2004; La Sorte et al., 2014). At a city scale, the introduction of a large number of exotic species may outweigh the loss of natives, thereby contributing to community differentiation (Olden & Poff, 2003) and enriching local α -diversity (Sax & Gaines, 2003; Thomas, 2013). Accordingly, while recent large-scale meta-analyses have revealed global biotic homogenization (Baiser et al., 2012; La Sorte et al., 2014), especially among cities on a

given continent (La Sorte et al., 2007), at a local scale, urbanization mostly causes biotic differentiation (Kühn & Klotz, 2006; Aronson et al., 2014; Bossu et al., 2014). Furthermore, the effects of exotic species have been found to vary at local scales. For instance, recently introduced species, i.e. neophytes, have not achieved yet their potential range and can therefore increase taxonomic differentiation (Kühn & Klotz, 2006; Lososová et al., 2012) while exotic species with a longer residence time, i.e. archeophytes, were found to promote homogenization (Kühn & Klotz, 2006; Lososová et al., 2012) similarly to native species (McCune & Vellend, 2013; Johnson et al., 2014; Li & Waller, 2015). Consequently, while exotic invasion and native extinction are posited as the major causes of global taxonomic homogenization (McKinney, 2004; Qian & Guo, 2010; La Sorte et al., 2014), their relative roles at a local scale are not as straightforward as predicted and remain controversial.

Because species selection operates on species functional traits, taxonomic homogenization is expected to be reflected in community trait composition (McKinney & Lockwood, 1999), which could in turn lead to functional homogenization (Olden et al., 2004). However, empirical evidence of a relationship between taxonomic and functional β -diversity is scarce and inconsistent (Smart et al., 2006; Abadie et al., 2011; Naaf & Wulf, 2012; Sonnier et al., 2014). This relationship apparently depends on trait redundancy between species, number of traits included in the study, regional pool species richness (Baiser & Lockwood, 2011), initial habitat conditions and species composition (Fukami et al., 2005; Smart et al., 2006). For instance, absence of functional homogenization despite an important decrease in taxonomic α and β -diversity through time reflects a high level of functional redundancy among communities, i.e. the replacement of species by other species with similar traits (Sonnier et al., 2014). Conversely, a reduction in local species richness concurrent with

taxonomic differentiation and functional homogenization indicates that different communities have converged toward more redundant traits, but retained their historical species distinctiveness (Smart et al., 2006). It remains unclear however whether taxonomic and functional homogenizations are correlated.

Biotic homogenization can be triggered by homogenization of natural environment and disturbance regimes. Yet, in urban ecosystems, this fundamental aspect of homogenization has received little attention compared to the role of invasion and extinction processes. Riparian forests are usually described as highly heterogeneous ecosystems due to the dynamic nature of hydrological regimes, which maintain a great diversity of habitats at multiple spatial and temporal scales (Décamps et al., 2004). However, regional homogenization of flood regimes, through human-induced decline in the magnitude and variability of floods (Poff et al., 2007), was hypothesized to contribute to the recent taxonomic homogenization in riparian communities (Johnson et al., 2014). Furthermore, numerous studies have reported that alteration of the flood regime, which usually results in floodplains being inundated less frequently and for shorter durations, reduces lateral connectivity and induces a shift in riparian community composition from wetland to terrestrial species (Shafroth et al., 2002; White & Greer, 2006; Burton et al., 2009; Catford et al., 2011; Sung et al., 2011). In fact, this terrestrialization of riparian communities represents an underestimated homogenization process, as they come to increasingly resemble terrestrial communities. While natural disturbances are usually thought to increase heterogeneity at large scales, flooding can also increase similarity between habitats and reduce β -diversity (Thomaz et al., 2007), since this severe disturbance requires numerous adaptations to waterlogging, fluctuating water levels and physical stress from currents (Catford & Jansson, 2014). As floods act directly on plant

population survival, especially through oxygen deficiency (Blom & Voeselek, 1996; Parent et al., 2008), their effect could therefore override the impact of urbanization on community. Since urbanization and flooding act synergistically and can both result in biotic homogenization yet lead to contrasting trait patterns (Chapter 1 of this work), traditional predictions relative to homogenization of terrestrial ecosystems in urban areas cannot be applied directly to riparian ecosystems.

This study aims to understand the effects of hydrological and anthropogenic disturbances on patterns of taxonomic and functional homogenization in urban riparian forests. Specifically, we address the following questions: (i) Is there a homogenization or differentiation trend in species and traits along urbanization and flooding gradients? (ii) Are the changes in taxonomic and functional β -diversity related to a change in local species richness, species and trait composition, or exotic species dominance? (iii) What is the relationship between α -diversity and taxonomic/functional β -diversity? We predicted (i) a taxonomic homogenization driven by the expansion of exotic species in urban forests; but (ii) a functional homogenization driven by strong hydrological disturbances rather than urbanization.

Methodology

Study area

The study was conducted in riparian forests of the Greater Montreal region, Québec, Canada (Fig. 3.1), the second most populous in Canada, with a population of about 3.8 million inhabitants (Statistics Canada, 2015). Prior to the 1960s, the region was predominantly agricultural, especially along the shores (see Chapter 1). Urban development then began

slowly, and farmland was progressively converted to residential use. Currently, about 60% of the studied area is covered by impervious surfaces, of which 41% is associated to residential land use. Some areas have remained rural (19%), especially along the north shore of des Mille Iles river, the eastern end of Laval Island, and on Bizard Island, while on Montreal Island rural areas are limited to a small portion of the north-western shores (Fig. 3.1). The area's forests belong to the sugar maple-bitternut hickory bioclimatic domain. Mesic forests are dominated by *Acer saccharum* with *Carya cordiformis*, *Tilia americana* and *Fraxinus americana*, while riparian forests are dominated by *Acer saccharinum* and *Fraxinus pennsylvanica* (Grandtner, 1966).

Site selection and vegetation sampling

The studied forests were selected using satellite imagery (1:5 000) and field reconnaissance surveys, according to size (area >0.5 ha) and vegetation structure (tree cover >80% and no turf). A total of 95 forests met these criteria, and 57 of these were selected (Fig. 3.1; Table S3.1) to represent a gradient of forest size, spatial position (from west to east on each shore), flood intensity (little to mostly flooded) and surrounding impervious surfaces (low to dense).

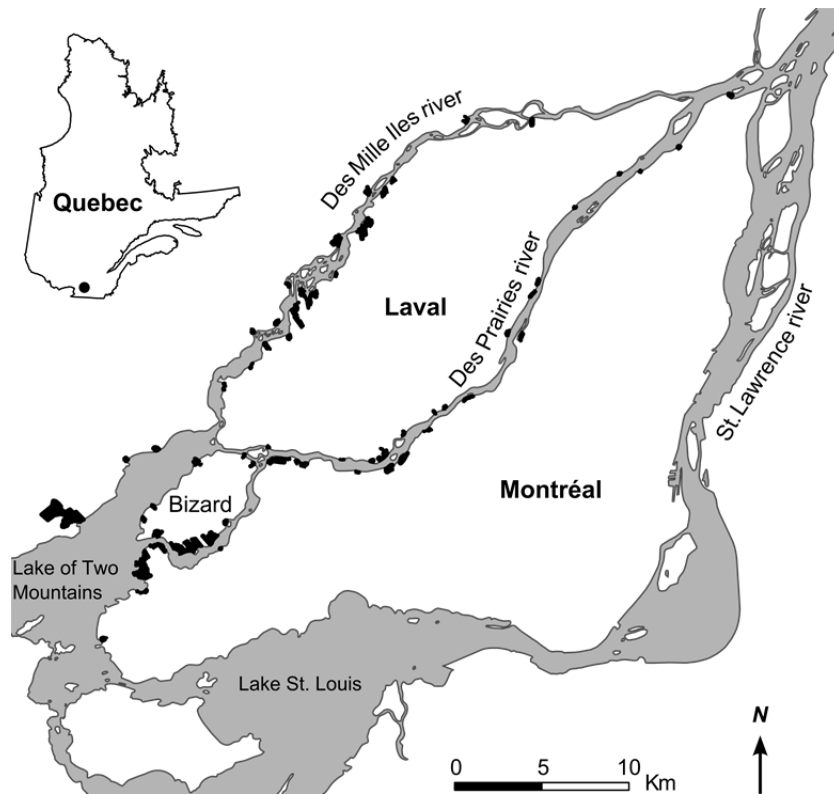


Figure 3.1. Location map of the 57 riparian forests (in black) sampled in the Greater Montreal region.

Within each of these forests, sample plots were positioned along transects perpendicular to the shoreline. Each forest contained 2 to 4 transects according to the length of its shore to ensure a similar sampling effort among forests, namely 2 transects for sites between 50 and 300 m long; 3 transects for sites between 301 and 500 m; and 4 transects for sites longer than 500 m. Each transect contained 2 or 3 plots, depending on forest width. The first plot was located at the shore tree line and the second plot was located 10 m from the first. When the forest was wider than 90 m, a third plot was located in the upland forest, at about 50 m from the second. A total of 438 plots (varying from 4 to 12 plots per site) was sampled in the 57 forests.

Vegetation sampling was carried out from mid-July to mid-August 2013. All herbaceous species were identified within 100 m² plots, 5 m × 20 m for the first plot (the length of the plot lying along the shoreline) and 10 m × 10 m for subsequent plots. Species cover was assessed using seven classes: <1%, 1-5%, 6-25%, 26-50%, 51-75% and 76-100%.

Urbanization and flooding intensity

The intensity of seasonal flooding was evaluated for each forest using flood hazard maps of the area (MMC & CEHQ, 2005), a digital elevation model (1 m resolution; MMC 2009) and based on field surveys during spring floods. Using this information, each forest was classified into three levels of intensity according to the proportion of area usually inundated during spring flooding, ranging from little to mostly flooded (Table 3.1).

The level of urbanization of the matrix surrounding each studied forest was evaluated by calculating the Normalized Difference Vegetation Index (NDVI) in a 500 m buffer zone around each forest from a satellite image (20 m resolution; Geobase 2008) using ArcGIS 10.1 software (ESRI, 2012). NDVI values characterize vegetation density and quality, and range from -1 to +1; negative values indicate the absence of vegetation or presence of sparse unhealthy vegetation, while positive values correspond to the presence of healthy vegetation. The NDVI values of all pixels in the surrounding buffer zone were averaged. A k-means clustering was performed using NDVI values to sort forests in three levels of urbanization intensity, ranging from weakly to highly urbanized (Table 3.1).

Table 3.1. Number of forest patches (N) and class ranges for the different levels of urbanization (mean NDVI values in the buffer zone) and flood intensity (proportion of flooded forest area during spring).

Levels	Urbanization levels		Flood levels	
	N	NDVI value	N	%
Low	20	[-0.20, -0.09[25	[0, 20[
Moderate	20	[-0.09, 0.05[16	[20, 50[
High	17	[0.05, 0.20]	16	[50, 100]

Functional traits

Each species was characterized according to nine functional traits (Table 3.2; see Table S3.2 for raw data) that were selected to represent dispersal ability and tolerance to hydrological and anthropogenic disturbances. Some traits were selected to serve as surrogates of many others (Violle et al., 2007), e.g., the wetness coefficient was used as a surrogate of many specific traits required to survive waterlogging. Trait data were gathered from the primary literature, published trait databases (Fitter and Peat, 1994; Kleyer et al., 2008;; Michigan Flora, 2011; Aubin et al., 2012) and knowledge of the species.

Data analyses

Prior to analyses, three species-by-site matrices were created containing total, native and exotic species respectively and were used individually in each of the subsequent analyses. For each of the 57 forests, species importance values (IV), a measure of the relative dominance of a species in a community (Barbour, 1987), were computed. They were calculated as the mean of the relative frequency (number of plots per forest in which a species occurred relative to the total number of occurrences of all species) and the relative dominance (cover of a species per forest relative to the total cover of all species).

Table 3.2. Description of the selected functional traits used to measure functional β -diversity changes in urban riparian forests.

Functional traits	Code	Units/Scale	Variable
Maximum height	height	cm	Quantitative
Life form	a.forb	annual forb	Nominal
	p.forb	perennial forb	
	fern	fern	
	graminoid	graminoid (i.e., grass and sedge)	
Shade tolerance	shade	1: intolerant	Ordinal
		2: mid-tolerant	
		3: tolerant	
Wetness coefficient	wetness	1: upland	Ordinal
		2: facultative upland	
		3: facultative	
		4: facultative wetland	
		5: obligate wetland	
Seed weight	seedWg	ln(mg)	Quantitative
Seed bank	seedBk	1: transient	Ordinal
		2: short-term persistent	
		3: long-term persistent	
Reproduction	veg	mostly vegetative	Nominal
	seed/veg	seed and vegetative	
	seed	seed only	
Diaspore morphology	wing	wing	Nominal
	nutrient.envelope	nutrient rich envelope (fleshy)	
	no.specialization	no specialization	
	appendages	appendages (e.g., hook or long structure)	
	aerenchym	aerenchym	
	nutrient.seed	nutrient rich seed	
	hairs	hairs	
	mucilaginous	mucilaginous	
Seed buoyancy	buoyancy	1: < 50% of seed float after 1 day	Ordinal
		2 : > 50% of seed float after 1 day	
		3 : > 50% of seed float after 1 week	

Local α -diversity

Total species richness (hereafter total species pool) and exotic richness were assessed for each forest patch, and the proportion of exotic species was then calculated (exotic richness/total richness). Because species richness depends on the number of sampling units, the observed number of species is a downward-biased estimator for the true species richness of a community (Gotelli & Colwell, 2001). Although sample-based richness estimators exist (Gotelli & Colwell, 2001), we preferred to use observed species richness because, at a low number of sampled plots, richness estimators are inaccurate (Chiarucci et al., 2003), which was particularly problematic for exotic species in our sample, as their estimated richness in the forests was always close to total species pool richness.

Mean functional traits for community

To measure changes in functional β -diversity along with urbanization and flood intensity in riparian forests, community weighted means of traits (CWM) were computed (e.g., Garnier et al., 2004, 2007; Lavorel et al., 2008). Compiled in a site-by-trait matrix, CWM for the total species pool, native and exotic species were obtained by matrix multiplication of the species-by-site matrix and a standardized species-by-trait matrix (trait standardization ensures equal weight for all traits, regardless of their units). For continuous traits, CWM was the average value of a trait for all species in the community, weighted by their relative abundance. For ordinal and binary traits, CWM was the relative abundance of species for each trait state.

Between-forest β -diversity

β -diversity can be defined as the variability in species or trait composition among sites of a study area, and can be measured as the average distance of sites to their centroid in multivariate space, using an appropriate distance measure (Anderson et al., 2006). Following

this framework, changes in taxonomic and functional β -diversity (homogenization or differentiation) for the total species pool, native and exotic species among urbanization and flood levels were analysed using tests of homogeneity of multivariate dispersions proposed by Anderson et al. (2006). This approach uses a sites-by-sites distance matrix to first compute the centroid of the sites for each group (here, either the three urbanization levels or the three flood levels), then calculate the distance of sites to the centroid of the urbanization/flood level to which they are associated (i.e., β -diversity), and finally test for differences in the average sites-to-centroid distances among groups with permutations (9999 permutations). This non-parametric test was originally developed to test for difference in taxonomic β -diversity between groups of sites, but can easily be extended to functional β -diversity when based on CWM data (Baiser & Lockwood, 2011). To calculate the taxonomic and functional distance matrices required for this test, Hellinger distance was used for species data and Euclidean distance for CWM, as recommended by Legendre and De Cáceres (2013).

To detect shifts in taxonomic and functional composition between urbanization and flood levels, permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001), which tests for location differences between centroids, was used. Each variable (urbanization and flood) was tested while controlling for the effect of the other and their interaction using MANOVA by RDA. Significance was tested with permutation tests (9999 permutations) with pseudo-F ratios. Like its univariate counterpart, which is sensitive to heterogeneity of variances, this test is sensitive to differences in multivariate dispersions (biotic homogenization or differentiation tested above; Anderson & Walsh, 2013). Consequently, caution should be exercised in interpreting a significant difference among groups that are highly dispersed, which may be due to differences in dispersion rather than to

true differences in location of the centroids. Visualization of the data can then support the interpretation of statistical tests. The differences in taxonomic and functional multivariate dispersion and composition among sites were therefore illustrated in a principal coordinate analysis ordination (PCoA) based on their respective distance matrix, for total pool, native and exotic species and for urbanization and flood gradients. To identify the trait shifts responsible for functional β -diversity changes, the CWM were projected in the PCoA ordination of sites.

Pearson correlations were used to assess the relations between α -diversity (total species richness), the proportion of exotic species in a community, taxonomic β -diversity and functional β -diversity for the total species pool. These correlations allow to better understand the mechanisms underlying all aspects of diversity changes within a community. Taxonomic and functional β -diversity of each forest was measured using site distance to their group (urbanization and flood levels) centroid in species space and in trait space, respectively. The probability values were adjusted using the Holm correction for multiple testing.

Finally, the effect of adding exotic species to a native community on taxonomic and functional β -diversity was tested with paired sample t-tests comparing distance of each site to its centroid calculated for the native species only and calculated for the total species pool (i.e., native + exotic). As for the test of homogeneity of multivariate dispersion, the observations (site distance to centroid) are not independent. However, with reasonable sample sizes, nonindependence is not a serious problem, as the correlation between two observations decreases with increasing sample size (Anderson, 2006). We ran a global paired sample t-test on all distances to determine the overall effect of exotic species in all sites. Subsequently, tests were computed for each urbanization and flood level to see whether exotics had an effect at all disturbance levels, and p-values were adjusted using Holm correction for multiple testing.

All statistical analyses were performed in the R environment (version 3.0.1; R Core Team, 2013). Multivariate beta dispersion analyses were performed using the *betadisper* and *permutest* functions, and multivariate ANOVA were performed using the *rda* and *anova.cca* functions in the *vegan* package (Oksanen et al., 2013).

Results

Taxonomic β -diversity

Taxonomic β -diversity changed with both urbanization and flood levels (Fig. 3.2), as all multivariate dispersion tests were significant for urbanization and flood, except for exotic species between urbanization levels (Table 3.3a). Dispersion was higher at high urbanization levels than at low levels, suggesting that urbanization caused a differentiation of species composition. Inversely, dispersion was lower at high flood levels, suggesting that flood caused a homogenization.

Changes in taxonomic β -diversity were followed by changes in taxonomic composition among urbanization and flood levels, as all multivariate ANOVA were significant (Table 3.3b). Taxonomic composition changes between levels are depicted in the PCoA by the change in the relative centroid locations (Fig. 3.2). The isolated location of the centroid of the high urbanization level relative to the moderate and low levels suggests that species composition (total, native and exotic) of highly urbanized forests differed from that of moderately and lowly urbanized forests (Fig. 3.2a,c,e). The even spacing between flood level centroids indicates a constant species composition turnover among all flood levels (Fig. 3.2b,d,f).

Table 3.3. Results of permutational test of multivariate dispersion (a, c) and permutational MANOVA (b, d) between urbanization and flood levels for taxonomic and functional β -diversity of total, native and exotic species (9999 permutations; on 2 and 54 df). In the permutational MANOVA, the effect of the second factor was partialled out while testing the first. Significant results ($P \geq 0.05$) are shown in bold.

Taxonomic β-diversity						
a. Multivariate test of dispersion around the centroid						
	Total species		Native species		Exotic species	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Urbanization	3.8341	0.029	4.6113	0.0126	2.0702	0.1382
Flood	11.145	0.0001	8.6903	0.0004	6.0009	0.0053
b. Multivariate test of centroid location						
	Total species		Native species		Exotic species	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Urbanization	1.8503	0.0074	1.6509	0.0195	1.816	0.0666
Flood	3.5037	0.0001	3.8964	0.0001	2.8614	0.0002
Functional β-diversity						
c. Multivariate test of dispersion around the centroid						
	Total species		Native species		Exotic species	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Urbanization	1.1913	0.307	2.0224	0.1439	0.233	0.7908
Flood	2.6886	0.0725	1.0548	0.3527	0.5872	0.5615
d. Multivariate test of centroid location						
	Total species		Native species		Exotic species	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Urbanization	3.4787	0.0028	1.6536	0.0935	3.7233	0.0029
Flood	6.1754	0.0001	7.6819	0.0001	3.096	0.0112

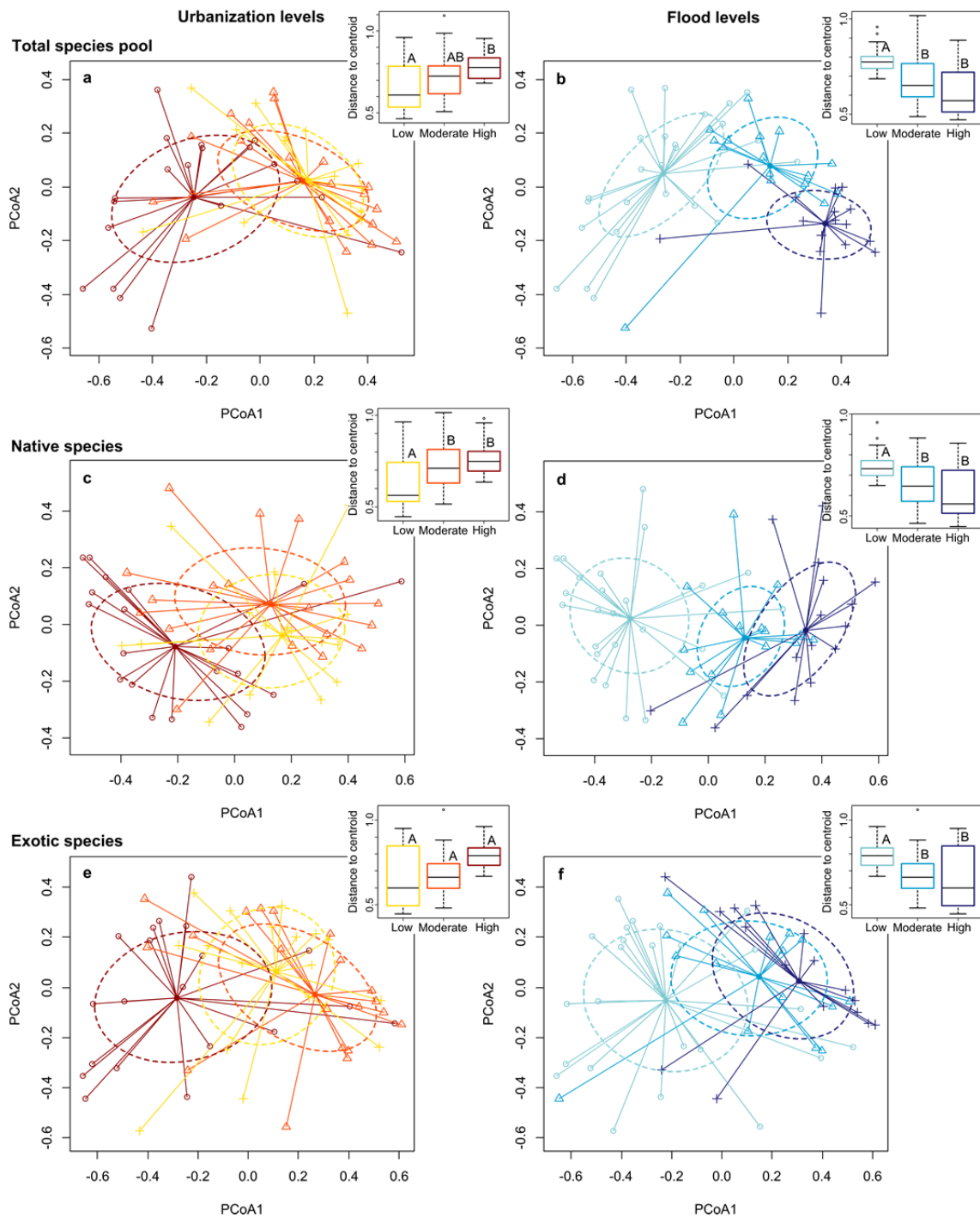


Figure 3.2. Taxonomic β -diversity. Influence of urbanization (a,c,e) and flood (b,d,f) levels on the multivariate dispersion (Hellinger distance) of species composition in the forest patches for total, native and exotic species. β -diversity is measured as the average distance of sites to their group centroid, here represented on the first two axes of a PCoA and using a boxplot (median and quartiles) of the sites-to-centroid distance.

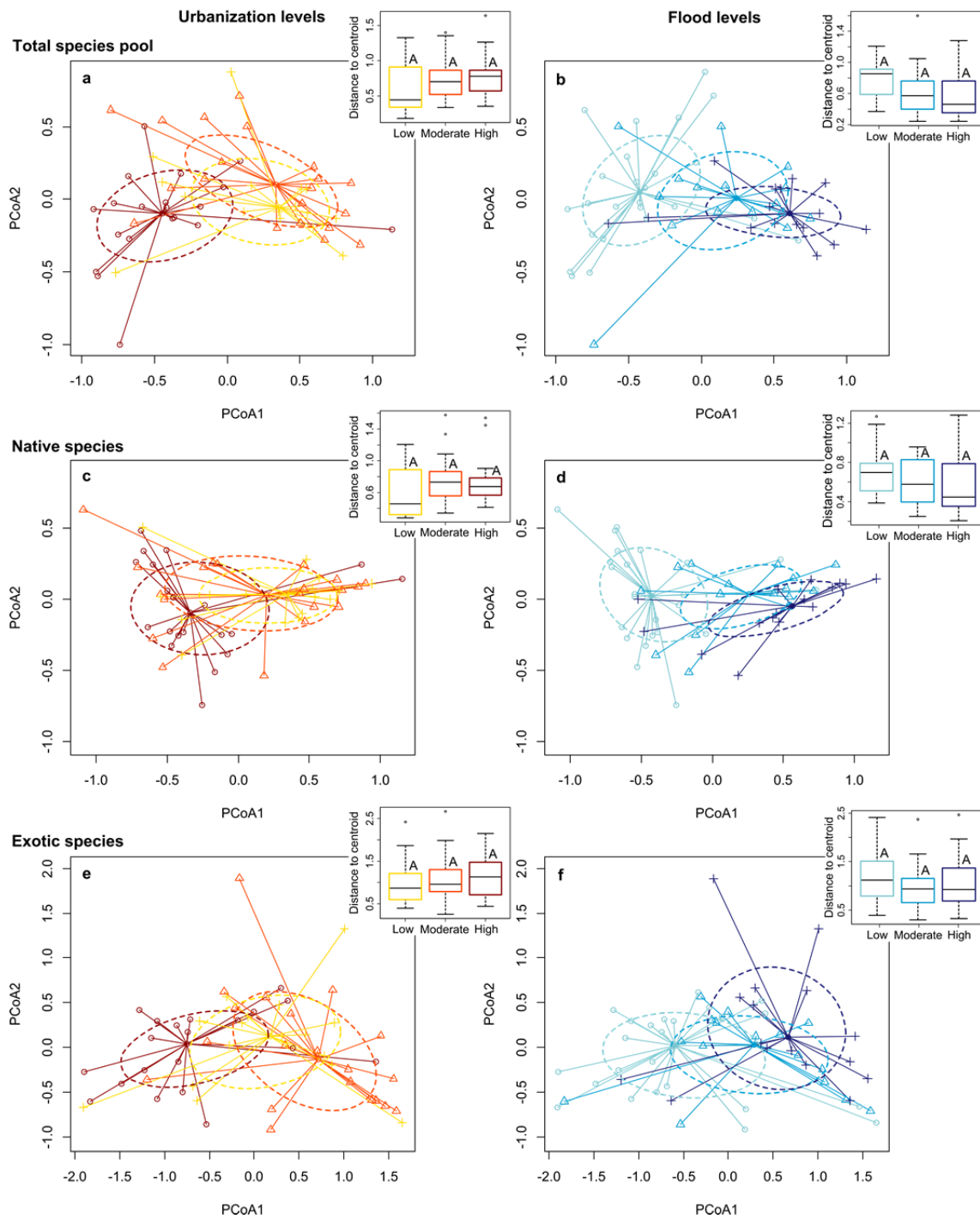


Figure 3.3. Functional β -diversity. Influence of urbanization (a,c,e) and flood (b,d,f) levels on the multivariate dispersion (Euclidean distance) of trait composition in the forest patches for total, native and exotic species. β -diversity is measured as the average distance of sites to their group centroid, here represented on the first two axes of a PCoA and using a boxplot (median and quartiles) of the sites-to-centroid distance.

Functional β -diversity

Functional β -diversity did not change across urbanization or flood levels, as none of the multivariate dispersion tests were significant (Table 3.3c), although total species pool functional dispersion between flood levels was almost significant ($p = 0.07$). Despite the absence of functional homogenization/differentiation, there were significant changes in functional composition across urbanization and flood levels (Table 3.3d). As observed for taxonomic composition, forests with a high urbanization level were generally more distinct in their functional composition than forests with low and moderate levels, as suggested by the remote location of their centroid (Fig. 3.3a,c,e). The centroids of the three flood levels were again evenly spaced, indicating that all levels had different functional composition (Fig. 3.3b,d,f). The observed changes in functional composition can be explained by changes in functional trait distribution (Fig. 3.4). Some traits presented a contrasted distribution across the urbanization/flood gradient; in highly flooded forests at low to moderate urbanization levels (the right end of the ordinations) there were more wetland, shade-tolerant species with buoyant seeds, notably ferns. In highly urban forests with a low flood level (the left end of the ordinations), there were intermediate-tolerant, terrestrial annual forbs, with non-buoyant heavy seeds.

Relation between α -diversity, taxonomic and functional β -diversity

For the total species pool across urbanization levels, we observed that functional β -diversity was strongly positively correlated with taxonomic β -diversity ($r = 0.83$, $P < 0.001$), while total species richness was correlated negatively to taxonomic ($r = -0.53$, $P < 0.001$) and functional β -diversity ($r = -0.49$, $P < 0.001$; Fig. 3.5). Furthermore, the proportion of exotic

species in a riparian forest was positively correlated to taxonomic β -diversity ($r = 0.34$, $P = 0.016$), but not to functional β -diversity ($r = 0.19$, $P = 0.16$). Similar correlations were found when using flood levels to measure β -diversity, except that there was a significant positive correlation between the proportion of exotic species and functional β -diversity ($r = 0.35$, $P = 0.017$).

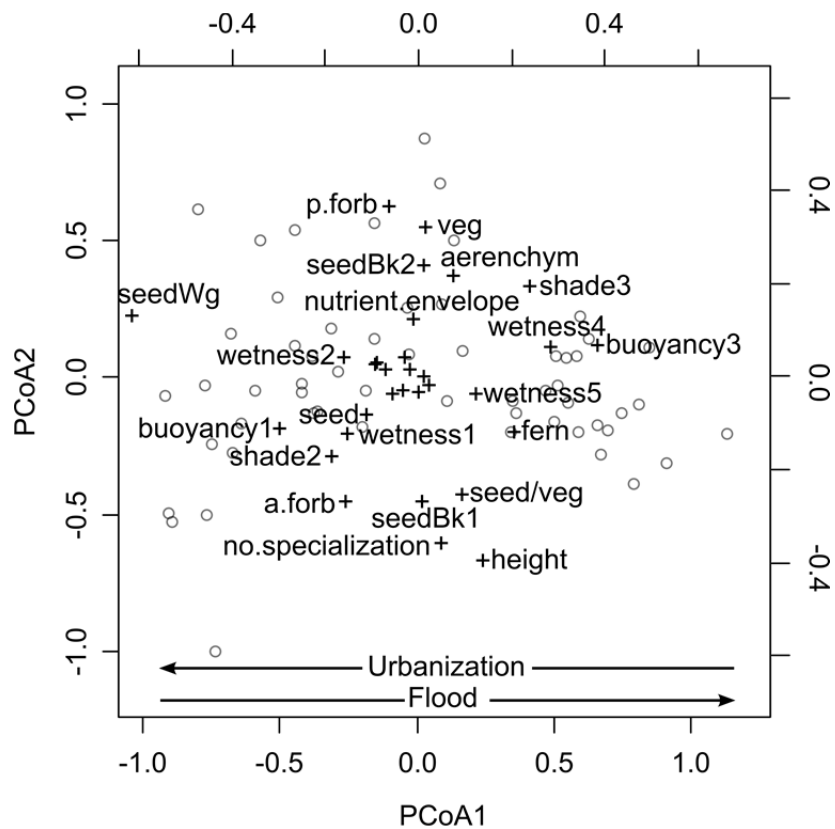


Figure 3.4. PCoA biplot of all forests (gray points) based on total species functional composition matrix (CWM). Functional traits (+) were projected on the PCoA ordination (same as Fig. 3.3 a,b) to show their contribution to β -diversity. The arrows summarize the urbanization/flood gradients observed in Fig. 3.3 a,b with the more urbanized sites (red) generally on the left side and the more flooded sites (dark blue) on the right side of the ordination. Only traits with correlations > 0.55 with one of the first two axes are shown. See Table 2 for trait codes.

The role of exotic species in β -diversity

A gain in exotic species generally increased taxonomic and functional β -diversity (Fig. 3.6), since adding them to a native community generally led to an increase in the mean site distance to the group centroid. More precisely, exotic species caused a global taxonomic differentiation in the studied forests for all disturbance levels pooled together, especially at low urbanization and low flood levels (Fig. 3.6 a, c). In contrast, they did not cause functional homogenization, or functional differentiation across urbanization levels (Fig. 3.6 b), while they did cause a slight functional differentiation across flood levels (Fig. 3.6 d), likely driven by the differentiation at low flood level, which was not significant after Holm correction.

Discussion

In this study, we showed a taxonomic differentiation at high levels of urbanization, while taxonomic homogenization, concomitant with shifts in species composition, was associated with high flood intensity. The introduction of exotic species into riparian forests was also partly responsible for the overall taxonomic differentiation, particularly at low urbanization and flood levels. Changes in taxonomic β -diversity between urbanization/flood levels were likely driven by changes in species richness, as suggested by the strong negative correlation with species richness (Fig. 3.5), as well as species turnover, as suggested the observed shift in species composition (Fig. 3.2). However, these taxonomic patterns were not followed by functional β -diversity changes, even though there was an important functional composition turnover and a high correlation between taxonomic and functional β -diversity.

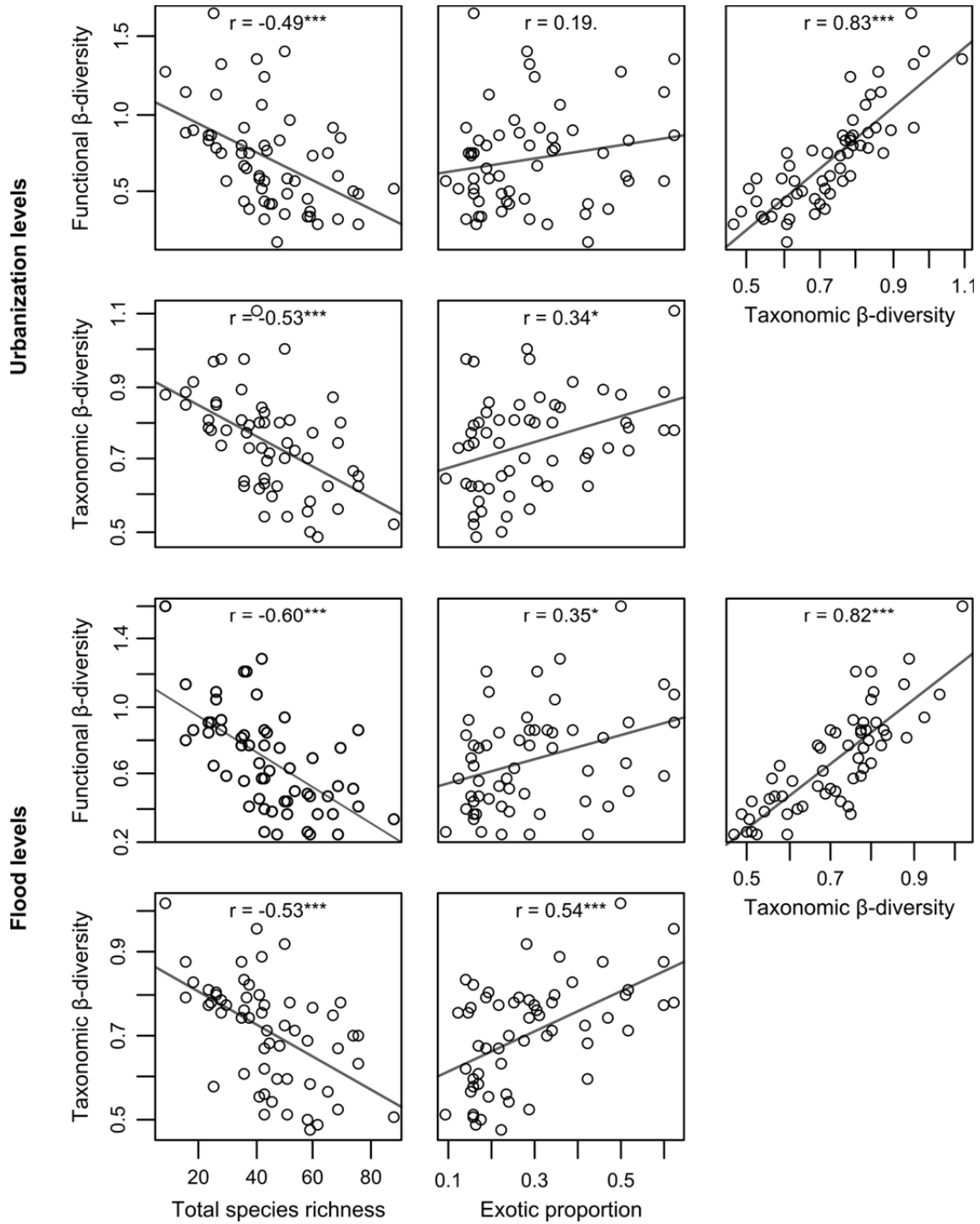


Figure 3.5. Correlations between total species richness, exotic proportion (exotic richness/total richness), taxonomic β -diversity (site distances to their centroid in species space) and functional β -diversity (site distances to their centroid in trait space) for the total species pool. β -diversity was measured as site distance to group centroid for urbanization levels (top) and for flood levels (bottom). Significance levels: * $P < 0.1$; ** $P < 0.01$; *** $P < 0.001$.

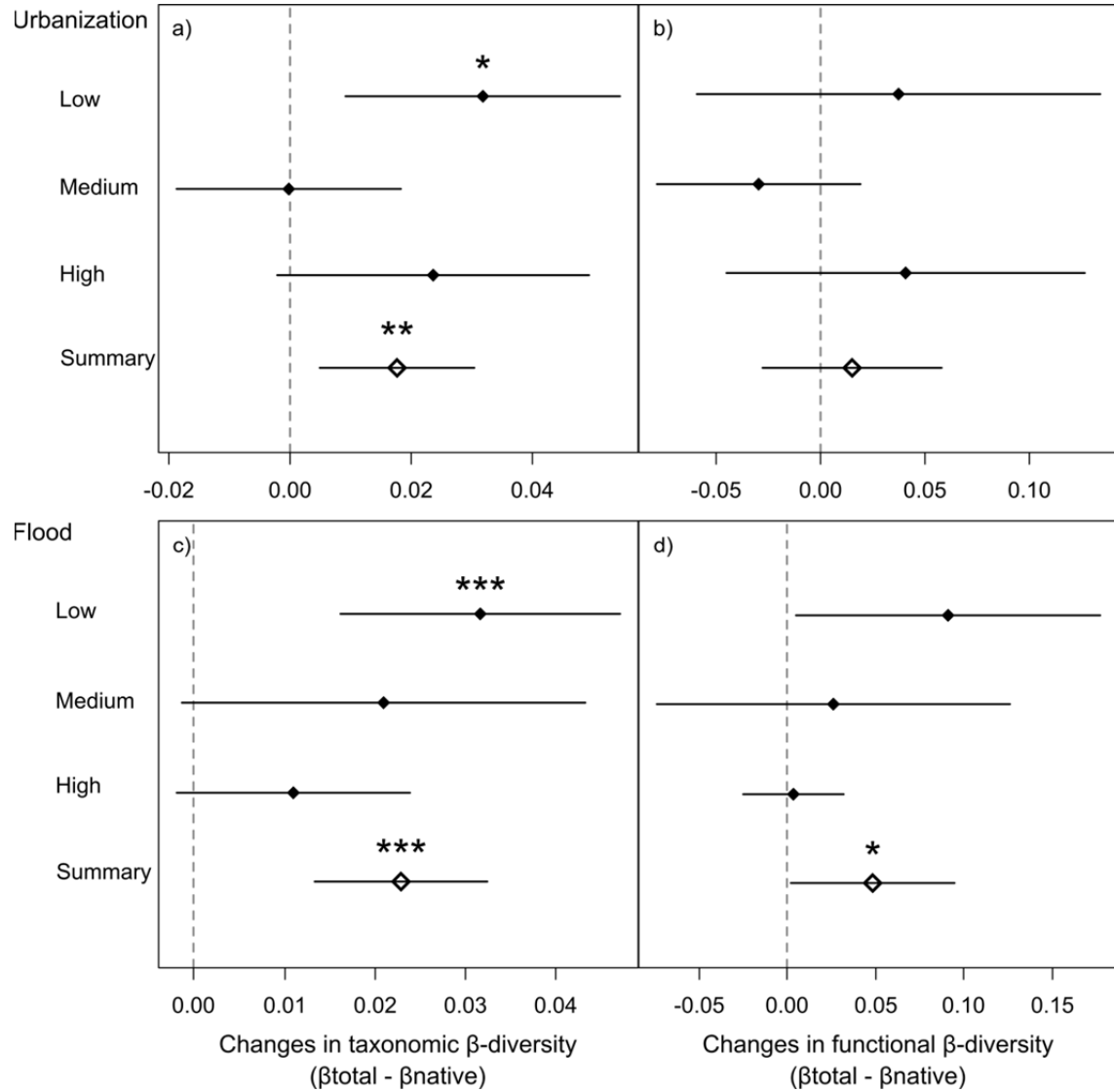


Figure 3.6. Differences in taxonomic (a, c) and functional (b, d) β -diversity caused by exotic species between different urbanization (a, b) and flood (c, d) levels. Changes in β -diversity were assessed by subtracting the site distance to group centroid of native species from the site distance to group centroid of total species (native + exotic). A positive value indicates differentiation, while a negative value indicates homogenization. Asterisks indicate a significant change in paired sample t-tests, Holm correction was used in tests between urbanization/flood levels. Significance levels: * $P < 0.1$; ** $P < 0.01$; *** $P < 0.001$.

Taxonomic differentiation with urbanization intensity

Urbanization has previously been linked to biotic homogenization (McKinney, 2006), but this pattern seemed to be strictly large-scale, among different cities (La Sorte et al., 2007). The role of exotic species in homogenization has usually been observed at large scales, where native floras of distant cities originally had very few species in common and became more similar through the introduction of a few widespread exotic species (McKinney, 2008). Olden and Poff (2003) predicted that, as the spatial extent studied decreases, the probability of observing the introduction of different species and extinction of unshared species is increased because among-site differences are accentuated at a finer sampling resolution. At a local scale, human disturbances are therefore more likely to cause biotic differentiation via the establishment of different species and differential patterns of extinction (Olden & Poff, 2003). Consequently, the differentiation pattern observed in this study was not unexpected.

In addition to this general prediction about differentiation at local scales, the unique abiotic conditions and disturbance regimes of localized urban habitats, driven by the accumulation of past land uses and their impact, increase habitat heterogeneity within cities (Pickett et al., 2001; Aronson et al., 2014). These novel local urban habitats thus harbor different plant communities relative to each other, driving the observed taxonomic differentiation, and relative to rural habitats, explaining the changes in species and trait composition found in this study. Furthermore, compared to rural areas, urban settings have rich exotic floras, which was previously hypothesized to cause taxonomic differentiation within cities (Aronson et al., 2014), particularly via neophytes (Aronson et al., 2014). However, our findings suggest that exotic species had an important role in differentiating communities at low urbanization levels (Fig. 3.6), even though taxonomic differentiation

occurred at high urbanization level. Highly urbanized forests are highly diversified thus adding new exotics has likely a negligible effect, while it can play a larger role in differentiating more homogeneous communities as those of low urbanization levels. Furthermore, as there were relatively few exotics relative to native species at low urbanization level, their presence possibly played a disproportionately large role in β -diversity changes. The positive correlation between exotic proportion and β -diversity indeed suggests that the proportion of exotics was lower in the rural than in the urban forests studied. The tendency of a colonizing species to cause biotic homogenization in its host community depends on this species frequency in other communities; the introduction of a rare species will cause differentiation while that of a widespread species will cause homogenization (Olden & Poff, 2003; McKinney, 2004). At a low urbanization level, most exotics were rare and scattered, so communities likely shared little or no common exotics.

The negative correlation between total species richness and β -diversity suggests that differentiation in highly urban forests may be caused by native species extinctions, and probably by a species turnover driven by the spread of generalist native species, rather than by the predicted exotic invasions (McCune & Vellend, 2013; Johnson et al., 2014; Li & Waller, 2015). Although species turnover is suggested as the basis of homogenization/differentiation processes (McKinney & Lockwood, 1999), the strength of the relationship between total species richness and β -diversity indicates that species loss may be the main mechanism underlying differentiation in urban riparian forests. The important role of species richness in β -diversity was identified by Baiser et al. (2012), who suggested that differentiation occurs when species richness gradients widen (i.e. "the rich get richer and/or the poor get poorer"). In this

study, we probably have a "poor get poorer" scenario, which increases the probability of not finding any species in common.

Taxonomic homogenization with flood intensity

Altered hydrologic regimes of rivers in urban areas may further influence β -diversity patterns. In the study area, the flooding gradient was highly correlated to human land use changes (Chapter 1 of this work) and may therefore provide a more complete picture of biodiversity changes in urban riparian forests. Human disturbances alter the magnitude and variability of floods through land use changes from pervious to impervious surfaces associated to urbanization (White & Greer, 2006; Burton et al., 2009; Sung et al., 2011) and through flow regulations (Ward & Stanford, 1995; Poff et al., 2007), which can lead to a regional homogenization of flood regimes (Poff et al., 2007). This increased similarity in flow regimes has been hypothesized to increase similarity among riparian communities (Johnson et al., 2014). Our results rather suggest that altered flood regimes allow community differentiation by enhancing local habitat heterogeneity. Floods can be an homogenizing force on community composition by exerting a strong selective pressure on species traits, while altered hydrological regimes result in floodplains being inundated less frequently and for shorter durations, promoting the establishment of new terrestrial species (Groffman et al., 2003; Stromberg et al., 2007; Pennington et al., 2010; Chapter 2 of this work). We did indeed find a high species turnover between flooding levels, higher than for urbanization levels. This species turnover likely favored differentiation by allowing different species to colonize these once restrictive habitats.

Relationship between taxonomic and functional homogenization

A loss or gain of taxonomic distinctiveness is followed by a loss or gain in functional distinctiveness. The positive relationship is stronger when multiple traits are considered (Naaf & Wulf, 2012). Predictions from a recent simulation study demonstrated that the strength of the relationship between changes in taxonomic and functional β -diversity increases as trait redundancy in the species pool decreases (Baiser & Lockwood, 2011). Thus, the use of multiple traits makes it possible to take into account the fact that species differ from each other in multiple ways and thereby reduce the degree of functional redundancy in the regional species pool (Baiser & Lockwood, 2011).

Despite this positive relationship, significant changes in taxonomic β -diversity did not imply significant changes in functional β -diversity in the studied riparian forests. Rather, we observed a high trait turnover among disturbance levels, without an increase or decrease in functional community similarity. Urbanization and flood intensity favored different traits through environmental filtering, but these traits were not more or less similar between sites, probably because niche differentiation maintains a minimal functional complementarity in communities (Tilman, 1997; Díaz & Cabido, 2001). As well, exotic species did not influence functional β -diversity, indicating that their traits are not different than that of native species. This result is expected because environmental filtering acts on species traits (Díaz & Cabido, 2001; Mayfield et al., 2010), whatever their origin. This study hence stresses the triviality of the native-vs-exotic dichotomy in assembly processes and diversity patterns (Davis, 2011). On the other hand, the absence of functional β -diversity changes concurrent with taxonomic changes could also be an artifact of the method itself. Indeed, there are many species that can differentiate two communities, while there are relatively few sampled traits, which in addition

show values that often overlap, especially for categorical traits. Hence, the magnitude of functional β -diversity changes is considerably lower than that of taxonomic β -diversity (Naaf & Wulf, 2012), and functional homogenization/differentiation could then remain undetected due to the restricted number of traits possible to document.

Conclusion

While urbanization led to taxonomic differentiation, flood intensity fostered taxonomic homogenization. Despite a high correlation between taxonomic and functional β -diversity changes, there was no functional homogenization or differentiation along disturbance gradients, implying that functional homogenization cannot be inferred from taxonomic homogenization and should be studied independently, as has been posited in other studies (Baiser & Lockwood, 2011; Naaf & Wulf, 2012). Our study also provides novel insights into the mechanisms involved in β -diversity changes. First, land use transformation seemed to be the main trigger of all biodiversity changes, as it caused a direct species loss in highly urban forests, and, through alteration of the hydrological regime, promoted an important species turnover between flood levels, both leading to a taxonomic differentiation at high urbanization and low flood levels. Although flood intensity favored homogenization at a local scale, it likely increases β -diversity at larger scales, as riparian habitats harbor different species relative to upland habitats (Sabo et al., 2005). Hence, while our study provided evidence of differentiation with flood alteration, the latter could ultimately lead to a homogenization of urbanized watersheds. Furthermore, urbanization altered the species pool by adding exotic species, which were partly accountable for the observed β -diversity patterns. However, it is increasingly recognized that the presence of exotic species is more a symptom of local habitat

degradation than a leading cause of diversity changes (Gurevitch & Padilla, 2004; MacDougall & Turkington, 2005; Davis, 2011), as anthropogenic filters act on species traits (Díaz & Cabido, 2001; Mayfield et al., 2010), whether native or exotic. Hence, future studies on biotic homogenization at local scales should focus more on the role of land use changes than on exotic species in order to improve our understanding of biodiversity responses to human disturbances.

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Chapitre 4

Conclusion

L'objectif global de ce mémoire de maîtrise était d'identifier et de comprendre les impacts de l'urbanisation sur la distribution des espèces et des traits dans les forêts riveraines de la région de Montréal. La première étude (chapitre 2) explore les changements dans la composition fonctionnelle des forêts riveraines en réponse à l'urbanisation et les questions suivantes ont été abordées: (1) Quels sont les filtres environnementaux clés qui structurent la composition fonctionnelle des communautés riveraines dans les villes? (2) Quelle est l'importance de la dispersion par la rivière dans la distribution des traits par rapport à la dispersion par voie terrestre dans un contexte de forêts à la fois fragmentées par l'urbanisation et connectées par les rivières? La seconde étude (chapitre 3) examine les effets des perturbations hydrologiques et anthropiques sur les tendances d'homogénéisation taxonomique et fonctionnelle dans les forêts riveraines urbaines et les questions suivantes ont été abordées: (1) Y a-t-il une tendance d'homogénéisation ou de différenciation des espèces et des traits le long de gradients d'urbanisation et d'inondation? (2) Les changements dans la diversité β taxonomique et fonctionnelle sont-ils liés à un changement de la composition en espèces ou en traits, de la richesse locale α , ou de la dominance des espèces exotiques? (3) Quelle est la relation entre diversité α et la diversité β fonctionnelle et taxonomique?

La première étude (chapitre 2) a montré que sous des régimes de perturbations naturelles sévères, l'effet des filtres naturels surpasse les effets délétères des filtres urbains. En effet, l'intensité des inondations saisonnières était la variable la plus importante pour expliquer la

composition fonctionnelle des communautés riveraines. La transformation du paysage par l'urbanisation jouait également un rôle important et exerçait une influence indirecte sur la distribution des traits via l'altération des régimes hydrologiques. Les changements de composition fonctionnelle observés dans cette étude suggèrent que l'urbanisation conduit à une tendance générale vers une terrestrialisation des forêts riveraines.

L'interdépendance entre les filtres naturels et anthropiques était à l'origine de la plupart des structures spatiales modélisées par les cartes des vecteurs propres asymétriques (AEM). Néanmoins, en plus des filtres environnementaux, la dispersion le long des rivières était aussi une force de structuration spatiale majeure. En effet, malgré la fragmentation importante des forêts en milieu urbain, la dispersion par la rivière (AEM) était plus importante que la dispersion par voie terrestre (cartes des vecteurs propres de Moran, MEM). Ce résultat souligne que les rivières offrent une grande connectivité entre les vestiges de forêts et jouent possiblement un rôle important pour le maintien de la biodiversité dans les paysages urbains.

La seconde étude (chapitre 3) a montré que, contrairement aux tendances prédites par la théorie, l'urbanisation favorise la différenciation taxonomique, tandis que les inondations favorisent l'homogénéisation taxonomique. Malgré une forte corrélation entre les changements de diversité β taxonomique et fonctionnelle, il n'y avait pas d'homogénéisation ni de différenciation fonctionnelle le long des gradients de perturbation, ce qui implique que l'homogénéisation fonctionnelle devrait être étudiée indépendamment de l'homogénéisation taxonomique puisque ces deux processus ne peuvent être déduits l'un de l'autre, tel que suggéré par d'autres études (Baiser & Lockwood, 2011; Naaf & Wulf, 2012).

Plusieurs mécanismes semblaient impliqués dans les changements de diversité β taxonomique observés entre les niveaux d'urbanisation et d'inondation. La diversité β

taxonomique présentait une forte corrélation négative avec la richesse en espèces et était associée à un changement dans la composition des espèces. De plus, l'introduction d'espèces exotiques dans les forêts riveraines était en partie responsable de la différenciation taxonomique globale. Par conséquent, l'urbanisation était probablement le principal élément déclencheur des changements de la diversité β , en causant un gain en espèces exotiques et une perte d'espèces dans les forêts fortement urbanisées, ainsi qu'en entraînant un important turnover d'espèces entre les niveaux d'inondation par la modification du régime hydrologique.

Dans l'ensemble, les résultats de ces deux études suggèrent que la modification des processus naturels par les activités anthropiques est le principal moteur de changements dans les forêts riveraines en milieu urbain. Tandis que les perturbations sont une caractéristique inhérente des écosystèmes riverains, les perturbations causées par l'Homme ont des conséquences à très long terme et altèrent les processus écologiques naturels. Bien que l'altération des régimes hydrologiques par l'urbanisation ait mené à une différenciation taxonomique dans les forêts riveraines, le processus de terrestrialisation révélé dans les changements de la composition fonctionnelle suggère une possible homogénéisation des milieux riverains avec le milieu terrestre à l'échelle du bassin versant. Comme les écosystèmes riverains intègres possèdent une flore distincte des écosystèmes terrestres (Sabo et al., 2005), en altérant les forêts riveraines, l'urbanisation risque de diminuer considérablement la biodiversité régionale, et ce malgré le gain en espèces exotiques.

Bien que l'élaboration de directives précises de gestion ne soit pas le but de ce travail, les résultats obtenus peuvent être utilisés pour guider la conservation de la biodiversité dans les villes. Compte tenu des changements extensifs et irréversibles du paysage en milieux urbains, la restauration complète des forêts riveraines à leur condition historique est impossible. Par

exemple, de nombreuses forêts riveraines de la région de Montréal ne pourront revenir à leur état initial de plaines inondables, car les modifications du régime hydrologique (notamment par les barrages) et du sol sont trop profondes. Toutefois, il demeure possible de conserver la biodiversité en villes. La plus grande priorité est de protéger les écosystèmes riverains restants puisque la biodiversité a besoin d'espace (Beninde et al., 2015). Ensuite, trois grandes recommandations peuvent être formulées, autant pour la gestion en régions urbaines que suburbaines, en regard des conclusions de ce mémoire. Les résultats issus des deux articles soulignent l'importance du régime hydrologique naturel dans la composition fonctionnelle et la diversité β des forêts riveraines. Par conséquent, les stratégies de gestion dans les milieux urbains devraient viser à (1) restaurer et préserver les processus naturels essentiels au maintien de l'intégrité des forêts riveraines, et ainsi limiter la terrestrialisation. Par exemple, une première étape simple est d'éviter ou d'enlever les constructions ou modifications qui déconnectent l'habitat riverain de la rivière (e.g., digues, remblais, murets) le long des rives. En outre, en raison de l'importance de la dispersion par le courant des rivières (chapitre 2), (2) le maintien de la connectivité amont-aval devrait également être privilégié en conservant et réhabilitant des bandes de végétation le long des rivières de manière à mitiger les effets délétères de la fragmentation. Enfin, la seconde étude (chapitre 3) a révélé que les espèces exotiques jouaient un rôle secondaire dans la différenciation taxonomique et n'influençaient pas la diversité fonctionnelle. Actuellement, les stratégies de restauration en milieu urbain investissent beaucoup de ressources dans l'élimination des espèces exotiques. Cependant, il est de plus en plus reconnu que, bien que parfois problématique, leur présence est davantage un symptôme de la dégradation des habitats, plutôt que la principale cause de changements de la diversité (Gurevitch & Padilla, 2004; MacDougall & Turkington, 2005; Davis, 2011), étant

donné que les filtres anthropiques agissent sur les traits des espèces (Díaz & Cabido, 2001; Mayfield et al., 2010), qu'elles soient indigènes ou exotiques. Par conséquent, la dichotomie indigène-exotique n'étant pas fondée sur les processus d'assemblage des communautés, (3) les efforts devraient davantage être orientés sur la restauration des habitats plutôt que sur l'élimination des espèces exotiques. Les espèces exotiques font aujourd'hui partie intégrante de la flore urbaine et leur élimination dans une forêt peut s'avérer plus dommageable que leur présence; celles-ci pourraient plutôt être considérées comme une forme de résilience des écosystèmes, une réponse aux changements environnementaux (Richardson et al., 2007).

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Annexes du chapitre 2

Table S2.1. Number of patches selected for each range of the selection criterion: patch area, patch position, proportion of flooded forest area, and proportion of surrounding impervious surfaces.

Area (ha)		Position*		Flood intensity (%)		Impervious surfaces (%)	
N	Value	N	Value	N	Value	N	Value
24	[0.4, 3[14	NE part	25	[0, 20[18	[0, 20[
24	[3, 20[27	middle	16]20, 50]	23	[20, 40[
9	[20, 160]	16	SO part	16]50, 100]	16	[40, 65]

* NE part: from the middle of Laval Island and eastward

Middle: from the western end to the middle of Laval Island

SW part: from the western end of Montreal Island to western end of Laval Island

Table S2.2. Pearson correlation coefficients between all explanatory variables from the local and landscape subsets. Only the lower triangle is shown.

	area	PAR	flood	altitude	slope	age	histo.human	histo.agricult	histo.area	forest	isolation	NDVI	rural	green	HII	impervious
PAR	-0.47															
flood	0.29	-0.43														
altitude	0.28	-0.18	-0.18													
slope	-0.12	0.29	-0.37	0.29												
age	0.16	-0.14	0.53	0.10	-0.19											
histo.human	-0.22	0.42	-0.32	-0.26	0.35	-0.22										
histo.agricult	0.04	-0.30	-0.02	0.10	-0.21	-0.38	-0.61									
histo.area	0.04	-0.11	0.30	0.13	-0.13	0.74	-0.24	-0.43								
forest	0.46	-0.53	0.28	0.07	-0.21	0.17	-0.24	0.17	-0.01							
isolation	-0.22	0.58	-0.38	-0.15	0.52	-0.26	0.42	-0.30	-0.15	-0.45						
NDVI	0.45	-0.54	0.35	-0.07	-0.33	0.16	-0.29	0.22	0.01	0.81	-0.52					
rural	0.11	-0.22	0.29	-0.08	-0.12	0.07	-0.24	0.25	-0.10	0.28	-0.18	0.29				
green	0.37	-0.46	0.34	-0.03	-0.30	0.19	-0.28	0.22	0.02	0.76	-0.43	0.89	0.24			
HII	-0.26	0.28	-0.47	0.20	0.40	-0.09	0.21	-0.12	0.00	-0.32	0.28	-0.34	-0.21	-0.22		
impervious	-0.39	0.35	-0.19	0.21	0.33	0.01	0.13	-0.21	0.11	-0.69	0.31	-0.85	-0.39	-0.77	0.35	
bridge	-0.19	0.19	-0.19	0.20	0.35	-0.15	0.12	-0.01	-0.08	-0.20	0.23	-0.34	-0.20	-0.18	0.26	0.18

Table S2.3. Species functional trait matrix for trees (a), shrubs (b) and herbs (c). See Table 2.2 for trait code.

a) Tree species code	height	veg	shade	wetness	seedBk	ln(seedWg)	bird	endozoo	hydro	anemo	anthropo	other
<i>Abies balsamea</i>	2500	1	3	3	1	2.0254	0	1	0	1	0	0
<i>Acer negundo</i>	2000	1	1	3	1	3.6869	1	0	0	1	1	0
<i>Acer nigrum</i>	3500	1	3	2	1	4.1668	0	1	0	1	0	0
<i>Acer platanoides</i>	3000	0	2	1	1	5.1462	0	0	0	1	1	0
<i>Acer rubrum</i>	2500	1	2	3	1	2.9938	0	0	1	1	0	0
<i>Acer saccharinum</i>	3500	1	2	4	1	5.6408	1	1	1	1	1	0
<i>Acer saccharum</i>	3500	1	3	2	1	4.2391	0	0	0	1	0	0
<i>Aesculus hippocastanum</i>	2500	0	2	1	1	9.4709	0	0	0	0	1	1
<i>Amelanchier laevis</i>	1300	1	3	1	1	1.6862	1	1	0	0	0	0
<i>Betula papyrifera</i>	2500	1	1	2	2	-1.1134	0	0	1	1	0	0
<i>Betula populifolia</i>	1000	1	1	3	3	-2.2391	0	0	0	1	0	0
<i>Carpinus caroliniana</i>	1200	0	3	3	2	2.5617	1	1	0	1	0	0
<i>Carya cordiformis</i>	2500	1	2	3	3	7.9749	0	1	0	0	0	1
<i>Carya ovata</i>	2500	1	2	2	3	8.4604	0	1	1	0	0	1
<i>Catalpa speciosa</i>	3000	1	1	2	1	3.0967	0	0	0	1	1	0
<i>Celtis occidentalis</i>	2400	0	3	3	2	2.3558	1	1	0	0	0	1
<i>Fagus grandifolia</i>	2500	1	3	2	1	5.647	1	1	0	0	0	1
<i>Fraxinus americana</i>	3000	1	1	2	2	3.8144	0	0	0	1	1	0
<i>Fraxinus nigra</i>	2000	1	1	4	2	3.8418	0	0	1	1	0	0
<i>Fraxinus pennsylvanica</i>	2500	1	2	4	2	3.4554	0	0	1	1	1	0
<i>Juglans cinerea</i>	2500	0	1	2	2	9.6243	0	1	0	0	0	1
<i>Malus pumila</i>	800	0	1	1	1	3.2862	0	1	0	0	1	0
<i>Malus sieboldii</i>	800	0	1	1	1	1.0296	0	1	0	0	1	0
<i>Ostrya virginiana</i>	1800	1	3	2	1	2.7158	1	0	0	1	0	0
<i>Picea glauca</i>	2500	0	3	2	1	0.8891	0	1	0	1	1	0
<i>Picea rubens</i>	2500	0	3	2	1	1.1754	0	1	0	1	0	0
<i>Pinus strobus</i>	3000	0	2	2	1	2.8197	1	1	0	1	0	0
<i>Populus balsamifera</i>	2500	1	1	4	1	-1.4271	0	0	1	1	0	0
<i>Populus deltoides</i>	3000	1	1	3	1	0.0649	0	0	1	1	1	0
<i>Populus grandidentata</i>	2000	1	1	2	1	-1.8893	0	0	1	1	0	0

a) Tree species code	height	veg	shade	wetness	seedBk	ln(seedWg)	bird	endozoo	hydro	anemo	anthropo	other
<i>Populus tremuloides</i>	2500	1	1	3	1	-1.9688	0	0	1	1	0	0
<i>Prunus serotina</i>	2200	1	1	2	3	4.5484	1	1	0	0	0	1
<i>Quercus macrocarpa</i>	1500	1	2	2	1	8.7073	1	1	1	0	0	1
<i>Quercus rubra</i>	3000	1	2	2	1	8.1965	1	1	0	0	1	1
<i>Robinia pseudoacacia</i>	2500	1	1	2	3	2.939	0	0	0	0	1	1
<i>Salix amygdaloides</i>	2500	1	1	4	1	-1.7462	0	0	1	1	0	0
<i>Salix fragilis</i>	3000	1	1	3	1	-1.9661	0	0	1	1	1	0
<i>Salix nigra</i>	3000	1	1	5	1	-1.707	0	0	1	1	0	0
<i>Thuja occidentalis</i>	1500	1	2	4	1	0.2717	0	1	0	1	1	0
<i>Tilia americana</i>	3500	1	3	2	2	4.5557	1	1	0	1	0	1
<i>Tilia cordata</i>	2500	1	3	1	1	3.4924	1	1	0	1	1	0
<i>Tsuga canadensis</i>	3000	0	3	2	1	0.8849	0	1	0	1	0	0
<i>Ulmus americana</i>	3500	1	2	4	1	1.8558	1	1	1	1	0	1
<i>Ulmus pumila</i>	3000	0	2	2	1	1.9433	1	1	0	1	0	0
<i>Ulmus rubra</i>	2500	1	2	3	1	2.4035	1	1	0	1	0	1

b) Shrub species code	height	veg	shade	wetness	seedBk	ln(seedWg)	bird	endozoo	hydro	anemo	anthropo	other
<i>Acer tataricum</i>	610	0	1	1	1	3.3957	0	0	0	1	1	0
<i>Alnus incana</i>	490	1	2	4	1	-0.8716	0	0	1	1	0	0
<i>Amelanchier sanguinea</i>	250	1	3	1	1	1.6862	1	1	0	0	0	0
<i>Amelanchier sp.</i>	250	1	3	1	1	1.6862	1	1	0	0	0	0
<i>Amorpha fruticosa</i>	400	1	1	4	1	1.7732	0	0	1	0	1	0
<i>Berberis thunbergii</i>	200	1	1	2	1	2.8197	1	1	0	0	1	0
<i>Berberis vulgaris</i>	300	1	1	2	3	2.5649	1	1	1	0	1	0
<i>Celastrus scandens</i>	1000	1	3	2	1	2.8559	1	0	0	0	0	0
<i>Cephalanthus occidentalis</i>	300	0	3	5	3	1.2192	0	0	1	0	0	0
<i>Clematis occidentalis</i>	350	1	2	1	1	1.2662	0	0	1	1	1	0
<i>Cornus alternifolia</i>	1000	1	3	2	1	4.0376	1	0	0	0	0	0
<i>Cornus amomum</i>	300	1	2	4	1	3.6156	1	0	0	0	0	0
<i>Cornus rugosa</i>	300	1	1	1	1	3.1726	1	0	0	0	0	0
<i>Cornus stolonifera</i>	300	1	2	4	1	3.1991	1	0	0	0	0	0

b) Shrub species code	height	veg	shade	wetness	seedBk	ln(seedWg)	bird	endozoo	hydro	anemo	anthropo	other
<i>Corylus cornuta</i>	300	1	3	2	1	6.7167	1	1	0	0	0	0
<i>Cotoneaster acutifolius</i>	305	0	2	1	2	2.9309	1	1	0	0	1	0
<i>Crataegus sp.</i>	600	0	2	2	1	3.8373	1	1	0	0	0	0
<i>Diervilla lonicera</i>	120	1	2	1	3	NA	0	1	0	0	0	0
<i>Dirca palustris</i>	200	1	3	3	1	2.4317	0	1	1	0	0	0
<i>Euonymus alatus</i>	250	1	3	1	2	2.8273	1	0	0	0	1	0
<i>Fallopia japonica</i>	200	1	2	2	1	0.7251	0	1	1	1	1	0
<i>Frangula alnus</i>	500	1	2	3	2	3.0253	1	0	1	0	1	0
<i>Ilex verticillata</i>	800	1	2	4	2	1.5952	1	0	0	0	0	0
<i>Lonicera dioica</i>	300	1	2	2	1	1.7829	1	1	0	0	1	0
<i>Lonicera morrowii</i>	244	1	2	2	1	1.0919	1	1	0	0	1	0
<i>Lonicera tatarica</i>	300	0	2	2	1	1.1612	1	1	0	0	1	0
<i>Menispermum canadense</i>	400	0	2	3	1	4.0413	1	0	0	0	0	0
<i>Morus alba</i>	1500	0	1	2	3	0.6574	1	1	0	0	1	0
<i>Parthenocissus quinquefolia</i>	1500	1	2	2	1	3.2065	1	0	0	0	1	0
<i>Philadelphus coronarius</i>	244	0	1	1	1	-2.4002	0	0	0	0	1	1
<i>Physocarpus opulifolius</i>	300	0	1	4	2	-0.8347	1	0	1	0	0	0
<i>Prunus nigra</i>	300	1	1	2	3	4.5329	1	1	0	0	0	1
<i>Prunus pensylvanica</i>	1200	1	1	2	3	3.4638	1	1	0	0	0	1
<i>Prunus virginiana</i>	900	1	2	2	3	4.5134	1	1	0	0	1	1
<i>Prunus virginiana var. Schubert</i>	900	1	2	2	3	4.5134	1	1	0	0	1	1
<i>Rhamnus cathartica</i>	800	1	1	3	3	3.0773	1	1	0	0	1	0
<i>Rhus typhina</i>	600	1	1	2	3	2.4159	1	0	0	0	0	0
<i>Ribes alpinum</i>	300	1	2	2	1	1.4816	1	1	0	0	1	0
<i>Ribes americanum</i>	150	0	3	4	3	0.3708	1	1	0	0	0	0
<i>Ribes cynosbati</i>	150	1	3	2	3	0.6931	1	1	0	0	0	0
<i>Ribes triste</i>	100	1	3	5	3	0.7464	1	1	0	0	0	0
<i>Rosa blanda</i>	150	1	1	2	2	2.3026	1	0	0	0	0	0
<i>Rubus allegheniensis</i>	200	1	1	2	3	0.5487	1	1	0	0	0	0
<i>Rubus idaeus</i>	150	1	1	3	3	0.5186	1	1	0	0	0	0
<i>Rubus occidentalis</i>	300	1	1	1	3	0.3029	1	1	0	0	0	0
<i>Rubus odoratus</i>	150	1	2	1	3	-0.0835	1	1	0	0	0	0

b) Shrub species code	height	veg	shade	wetness	seedBk	ln(seedWg)	bird	endozoo	hydro	anemo	anthropo	other
<i>Salix bebbiana</i>	800	1	1	4	1	-1.707	0	0	1	1	0	0
<i>Salix discolor</i>	800	1	1	4	1	-1.1394	0	0	1	1	0	0
<i>Salix eriocephala</i>	400	1	1	4	1	-2.7489	0	0	1	1	0	0
<i>Salix interior</i>	200	1	1	4	1	-3.1942	0	0	1	1	0	0
<i>Salix lucida</i>	800	1	2	4	1	-1.7545	0	0	1	1	0	0
<i>Sambucus canadensis</i>	300	1	2	4	3	1.3083	1	1	0	0	0	0
<i>Sambucus racemosa</i>	400	1	3	2	3	0.8755	1	1	0	0	0	0
<i>Sorbus aucuparia</i>	1219	0	2	1	1	1.2887	1	1	0	0	1	0
<i>Spiraea latifolia</i>	200	0	1	4	1	-0.1265	0	0	1	1	0	0
<i>Staphylea trifolia</i>	500	1	3	3	2	3.7265	0	0	1	1	0	0
<i>Symphoricarpos albus</i>	100	1	2	2	1	1.7859	1	1	0	0	1	0
<i>Syringa reticulata</i>	1000	1	1	3	2	2.568	0	0	0	1	1	0
<i>Syringa vulgaris</i>	800	1	1	1	2	1.6092	0	1	0	1	1	0
<i>Taxus canadensis</i>	200	1	3	2	3	3.2878	1	0	0	1	0	0
<i>Toxicodendron radicans</i>	100	1	2	3	3	2.7014	1	1	0	0	0	0
<i>Viburnum lantana</i>	274	0	1	1	1	3.9537	1	0	0	0	1	0
<i>Viburnum lentago</i>	400	1	3	3	1	4.0574	1	0	0	0	0	0
<i>Viburnum opulus</i>	500	0	2	4	1	3.507	1	0	0	0	1	0
<i>Viburnum trilobum</i>	500	0	2	4	1	3.507	1	0	0	0	0	0
<i>Vitis riparia</i>	1500	1	2	3	1	3.4429	1	1	0	0	1	0
<i>Zanthoxylum americanum</i>	500	1	3	2	2	2.7788	1	1	0	0	0	0

c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Achillea millefolium</i>	1	60	1	1	2	2	-1.839	1	0	0	1	1	0
<i>Acorus calamus</i>	1	200	1	1	5	1	-0.095	0	0	1	0	0	1
<i>Actaea rubra</i>	1	40	1	3	2	1	1.7047	1	0	0	0	0	0
<i>Aegopodium podagraria</i>	1	90	1	2	3	3	0.7885	0	0	0	1	1	1
<i>Ageratina altissima</i>	1	120	1	2	2	3	-1.791	0	0	0	1	0	0
<i>Agrimonia gryposepala</i>	1	200	1	2	2	3	0.5956	0	1	0	0	0	0
<i>Agrostis stolonifera</i>	1	70	1	1	4	3	-2.604	0	0	0	1	0	1
<i>Alisma triviale</i>	1	15	1	1	5	3	-0.862	0	0	1	0	0	0

c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Alliaria petiolata</i>	0	130	0	2	2	1	0.9783	0	1	0	0	1	1
<i>Ambrosia artemisiifolia</i>	0	200	0	1	2	3	1.2892	1	1	0	0	1	0
<i>Amphicarpaea bracteata</i>	0	250	0	3	3	1	3.2992	1	0	0	0	0	1
<i>Andropogon gerardii</i>	1	200	1	1	3	1	1.1455	0	0	1	1	0	0
<i>Anemone americana</i>	1	15	1	3	1	1	1.0296	1	0	0	0	0	1
<i>Anemone canadensis</i>	1	80	1	1	4	1	0.818	0	0	0	1	0	0
<i>Anemone virginiana</i>	1	90	1	1	2	1	0.1296	0	0	0	1	0	1
<i>Anthriscus sylvestris</i>	0	100	1	2	1	1	1.3376	0	1	0	1	1	0
<i>Apios americana</i>	1	30	1	3	4	1	NA	0	0	1	0	1	1
<i>Apocynum androsaemifolium</i>	1	120	1	2	1	1	-1.238	0	0	1	1	0	0
<i>Apocynum cannabinum</i>	1	120	1	2	3	2	-0.098	0	0	1	1	0	1
<i>Aquilegia vulgaris</i>	1	60	1	2	1	2	0.4055	0	0	0	0	1	1
<i>Aralia nudicaulis</i>	1	30	1	3	2	2	1.5219	1	0	0	0	0	0
<i>Aralia racemosa</i>	1	200	1	3	2	2	-0.029	1	0	0	0	0	0
<i>Arctium lappa</i>	0	300	0	1	2	3	2.3979	0	1	0	0	0	0
<i>Arctium minus</i>	0	150	0	1	2	2	2.1748	0	1	0	0	0	0
<i>Arisaema triphyllum</i>	1	100	1	3	3	3	1.4165	1	0	0	0	0	0
<i>Artemisia vulgaris</i>	1	150	1	1	1	2	-1.833	0	0	0	1	0	0
<i>Asarum canadense</i>	1	18	1	3	1	2	2.0516	0	0	0	0	0	1
<i>Asclepias incarnata</i>	1	120	1	1	5	1	1.0816	0	0	1	1	0	0
<i>Asclepias syriaca</i>	1	150	1	1	1	3	1.8245	0	0	1	1	0	0
<i>Asparagus officinalis</i>	1	250	1	1	2	1	3.2581	1	0	0	0	1	0
<i>Athyrium filix-femina</i>	1	90	1	3	3	2	-4.605	0	0	0	1	0	1
<i>Barbarea vulgaris</i>	0	60	0	1	3	3	-0.511	0	0	0	0	0	1
<i>Bidens cernua</i>	0	100	0	2	5	1	2.3483	0	1	1	0	0	0
<i>Bidens frondosa</i>	0	100	0	2	4	3	0.8425	0	1	1	0	0	0
<i>Bidens tripartita</i>	0	60	0	2	4	3	1.2495	0	1	1	0	0	0
<i>Boehmeria cylindrica</i>	1	100	0	3	5	3	0.3332	0	0	1	1	0	0
<i>Bolboschoenus fluviatilis</i>	1	200	1	1	5	1	1.6034	0	1	1	0	0	0
<i>Botrychium matricariifolium</i>	1	30	1	2	2	3	-4.605	0	0	0	1	0	1
<i>Brachyelytrum erectum</i>	1	100	1	3	1	3	1.8804	0	1	0	0	0	1
<i>Bromus inermis</i>	1	130	1	1	1	3	1.155	1	0	0	0	0	0

c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Butomus umbellatus</i>	1	150	1	1	5	3	-1.704	0	0	1	1	1	0
<i>Calamagrostis canadensis</i>	1	110	1	1	5	2	-2.136	0	1	1	1	0	0
<i>Calystegia sepium</i>	1	300	1	1	3	3	3.3429	0	0	1	0	1	1
<i>Campanula rapunculoides</i>	1	60	1	2	1	1	-1.772	0	1	0	1	1	1
<i>Campanula trachelium</i>	1	100	0	2	1	3	-1.897	0	1	0	1	1	0
<i>Cardamine pratensis</i>	1	35	1	3	5	3	-0.562	0	0	0	0	0	1
<i>Carex blanda</i>	1	60	0	3	3	3	0.6195	0	1	0	1	0	1
<i>Carex bromoides</i>	1	80	1	2	4	3	-0.679	0	1	1	1	0	1
<i>Carex cephaloidea</i>	1	90	1	2	2	3	-0.374	0	1	1	1	0	1
<i>Carex crinita</i>	1	150	1	2	5	3	-0.462	0	1	1	1	0	1
<i>Carex deweyana</i>	1	90	0	3	2	3	-0.025	1	1	1	1	0	1
<i>Carex gracillima</i>	1	90	1	3	2	3	0.1204	1	1	1	1	0	1
<i>Carex grayi</i>	1	100	1	3	4	3	2.7283	0	1	1	1	0	1
<i>Carex grisea</i>	1	80	0	2	3	3	0.88	0	1	1	1	0	1
<i>Carex gynandra</i>	1	140	1	2	5	3	-0.167	0	1	1	1	0	1
<i>Carex intumescens</i>	1	75	0	3	4	3	2.3702	0	1	1	1	0	1
<i>Carex leptoneuria</i>	1	45	0	3	3	3	0.7634	1	1	0	1	0	1
<i>Carex pedunculata</i>	1	30	1	3	2	1	0.1931	1	1	0	1	0	1
<i>Carex pellita</i>	1	100	1	2	5	3	0.5931	0	1	1	1	0	1
<i>Carex plantaginea</i>	1	60	0	3	1	3	0.839	0	1	0	1	0	1
<i>Carex prasina</i>	1	80	1	3	5	3	-0.587	0	1	1	1	0	1
<i>Carex radiata</i>	1	50	0	3	3	3	1.7805	0	1	1	1	0	1
<i>Carex retrorsa</i>	1	105	1	1	5	2	0.3784	1	1	1	1	0	1
<i>Carex rosea</i>	1	50	1	3	1	3	-0.026	0	1	1	1	0	1
<i>Carex sparganioides</i>	1	100	0	3	2	3	-0.374	0	1	1	1	0	1
<i>Carex tenera</i>	1	75	1	3	3	3	-0.657	0	1	1	1	0	1
<i>Carex tribuloides</i>	1	90	1	3	4	3	-1.699	0	1	1	1	0	1
<i>Carex typhina</i>	1	100	1	3	5	3	0.3896	0	1	1	1	0	1
<i>Carex vesicaria</i>	1	100	1	2	5	3	0.5878	0	1	1	1	0	1
<i>Carex vulpinoidea</i>	1	100	0	2	5	3	-1.051	1	1	1	1	0	1
<i>Caulophyllum thalictroides</i>	1	100	1	3	1	1	5.2913	1	0	0	1	0	0
<i>Centaurea jacea</i>	1	70	0	1	1	3	0.3001	1	1	0	0	1	1

c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Chelidonium majus</i>	0	60	0	3	1	3	-0.288	1	1	0	0	1	1
<i>Chelone glabra</i>	1	100	0	2	5	1	-0.552	0	0	1	1	0	0
<i>Cichorium intybus</i>	1	100	0	1	2	2	0.0616	0	1	0	1	1	0
<i>Cicuta bulbifera</i>	1	100	1	2	5	1	0.4555	0	1	1	0	0	0
<i>Cicuta maculata</i>	0	200	1	2	5	1	0.8329	0	1	1	0	0	0
<i>Cinna arundinacea</i>	1	130	1	3	4	3	-0.65	1	0	1	0	0	0
<i>Circaea canadensis</i>	1	100	1	3	2	1	1.1887	0	1	0	0	0	0
<i>Cirsium arvense</i>	1	100	1	1	2	3	0.2624	0	1	1	1	1	0
<i>Cirsium discolor</i>	0	200	0	1	1	3	1.7336	0	1	1	1	1	0
<i>Cirsium palustre</i>	0	200	1	2	4	3	0.5481	1	1	1	1	1	0
<i>Comandra umbellata</i>	1	40	1	1	2	1	4.7232	1	0	0	0	0	0
<i>Comarum palustre</i>	1	50	1	1	5	3	-1.304	1	1	1	0	1	0
<i>Convallaria majalis</i>	1	30	1	3	1	1	2.8904	1	0	0	0	0	0
<i>Cryptotaenia canadensis</i>	1	100	0	3	3	2	0.7467	0	0	0	0	0	1
<i>Cuscuta gronovii</i>	0	45	0	2	4	3	0.6931	0	0	0	0	1	1
<i>Dactylis glomerata</i>	1	150	0	3	2	1	0.0598	1	1	1	1	1	0
<i>Daucus carota</i>	0	100	0	1	1	2	0	1	1	0	1	1	0
<i>Desmodium canadense</i>	1	250	0	1	3	3	1.6292	0	1	0	0	0	0
<i>Dianthus armeria</i>	0	45	0	1	1	3	-1.402	0	0	0	0	0	0
<i>Dichanthelium acuminatum</i>	1	75	0	1	3	3	-0.669	0	0	0	1	0	0
<i>Doellingeria umbellata</i>	1	200	1	1	4	2	-0.357	0	0	0	1	0	0
<i>Dryopteris carthusiana</i>	1	75	1	3	4	2	-4.605	0	0	0	1	0	0
<i>Dryopteris cristata</i>	1	55	1	3	5	2	-4.605	0	0	0	1	0	1
<i>Dryopteris intermedia</i>	1	50	1	3	3	2	-4.605	0	0	0	1	0	1
<i>Dryopteris marginalis</i>	1	60	1	3	2	2	-4.605	0	0	0	1	0	1
<i>Dulichium arundinaceum</i>	1	100	1	2	5	3	-0.635	0	0	1	1	0	0
<i>Echinocystis lobata</i>	0	800	0	1	4	2	5.5219	1	0	1	0	0	0
<i>Eleocharis acicularis</i>	1	20	1	1	5	2	-0.685	0	1	1	0	0	0
<i>Eleocharis erythropoda</i>	1	17	1	1	5	2	-1.171	0	1	1	0	0	0
<i>Eleocharis palustris</i>	1	115	1	1	5	3	-0.288	0	1	1	0	0	0
<i>Elymus repens</i>	1	100	1	1	2	2	1.4165	1	1	0	1	1	0
<i>Elymus trachycaulus</i>	1	100	0	1	2	3	1.2809	1	1	0	1	1	0

c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Elymus virginicus</i>	1	100	0	3	4	2	1.5119	1	1	0	1	1	0
<i>Epipactis helleborine</i>	1	60	1	3	3	1	-4.67	0	0	0	1	0	0
<i>Equisetum arvense</i>	1	40	1	2	3	1	-4.605	0	0	1	1	0	1
<i>Equisetum hyemale</i>	1	100	1	2	3	1	-4.605	0	0	1	1	0	0
<i>Equisetum palustre</i>	1	40	1	1	4	1	-4.605	0	0	1	1	0	0
<i>Equisetum sylvaticum</i>	1	50	1	3	4	1	-4.605	0	0	1	1	0	0
<i>Erigeron annuus</i>	0	100	0	1	2	2	-3.507	0	0	0	1	0	0
<i>Erigeron philadelphicus</i>	1	100	0	1	3	2	-3.219	0	0	0	1	0	0
<i>Erysimum inconspicuum</i>	1	70	0	1	1	2	-1.609	1	1	0	0	1	0
<i>Eupatorium perfoliatum</i>	1	200	1	2	4	2	-2.207	0	0	1	1	0	0
<i>Euthamia graminifolia</i>	1	120	1	1	3	2	-2.659	0	0	0	1	0	0
<i>Eutrochium maculatum</i>	1	200	1	1	5	2	-1.273	0	0	1	1	0	0
<i>Fallopia convolvulus</i>	0	100	0	1	2	3	1.7647	1	0	0	0	1	0
<i>Festuca ovina</i>	1	15	0	2	1	2	-0.511	1	1	1	1	1	0
<i>Fragaria virginiana</i>	1	15	1	1	2	2	-0.774	1	0	0	0	0	0
<i>Galium palustre</i>	1	50	1	2	5	3	0.2151	1	0	1	0	0	0
<i>Galium triflorum</i>	1	60	1	3	2	2	-0.216	1	1	1	0	0	0
<i>Geum aleppicum</i>	1	150	1	1	3	2	0	0	1	0	0	0	0
<i>Geum canadense</i>	1	100	1	3	3	3	0.1256	0	1	0	0	0	0
<i>Geum laciniatum</i>	1	95	0	2	4	2	0.1256	0	1	0	0	0	0
<i>Glechoma hederacea</i>	1	30	1	2	2	2	-0.431	1	0	0	0	1	1
<i>Glyceria striata</i>	1	100	1	3	5	3	-1.842	0	1	0	0	0	0
<i>Helenium autumnale</i>	1	100	0	1	4	1	-1.172	0	0	1	1	0	0
<i>Heliopsis helianthoides</i>	1	120	0	1	2	1	1.4241	1	0	0	0	0	1
<i>Hemerocallis fulva</i>	1	150	1	2	1	1	3.3286	0	1	0	0	1	1
<i>Hesperis matronalis</i>	1	100	0	2	2	3	0.7054	0	0	0	0	0	1
<i>Hydrocharis morsus-ranae</i>	1	8	1	1	5	2	-1.772	1	1	1	0	1	0
<i>Hydrophyllum virginianum</i>	1	80	1	3	3	2	2.2057	0	0	0	0	0	1
<i>Hylodesmum glutinosum</i>	1	120	0	2	1	1	2.8497	0	1	0	0	0	0
<i>Hypericum ellipticum</i>	1	50	1	1	5	3	-3.507	0	1	1	1	0	0
<i>Hypericum perforatum</i>	1	100	1	1	1	3	-1.609	0	1	1	1	0	0
<i>Hypericum punctatum</i>	1	60	0	3	3	3	-3.079	0	1	0	1	0	0

c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Impatiens capensis</i>	0	100	0	2	4	1	-0.434	0	0	1	0	0	1
<i>Impatiens pallida</i>	0	150	0	2	4	1	-0.434	0	0	1	0	0	1
<i>Iris pseudacorus</i>	1	150	1	1	5	1	3.8918	0	1	1	0	1	0
<i>Iris versicolor</i>	1	90	1	1	5	1	2.7094	0	0	1	0	0	1
<i>Juncus tenuis</i>	1	60	0	2	3	3	-4.605	1	0	0	0	0	0
<i>Lactuca biennis</i>	0	400	0	1	3	3	-0.02	0	0	0	1	0	0
<i>Lactuca canadensis</i>	0	200	0	1	2	2	0.3912	0	0	0	1	0	0
<i>Lactuca serriola</i>	0	200	0	1	2	2	-0.545	0	0	0	1	0	0
<i>Laportea canadensis</i>	1	120	1	3	4	1	0.7542	0	0	1	0	0	1
<i>Lapsana communis</i>	0	100	0	2	2	2	0	0	1	0	0	1	0
<i>Lathyrus palustris</i>	1	120	1	1	4	1	2.7279	0	0	0	0	0	1
<i>Leersia oryzoides</i>	1	130	1	1	5	3	-0.095	0	1	1	0	0	0
<i>Leersia virginica</i>	1	100	1	3	4	3	-0.031	0	1	1	0	0	0
<i>Lemna minor</i>	1	1	1	1	5	1	-2.861	0	1	1	0	0	0
<i>Leonurus cardiaca</i>	1	120	1	1	1	1	0	0	1	0	0	0	0
<i>Leucanthemum vulgare</i>	1	60	0	1	1	3	0.8187	0	1	0	1	1	0
<i>Lilium canadense</i>	1	200	1	2	2	1	1.7078	0	0	0	1	0	1
<i>Linaria vulgaris</i>	1	80	1	1	1	2	-1.966	1	0	1	1	1	1
<i>Lithospermum officinale</i>	1	100	0	2	1	1	2.4062	1	0	1	0	0	1
<i>Lobelia cardinalis</i>	1	150	0	2	5	2	-3.215	0	0	1	1	0	0
<i>Lotus corniculatus</i>	1	60	1	1	2	2	0.204	1	0	0	0	1	1
<i>Ludwigia palustris</i>	1	35	1	1	5	1	-3.219	0	0	1	0	0	0
<i>Lycopus americanus</i>	1	60	1	3	5	2	-1.898	1	1	1	0	0	0
<i>Lycopus europaeus</i>	1	100	1	1	5	2	-1.204	1	1	1	0	0	0
<i>Lycopus uniflorus</i>	1	80	1	2	5	2	-1.77	0	0	1	1	0	0
<i>Lycopus virginicus</i>	1	122	1	3	5	2	1.4349	1	1	1	0	0	0
<i>Lysimachia ciliata</i>	1	120	1	2	4	2	0.062	0	0	1	0	0	1
<i>Lysimachia nummularia</i>	1	20	1	3	4	2	-1.72	0	1	1	0	1	1
<i>Lysimachia terrestris</i>	1	60	1	1	5	1	-0.594	0	0	1	0	0	1
<i>Lysimachia thyrsoiflora</i>	1	80	1	2	5	2	-0.3	0	0	1	0	0	1
<i>Lythrum salicaria</i>	1	100	1	1	5	3	-2.813	0	1	1	1	1	0
<i>Maianthemum canadense</i>	1	22	1	3	2	1	2.1972	1	0	0	0	0	0

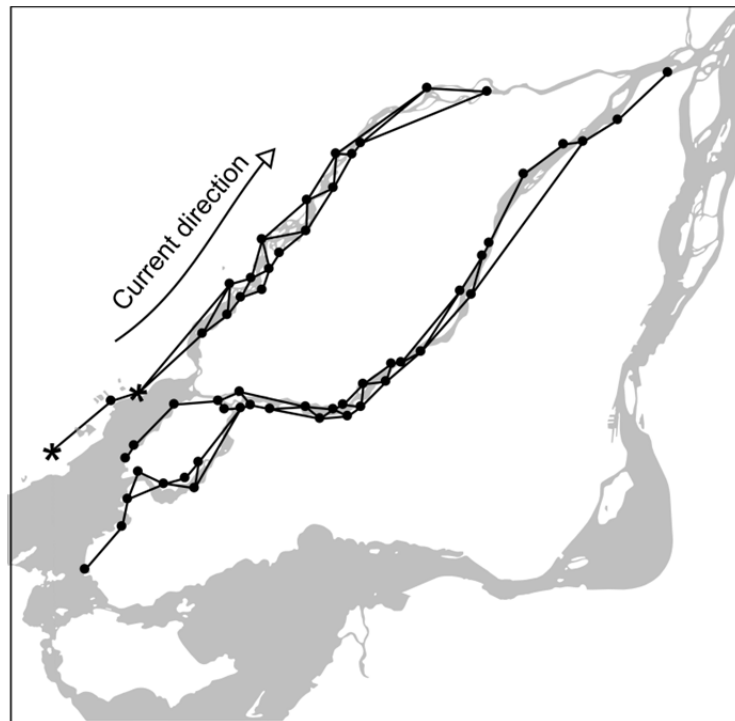
c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Maianthemum racemosum</i>	1	90	1	3	2	1	3.4242	1	0	0	0	0	0
<i>Maianthemum stellatum</i>	1	50	1	2	3	1	2.7892	1	0	0	0	0	0
<i>Matteuccia struthiopteris</i>	1	230	1	3	3	3	-4.605	0	0	0	1	0	1
<i>Medicago lupulina</i>	0	30	0	1	2	3	0.5341	1	0	0	0	1	1
<i>Medicago sativa</i>	1	50	0	1	1	3	0.693	1	0	0	0	1	1
<i>Melilotus albus</i>	0	150	0	1	2	3	0.7747	1	0	0	0	1	0
<i>Mentha arvensis</i>	1	60	1	2	4	3	-1.609	0	0	1	0	1	0
<i>Mentha xipiperita</i>	1	90	1	1	5	3	-2.311	0	0	1	0	1	0
<i>Mimulus ringens</i>	1	100	1	2	5	3	-3.507	0	0	1	1	0	0
<i>Monotropa uniflora</i>	1	30	0	3	2	2	-5.444	0	0	0	1	0	1
<i>Muhlenbergia frondosa</i>	1	120	1	3	4	3	-1.196	0	0	1	0	0	1
<i>Myosotis laxa</i>	1	50	0	1	5	3	-1.743	0	0	0	0	0	0
<i>Myosotis scorpioides</i>	1	60	1	2	5	3	0.7009	0	0	1	0	0	0
<i>Myosotis stricta</i>	0	20	0	2	1	3	-1.834	1	1	0	0	0	0
<i>Nabalus altissimus</i>	1	200	1	3	2	2	0.4047	0	0	0	1	0	0
<i>Oenothera parviflora</i>	0	95	0	1	2	3	-0.673	0	0	0	0	0	1
<i>Onoclea sensibilis</i>	1	150	1	3	4	1	-4.605	0	0	1	1	0	0
<i>Origanum vulgare</i>	1	70	0	2	1	3	-2.303	0	1	1	1	1	1
<i>Osmorhiza claytonii</i>	1	100	0	3	2	2	2.3144	0	1	0	0	0	0
<i>Osmunda regalis</i>	1	300	1	3	5	1	-4.605	0	0	1	1	0	0
<i>Oxalis stricta</i>	1	25	1	1	2	2	-1.645	0	0	0	0	0	1
<i>Pastinaca sativa</i>	0	100	0	1	1	1	1.0986	0	0	0	1	0	0
<i>Penthorum sedoides</i>	1	60	1	2	5	3	-4.597	0	0	1	0	0	0
<i>Persicaria amphibia</i>	1	120	1	1	5	1	0.8961	1	0	1	0	0	0
<i>Persicaria pensylvanica</i>	0	100	0	1	4	3	1.8145	1	0	0	0	0	0
<i>Phalaris arundinacea</i>	1	230	1	1	4	3	-0.171	1	1	1	1	1	0
<i>Phleum pratense</i>	1	150	1	2	2	2	-0.942	0	1	0	1	0	0
<i>Phragmites australis subsp. australis</i>	1	500	1	1	4	1	-2.303	0	1	1	1	1	0
<i>Phryma leptostachya</i>	1	100	0	3	2	1	1.6094	0	1	0	0	0	0
<i>Physalis alkekengi</i>	1	100	0	1	1	3	0.47	1	0	0	0	1	0
<i>Physostegia virginiana</i>	1	80	1	1	4	1	0.9555	0	0	0	0	0	1
<i>Pilosella piloselloides</i>	1	100	1	1	1	1	-2.031	0	0	0	1	1	0

c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Plantago major</i>	1	50	1	1	2	3	-1.728	1	1	0	0	1	0
<i>Plantago rugelii</i>	1	20	0	1	3	3	-0.693	1	1	0	0	1	0
<i>Poa compressa</i>	1	50	1	1	2	3	-1.663	1	1	0	1	1	0
<i>Poa nemoralis</i>	1	80	1	2	2	1	-1.609	1	1	0	1	1	0
<i>Poa palustris</i>	1	120	1	2	4	1	-1.433	1	1	0	1	1	0
<i>Poa pratensis</i>	1	90	1	1	2	3	-1.12	1	1	0	1	1	0
<i>Polygonatum pubescens</i>	1	90	1	3	1	1	3.163	1	0	0	0	0	0
<i>Potentilla anserina</i>	1	20	1	1	4	2	-0.105	0	0	1	0	0	1
<i>Potentilla argentea</i>	1	50	1	1	2	3	-2.465	0	0	0	0	0	1
<i>Potentilla recta</i>	1	70	1	1	1	2	-1.204	0	0	0	0	0	1
<i>Prunella vulgaris</i>	1	70	1	1	3	3	-0.387	1	1	1	0	0	1
<i>Pteridium aquilinum</i>	1	100	1	2	2	3	-4.605	0	0	0	1	0	1
<i>Pycnanthemum virginianum</i>	1	120	1	1	4	1	-1.958	0	0	0	1	0	1
<i>Pyrola elliptica</i>	1	25	1	3	2	1	-4.605	0	0	0	1	0	0
<i>Ranunculus abortivus</i>	1	60	0	3	3	2	-1.064	0	0	0	0	0	1
<i>Ranunculus acris</i>	1	100	1	1	3	2	0.47	1	1	0	0	0	0
<i>Ranunculus repens</i>	1	30	1	2	3	2	0.8755	1	1	1	0	0	0
<i>Rorippa amphibia</i>	1	90	1	1	5	3	-2.43	0	0	1	0	0	1
<i>Rubus pubescens</i>	1	50	1	3	4	3	0.9163	1	0	0	0	0	0
<i>Rumex verticillatus</i>	1	150	0	1	5	3	0.5481	0	0	1	1	0	0
<i>Sagittaria latifolia</i>	1	140	0	1	5	1	1.9123	0	1	1	0	0	0
<i>Sanguinaria canadensis</i>	1	30	1	3	2	2	2.4432	0	0	0	0	0	1
<i>Sanicula marilandica</i>	1	130	0	2	2	1	1.6152	0	1	0	0	0	0
<i>Saponaria officinalis</i>	1	60	1	2	2	1	0.5956	0	0	0	0	1	1
<i>Schedonorus arundinaceus</i>	1	200	1	1	2	2	0.8755	0	1	0	1	1	0
<i>Schoenoplectus acutus</i>	1	130	1	1	5	3	0.1519	0	0	1	1	0	0
<i>Scirpus atrocinctus</i>	1	150	1	2	5	2	-3.219	1	0	1	0	0	0
<i>Scirpus cyperinus</i>	1	150	1	2	5	3	-4.374	0	1	1	1	0	0
<i>Scutellaria lateriflora</i>	1	70	1	2	5	1	-1.191	0	0	1	0	0	0
<i>Silene latifolia</i>	0	100	1	1	1	3	-0.34	0	0	0	0	1	1
<i>Silene vulgaris</i>	1	45	1	1	1	3	-0.336	0	0	0	0	1	1
<i>Sisyrinchium montanum</i>	1	45	1	1	3	1	-0.174	0	0	0	0	0	1

c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Sium suave</i>	1	200	0	1	5	2	0	0	0	1	0	0	0
<i>Smilax herbacea</i>	1	500	0	3	3	1	3.6089	1	0	0	0	0	0
<i>Solanum dulcamara</i>	1	300	1	1	3	1	0.4371	1	0	0	0	1	0
<i>Solidago altissima</i>	1	200	1	2	2	3	-2.408	0	0	0	1	0	0
<i>Solidago caesia</i>	1	100	1	2	2	2	-0.434	0	0	0	1	0	0
<i>Solidago canadensis</i>	1	150	1	1	2	2	-2.317	0	0	0	1	0	0
<i>Solidago flexicaulis</i>	1	100	1	3	2	2	-0.434	0	0	0	1	0	0
<i>Solidago gigantea</i>	1	300	1	1	4	2	-0.434	0	0	0	1	0	0
<i>Solidago nemoralis</i>	1	80	1	1	1	2	-0.799	0	0	0	1	0	0
<i>Solidago rugosa</i>	1	200	1	1	3	2	-0.791	0	0	0	1	0	0
<i>Sonchus arvensis</i>	1	120	1	1	2	2	-0.713	0	0	0	1	0	0
<i>Sonchus asper</i>	0	80	0	1	2	3	-1.273	0	0	0	1	0	0
<i>Sparganium eurycarpum</i>	1	150	1	2	5	1	5.7331	0	0	1	0	0	0
<i>Spartina pectinata</i>	1	250	1	1	4	1	-0.343	0	1	1	0	0	0
<i>Stachys hispida</i>	1	100	0	2	4	3	-0.078	0	1	1	0	0	0
<i>Stachys pilosa</i>	1	120	1	2	4	3	0.182	0	1	1	0	0	0
<i>Symphyotrichum cordifolium</i>	1	100	1	1	1	1	-1.484	0	0	0	1	0	0
<i>Symphyotrichum lanceolatum</i>	1	250	1	2	4	2	-1.815	0	0	0	1	0	0
<i>Symphyotrichum lateriflorum</i>	1	150	1	2	3	1	-0.503	0	0	0	1	0	0
<i>Symphyotrichum novae-angliae</i>	1	150	1	1	4	1	-0.416	0	0	0	1	0	0
<i>Tanacetum vulgare</i>	1	100	1	1	2	2	-1.609	0	1	0	0	0	1
<i>Taraxacum officinale</i>	1	50	0	1	2	3	-0.215	0	0	0	1	0	0
<i>Teucrium canadense</i>	1	60	1	2	4	1	0.5585	1	0	1	0	0	1
<i>Thalictrum dioicum</i>	1	60	1	3	2	1	0.7669	0	1	0	0	0	1
<i>Thalictrum pubescens</i>	1	250	1	2	4	1	0.5176	0	1	0	0	0	1
<i>Thelypteris palustris</i>	1	70	1	1	4	2	-4.605	0	0	1	1	0	0
<i>Tragopogon pratensis</i>	0	100	0	1	1	1	1.5686	0	0	0	1	0	0
<i>Trifolium arvense</i>	0	40	0	1	1	3	-0.916	1	1	0	1	0	0
<i>Trifolium aureum</i>	0	50	0	1	1	2	-1.204	0	1	0	1	0	0
<i>Trifolium pratense</i>	1	40	0	1	2	3	0.5106	1	1	0	1	0	0
<i>Trifolium repens</i>	1	40	1	1	2	3	-0.451	1	0	0	1	0	0
<i>Trillium erectum</i>	1	40	1	3	2	1	0.7885	1	0	0	0	0	1

c) Herb species code	lifespan	height	veg	shade	wetness	seedBk	ln(seedWg)	endozoo	epizoo	hydro	anemo	anthropo	other
<i>Trillium grandiflorum</i>	1	45	1	3	2	1	2.1805	0	0	0	0	0	1
<i>Trillium undulatum</i>	1	60	1	3	2	1	1.6385	0	0	0	0	0	1
<i>Tussilago farfara</i>	1	20	1	1	2	1	-1.204	0	0	0	1	0	0
<i>Typha latifolia</i>	1	270	1	1	5	2	-2.813	0	1	1	1	0	0
<i>Uvularia grandiflora</i>	1	75	1	3	1	1	1.6136	0	0	0	0	0	1
<i>Valeriana officinalis</i>	1	150	1	1	2	1	-0.01	0	0	0	1	0	0
<i>Verbena urticifolia</i>	1	160	0	3	3	3	-0.693	1	0	0	0	0	1
<i>Veronica anagallis-aquatica</i>	1	30	1	1	5	3	-2.668	0	1	1	0	0	1
<i>Veronica scutellata</i>	1	30	1	1	5	3	-1.58	0	1	1	0	0	1
<i>Vicia cracca</i>	1	200	1	1	1	2	2.4281	1	0	0	0	0	1
<i>Viola pubescens</i>	1	15	1	3	2	2	0.6821	0	0	0	0	0	1
<i>Viola sp.</i>	1	10	1	3	2	2	0	0	0	1	0	0	1

Figure S2.1. Connectivity diagram, based on the current direction, used to generate the AEM and the dbMEM eigenfunctions. The asterisks represent the two sites that were excluded from shrub analyses, and the connectivity diagram was adjusted accordingly.



Appendix S2.1. Steps to create the connectivity matrix

As shown in the connectivity diagram (Fig. S2.1), the spatial processes on each river of the study area were hypothesized to be independent from each other. To properly model the distinction between both rivers, the method developed by Blanchet et al. (2008, 2011) was therefore modified slightly.

Conceptually, the connection diagram was translated into a matrix E (sites-by-edges) in 4 steps:

1. For each river, separately, build a sites-by-edges matrix, E_1 and E_2 , in which, for each forest, the links that connect it with the most upstream site (at the base of the connection diagram) are coded "1", while others are coded "0".
2. Center the matrices E_1 and E_2 by columns.
3. Create a new sites-by-edges matrix E that contains the information for the two rivers by joining E_1 and E_2 in a checkerboard pattern (Fig. S2.2). Since both rivers are independent, no link in the new matrix E will connect sites located on different rivers, and two blocks of independent information are therefore obtained.
4. Add to the matrix E a binary column that distinguishes the two rivers. It must be added after the centering by block of step 2, or else it would be centered to zero. This column is the equivalent of adding a single origin point upstream of the two rivers or two origin points ahead of both rivers. Indeed, adding two binary columns to model two distinct origin points is useless, since they contain the exact same information (they are perfectly collinear).

This procedure with centering by block before AEM analysis makes it possible to properly model each river independently from the other by creating eigenfunctions that model one river at a time. Without centering by block, the R function `aem()` centers the entire connectivity matrix by column, including the block of zeros in the calculation, which masks the distinction between the rivers. The subsequent addition of the binary column simply creates an AEM vector that clearly separates the two rivers (in this study, AEM4-6-7).

In fact, this method makes it possible to study several spatial processes with various or parallel directions in a single AEM analysis instead of computing one analysis per process of interest. In such cases of multiple spatial processes, Blanchet et al. (2011) originally suggested

joining E_{1-n} matrices side by side. However, this method is only applicable in the particular case of an equal number of sites in all E_{1-n} matrices, which is often not the case in ecology.

References

Blanchet F.G., Legendre P., & Borcard D. (2008) Modelling directional spatial processes in ecological data. *Ecological Modelling*, **215**, 325–336.

Blanchet F.G., Legendre P., Maranger R., Monti D., & Pepin P. (2011) Modelling the effect of directional spatial ecological processes at different scales. *Oecologia*, **166**, 357–68.

Table S2.4. Comparison of weights based on RDA models of CWM (for trees, shrubs and herbs separately) constrained by the AEM functions, measuring the positive spatial autocorrelation, created with different weighting vectors described in the main text. Combinations of weights were obtained through multiplication of their vectors. R^2_{adj} in bold are the selected combinations.

weight function	Trees		Shrubs		Herbs	
	# selected vectors	R^2_{adj}	# selected vectors	R^2_{adj}	# selected vectors	R^2_{adj}
No weight	2	19.06	7	25.55	5	35.93
f_1	2	19.12	6	22.65	4	34.74
f_2	2	10.03	6	22.96	5	35.95
fragmentation	3	21.55	7	25.59	5	35.86
f_1 *fragmentation	2	19.01	5	21.37	5	36.69
f_2 *fragmentation	4	24.45	7	25.22	4	34.65

Table S2.5. Selected explanatory variables using the forward selection procedure. The cumulative adjusted R^2 and the p-value of each variable are given. Where appropriate, the transformation applied to each variable is indicated.

	<i>Landscape context</i>			<i>Local conditions</i>			<i>Spatial process</i>		
	variables	$R^2_{adj}Cum$	p-value	variables	$R^2_{adj}Cum$	p-value	variables	$R^2_{adj}Cum$	p-value
Trees	NDVI	8.13	0.0013	flood	21.75	0.0001	AEM6	10.04	0.0003
	$^4\sqrt{rural}$	11.58	0.0304	histo.human	26.60	0.0027	AEM1	19.02	0.0002
	$green^2$	14.17	0.0479	histo.area	30.11	0.0104	AEM17	21.88	0.0328
				PAR	32.21	0.0372	AEM10	24.45	0.0387
			slope	34.26	0.0378				
Shrubs	bridge	10.21	0.0001	flood	12.35	0.001	AEM7	9.39	0.0002
	$NDVI^2$	13.96	0.0088	histo.area	18.48	0.001	AEM10	12.99	0.0094
	$^2\sqrt{forest}$	16.35	0.0308	$\ln(PAR)$	20.69	0.039	AEM9	15.78	0.0209
				slope	23.19	0.023	AEM1	18.38	0.0231
							AEM13	20.99	0.0196
							AEM11	23.39	0.0284
						AEM6	25.59	0.0370	
Herbs	$\ln(green+1)$	16.29	0.0001	flood	27.96	0.0001	AEM4	16.00	0.0001
	bridge	19.76	0.0099	histo.human	34.04	0.0003	AEM1	30.50	0.0001
	$^4\sqrt{rural}$	21.86	0.0396	$^2\sqrt{PAR}$	37.60	0.0014	AEM15	32.63	0.0174
	impervious	25.41	0.0059	altitude ²	39.19	0.0305	AEM13	34.77	0.0117
	HII	27.20	0.0422	slope	40.66	0.0319	AEM3	36.69	0.0175

Annexes du chapitre 3

Table S3.1. Number of patches selected for each range of the selection criterion: patch area, patch position, proportion of flooded forest area, and proportion of surrounding impervious surfaces.

Area (ha)		Position*		Flood intensity (%)		Impervious surface (%)	
N	Value	N	Value	N	Value	N	Value
24	[0.4, 3[14	NE part	25	[0, 20[18	[0, 20[
24	[3, 20[27	middle	16]20, 50]	23	[20, 40[
9	[20, 160]	16	SO part	16]50, 100]	16	[40, 65]

* NE part: from the middle of Laval Island and eastward

 Middle: from the western end to the middle of Laval Island

 SW part: from the western end of Montreal Island to western end of Laval Island

Table S3.2. Herb species functional traits and immigration status. See Table 3.2 for trait code.

species code	origin	lifespan	height	reproduction	shade	wetness	seedBk	seedWg	diaspore morphology	buoyancy
<i>Achillea millefolium</i>	exotic	p.forb	60	veg	1	2	2	-1.8388	wing	1
<i>Acorus calamus</i>	native	p.forb	200	veg	1	5	1	-0.0945	nutrient.envelope	3
<i>Actaea rubra</i>	native	p.forb	40	seed/veg	3	2	1	1.7047	nutrient.envelope	2
<i>Aegopodium podagraria</i>	exotic	p.forb	90	veg	2	3	3	0.7885	no.specialization	1
<i>Ageratina altissima</i>	native	p.forb	120	seed/veg	2	2	3	-1.791	hairs	1
<i>Agrimonia gryposepala</i>	native	p.forb	200	seed/veg	2	2	3	0.5956	appendages	1
<i>Agrostis stolonifera</i>	native	graminoid	70	veg	1	4	3	-2.6039	wing	3
<i>Alisma triviale</i>	native	p.forb	15	seed/veg	1	5	3	-0.8618	aerenchym	3
<i>Alliaria petiolata</i>	exotic	a.forb	130	seed	2	2	1	0.9783	no.specialization	1
<i>Ambrosia artemisiifolia</i>	exotic	a.forb	200	seed	1	2	3	1.2892	appendages	1
<i>Amphicarpaea bracteata</i>	native	a.forb	250	seed	3	3	1	3.2992	nutrient.seed	1
<i>Andropogon gerardii</i>	native	graminoid	200	veg	1	3	1	1.1455	hairs	3
<i>Anemone americana</i>	native	p.forb	15	seed/veg	3	1	1	1.0296	nutrient.envelope	3
<i>Anemone canadensis</i>	native	p.forb	80	seed/veg	1	4	1	0.818	wing	3
<i>Anemone virginiana</i>	native	p.forb	90	seed/veg	1	2	1	0.1296	hairs	3
<i>Anthriscus sylvestris</i>	exotic	a.forb	100	seed/veg	2	1	1	1.3376	no.specialization	1
<i>Apios americana</i>	native	p.forb	30	veg	3	4	1	NA	nutrient.seed	1
<i>Apocynum androsaemifolium</i>	native	p.forb	120	veg	2	1	1	-1.2379	hairs	3
<i>Apocynum cannabinum</i>	native	p.forb	120	veg	2	3	2	-0.0976	hairs	3
<i>Aquilegia vulgaris</i>	exotic	p.forb	60	seed/veg	2	1	2	0.4055	no.specialization	1
<i>Aralia nudicaulis</i>	native	p.forb	30	veg	3	2	2	1.5219	nutrient.envelope	2
<i>Aralia racemosa</i>	native	p.forb	200	veg	3	2	2	-0.0294	nutrient.envelope	2
<i>Arctium lappa</i>	exotic	a.forb	300	seed	1	2	3	2.3979	appendages	1
<i>Arctium minus</i>	exotic	a.forb	150	seed	1	2	2	2.1748	appendages	1
<i>Arisaema triphyllum</i>	native	p.forb	100	veg	3	3	3	1.4165	nutrient.envelope	1
<i>Artemisia vulgaris</i>	exotic	p.forb	150	veg	1	1	2	-1.8326	mucilaginous	1
<i>Asarum canadense</i>	native	p.forb	18	veg	3	1	2	2.0516	nutrient.envelope	1
<i>Asclepias incarnata</i>	native	p.forb	120	seed/veg	1	5	1	1.0816	hairs	3
<i>Asclepias syriaca</i>	native	p.forb	150	veg	1	1	3	1.8245	hairs	3

species code	origin	lifespan	height	reproduction	shade	wetness	seedBk	seedWg	diaspore morphology	buoyancy
<i>Asparagus officinalis</i>	exotic	p.forb	250	seed/veg	1	2	1	3.2581	nutrient.envelope	1
<i>Athyrium filix-femina</i>	native	fern	90	seed/veg	3	3	2	-4.6052	no.specialization	3
<i>Barbarea vulgaris</i>	exotic	a.forb	60	seed	1	3	3	-0.5108	no.specialization	3
<i>Bidens cernua</i>	native	a.forb	100	seed	2	5	1	2.3483	appendages	3
<i>Bidens frondosa</i>	native	a.forb	100	seed	2	4	3	0.8425	appendages	3
<i>Bidens tripartita</i>	native	a.forb	60	seed	2	4	3	1.2495	appendages	3
<i>Boehmeria cylindrica</i>	native	p.forb	100	seed	3	5	3	0.3332	wing	3
<i>Bolboschoenus fluviatilis</i>	native	graminoid	200	veg	1	5	1	1.6034	aerenchym	3
<i>Botrychium matricariifolium</i>	native	fern	30	veg	2	2	3	-4.6052	no.specialization	3
<i>Brachyelytrum erectum</i>	native	graminoid	100	seed/veg	3	1	3	1.8804	appendages	3
<i>Bromus inermis</i>	native	graminoid	130	veg	1	1	3	1.155	appendages	1
<i>Butomus umbellatus</i>	exotic	p.forb	150	veg	1	5	3	-1.7037	aerenchym	3
<i>Calamagrostis canadensis</i>	native	graminoid	110	seed/veg	1	5	2	-2.1355	hairs	3
<i>Calystegia sepium</i>	native	p.forb	300	veg	1	3	3	3.3429	no.specialization	3
<i>Campanula rapunculoides</i>	exotic	p.forb	60	seed/veg	2	1	1	-1.772	no.specialization	2
<i>Campanula trachelium</i>	exotic	p.forb	100	seed	2	1	3	-1.8971	no.specialization	2
<i>Cardamine pratensis</i>	exotic	p.forb	35	veg	3	5	3	-0.5621	no.specialization	1
<i>Carex blanda</i>	native	graminoid	60	seed	3	3	3	0.6195	aerenchym	2
<i>Carex bromoides</i>	native	graminoid	80	veg	2	4	3	-0.6792	aerenchym	3
<i>Carex cephaloidea</i>	native	graminoid	90	seed/veg	2	2	3	-0.374	aerenchym	3
<i>Carex crinita</i>	native	graminoid	150	seed/veg	2	5	3	-0.4622	aerenchym	3
<i>Carex deweyana</i>	native	graminoid	90	seed	3	2	3	-0.0253	aerenchym	3
<i>Carex gracillima</i>	native	graminoid	90	seed/veg	3	2	3	0.1204	aerenchym	3
<i>Carex grayi</i>	native	graminoid	100	seed/veg	3	4	3	2.7283	aerenchym	3
<i>Carex grisea</i>	native	graminoid	80	seed	2	3	3	0.88	aerenchym	3
<i>Carex gynandra</i>	native	graminoid	140	seed/veg	2	5	3	-0.1672	aerenchym	3
<i>Carex intumescens</i>	native	graminoid	75	seed	3	4	3	2.3702	aerenchym	3
<i>Carex leptonevia</i>	native	graminoid	45	seed	3	3	3	0.7634	aerenchym	2
<i>Carex pedunculata</i>	native	graminoid	30	seed/veg	3	2	1	0.1931	aerenchym	2
<i>Carex pellita</i>	native	graminoid	100	veg	2	5	3	0.5931	aerenchym	3
<i>Carex plantaginea</i>	native	graminoid	60	seed	3	1	3	0.839	aerenchym	2

species code	origin	lifespan	height	reproduction	shade	wetness	seedBk	seedWg	diaspore morphology	buoyancy
<i>Carex prasina</i>	native	graminoid	80	seed/veg	3	5	3	-0.587	aerenchym	3
<i>Carex radiata</i>	native	graminoid	50	seed	3	3	3	1.7805	aerenchym	3
<i>Carex retrorsa</i>	native	graminoid	105	seed/veg	1	5	2	0.3784	aerenchym	3
<i>Carex rosea</i>	native	graminoid	50	seed/veg	3	1	3	-0.0255	aerenchym	3
<i>Carex sparganioides</i>	native	graminoid	100	seed	3	2	3	-0.374	aerenchym	3
<i>Carex tenera</i>	native	graminoid	75	seed/veg	3	3	3	-0.657	aerenchym	3
<i>Carex tribuloides</i>	native	graminoid	90	seed/veg	3	4	3	-1.6994	aerenchym	3
<i>Carex typhina</i>	native	graminoid	100	seed/veg	3	5	3	0.3896	aerenchym	3
<i>Carex vesicaria</i>	native	graminoid	100	veg	2	5	3	0.5878	aerenchym	3
<i>Carex vulpinoidea</i>	native	graminoid	100	seed	2	5	3	-1.0508	aerenchym	3
<i>Caulophyllum thalictroides</i>	native	p.forb	100	veg	3	1	1	5.2913	nutrient.envelope	2
<i>Centaurea jacea</i>	exotic	p.forb	70	seed	1	1	3	0.3001	appendages	2
<i>Chelidonium majus</i>	exotic	a.forb	60	seed	3	1	3	-0.2877	nutrient.envelope	1
<i>Chelone glabra</i>	native	p.forb	100	seed	2	5	1	-0.5516	wing	3
<i>Cichorium intybus</i>	exotic	p.forb	100	seed	1	2	2	0.0616	appendages	1
<i>Cicuta bulbifera</i>	native	p.forb	100	seed/veg	2	5	1	0.4555	aerenchym	3
<i>Cicuta maculata</i>	native	a.forb	200	seed/veg	2	5	1	0.8329	aerenchym	3
<i>Cinna arundinacea</i>	native	graminoid	130	seed/veg	3	4	3	-0.6501	wing	3
<i>Circaea canadensis</i>	native	p.forb	100	veg	3	2	1	1.1887	appendages	1
<i>Cirsium arvense</i>	exotic	p.forb	100	veg	1	2	3	0.2624	hairs	3
<i>Cirsium discolor</i>	native	a.forb	200	seed	1	1	3	1.7336	hairs	3
<i>Cirsium palustre</i>	exotic	a.forb	200	seed/veg	2	4	3	0.5481	hairs	3
<i>Comandra umbellata</i>	native	p.forb	40	veg	1	2	1	4.7232	nutrient.envelope	2
<i>Comarum palustre</i>	native	p.forb	50	seed/veg	1	5	3	-1.3038	aerenchym	3
<i>Convallaria majalis</i>	exotic	p.forb	30	veg	3	1	1	2.8904	nutrient.envelope	1
<i>Cryptotaenia canadensis</i>	native	p.forb	100	seed	3	3	2	0.7467	no.specialization	1
<i>Cuscuta gronovii</i>	native	a.forb	45	seed	2	4	3	0.6931	no.specialization	1
<i>Dactylis glomerata</i>	exotic	graminoid	150	seed	3	2	1	0.0598	wing	3
<i>Daucus carota</i>	exotic	a.forb	100	seed	1	1	2	0	appendages	1
<i>Desmodium canadense</i>	native	p.forb	250	seed	1	3	3	1.6292	appendages	1
<i>Dianthus armeria</i>	exotic	a.forb	45	seed	1	1	3	-1.4024	no.specialization	1

species code	origin	lifespan	height	reproduction	shade	wetness	seedBk	seedWg	diaspore morphology	buoyancy
<i>Dichanthelium acuminatum</i>	native	graminoid	75	seed	1	3	3	-0.6694	wing	2
<i>Doellingeria umbellata</i>	native	p.forb	200	seed/veg	1	4	2	-0.3567	hairs	2
<i>Dryopteris carthusiana</i>	native	fern	75	seed/veg	3	4	2	-4.6052	no.specialization	3
<i>Dryopteris cristata</i>	native	fern	55	veg	3	5	2	-4.6052	no.specialization	3
<i>Dryopteris intermedia</i>	native	fern	50	veg	3	3	2	-4.6052	no.specialization	3
<i>Dryopteris marginalis</i>	native	fern	60	veg	3	2	2	-4.6052	no.specialization	3
<i>Dulichium arundinaceum</i>	native	graminoid	100	seed/veg	2	5	3	-0.635	aerenchym	3
<i>Echinocystis lobata</i>	native	a.forb	800	seed	1	4	2	5.5219	no.specialization	2
<i>Eleocharis acicularis</i>	native	graminoid	20	veg	1	5	2	-0.6854	appendages	1
<i>Eleocharis erythropoda</i>	native	graminoid	17	veg	1	5	2	-1.1712	appendages	1
<i>Eleocharis palustris</i>	native	graminoid	115	seed/veg	1	5	3	-0.2877	appendages	1
<i>Elymus repens</i>	exotic	graminoid	100	veg	1	2	2	1.4165	wing	2
<i>Elymus trachycaulus</i>	native	graminoid	100	seed	1	2	3	1.2809	wing	2
<i>Elymus virginicus</i>	native	graminoid	100	seed	3	4	2	1.5119	wing	2
<i>Epipactis helleborine</i>	exotic	p.forb	60	seed/veg	3	3	1	-4.6699	wing	3
<i>Equisetum arvense</i>	native	fern	40	veg	2	3	1	-4.6052	no.specialization	3
<i>Equisetum hyemale</i>	native	fern	100	veg	2	3	1	-4.6052	no.specialization	3
<i>Equisetum palustre</i>	native	fern	40	veg	1	4	1	-4.6052	no.specialization	3
<i>Equisetum sylvaticum</i>	native	fern	50	veg	3	4	1	-4.6052	no.specialization	3
<i>Erigeron annuus</i>	native	a.forb	100	seed	1	2	2	-3.5066	hairs	1
<i>Erigeron philadelphicus</i>	native	p.forb	100	seed	1	3	2	-3.2189	hairs	1
<i>Erysimum inconspicuum</i>	native	p.forb	70	seed	1	1	2	-1.6094	mucilaginous	1
<i>Eupatorium perfoliatum</i>	native	p.forb	200	seed/veg	2	4	2	-2.2073	hairs	3
<i>Euthamia graminifolia</i>	native	p.forb	120	veg	1	3	2	-2.6593	hairs	1
<i>Eutrochium maculatum</i>	native	p.forb	200	seed/veg	1	5	2	-1.273	hairs	3
<i>Fallopia convolvulus</i>	exotic	a.forb	100	seed	1	2	3	1.7647	wing	1
<i>Festuca ovina</i>	exotic	p.forb	15	seed	2	1	2	-0.5108	wing	2
<i>Fragaria virginiana</i>	native	p.forb	15	veg	1	2	2	-0.7744	nutrient.envelope	1
<i>Galium palustre</i>	native	p.forb	50	veg	2	5	3	0.2151	no.specialization	3
<i>Galium triflorum</i>	native	p.forb	60	veg	3	2	2	-0.2157	appendages	3
<i>Geum aleppicum</i>	native	p.forb	150	seed/veg	1	3	2	0	appendages	2

species code	origin	lifespan	height	reproduction	shade	wetness	seedBk	seedWg	diaspore morphology	buoyancy
<i>Geum canadense</i>	native	p.forb	100	veg	3	3	3	0.1256	appendages	2
<i>Geum laciniatum</i>	native	p.forb	95	seed	2	4	2	0.1256	appendages	2
<i>Glechoma hederacea</i>	exotic	p.forb	30	veg	2	2	2	-0.4308	mucilaginous	1
<i>Glyceria striata</i>	native	graminoid	100	seed/veg	3	5	3	-1.8416	wing	3
<i>Helenium autumnale</i>	native	p.forb	100	seed	1	4	1	-1.1723	appendages	2
<i>Heliopsis helianthoides</i>	native	p.forb	120	seed	1	2	1	1.4241	no.specialization	1
<i>Hemerocallis fulva</i>	exotic	p.forb	150	veg	2	1	1	3.3286	no.specialization	1
<i>Hesperis matronalis</i>	exotic	p.forb	100	seed	2	2	3	0.7054	no.specialization	2
<i>Hydrocharis morsus-ranae</i>	exotic	p.forb	8	veg	1	5	2	-1.772	no.specialization	3
<i>Hydrophyllum virginianum</i>	native	p.forb	80	seed/veg	3	3	2	2.2057	appendages	1
<i>Hylodesmum glutinosum</i>	native	p.forb	120	seed	2	1	1	2.8497	appendages	1
<i>Hypericum ellipticum</i>	native	p.forb	50	seed/veg	1	5	3	-3.5066	no.specialization	2
<i>Hypericum perforatum</i>	exotic	p.forb	100	veg	1	1	3	-1.6094	no.specialization	2
<i>Hypericum punctatum</i>	native	p.forb	60	seed	3	3	3	-3.0791	no.specialization	2
<i>Impatiens capensis</i>	native	a.forb	100	seed	2	4	1	-0.4341	no.specialization	3
<i>Impatiens pallida</i>	native	a.forb	150	seed	2	4	1	-0.4341	no.specialization	3
<i>Iris pseudacorus</i>	exotic	p.forb	150	seed/veg	1	5	1	3.8918	aerenchym	3
<i>Iris versicolor</i>	native	p.forb	90	seed/veg	1	5	1	2.7094	aerenchym	3
<i>Juncus tenuis</i>	native	p.forb	60	seed	2	3	3	-4.6052	mucilaginous	1
<i>Lactuca biennis</i>	native	a.forb	400	seed	1	3	3	-0.0202	hairs	1
<i>Lactuca canadensis</i>	native	a.forb	200	seed	1	2	2	0.3912	hairs	1
<i>Lactuca serriola</i>	exotic	a.forb	200	seed	1	2	2	-0.5447	hairs	1
<i>Laportea canadensis</i>	native	p.forb	120	veg	3	4	1	0.7542	no.specialization	3
<i>Lapsana communis</i>	exotic	a.forb	100	seed	2	2	2	0	no.specialization	1
<i>Lathyrus palustris</i>	native	p.forb	120	veg	1	4	1	2.7279	nutrient.seed	1
<i>Leersia oryzoides</i>	native	graminoid	130	seed/veg	1	5	3	-0.0945	wing	3
<i>Leersia virginica</i>	native	graminoid	100	veg	3	4	3	-0.0313	wing	3
<i>Lemna minor</i>	native	p.forb	1	veg	1	5	1	-2.8612	no.specialization	3
<i>Leonurus cardiaca</i>	exotic	p.forb	120	veg	1	1	1	0	appendages	2
<i>Leucanthemum vulgare</i>	exotic	p.forb	60	seed	1	1	3	0.8187	no.specialization	1
<i>Lilium canadense</i>	native	p.forb	200	veg	2	2	1	1.7078	wing	1

species code	origin	lifespan	height	reproduction	shade	wetness	seedBk	seedWg	diaspore morphology	buoyancy
<i>Linaria vulgaris</i>	exotic	p.forb	80	veg	1	1	2	-1.9661	wing	3
<i>Lithospermum officinale</i>	exotic	p.forb	100	seed	2	1	1	2.4062	no.specialization	1
<i>Lobelia cardinalis</i>	native	p.forb	150	seed	2	5	2	-3.2149	no.specialization	3
<i>Lotus corniculatus</i>	exotic	p.forb	60	seed/veg	1	2	2	0.204	nutrient.seed	1
<i>Ludwigia palustris</i>	native	p.forb	35	seed/veg	1	5	1	-3.2189	no.specialization	3
<i>Lycopus americanus</i>	native	p.forb	60	seed/veg	3	5	2	-1.8977	mucilaginous	3
<i>Lycopus europaeus</i>	exotic	p.forb	100	seed/veg	1	5	2	-1.204	mucilaginous	3
<i>Lycopus uniflorus</i>	native	p.forb	80	seed/veg	2	5	2	-1.7696	mucilaginous	3
<i>Lycopus virginicus</i>	native	p.forb	122	seed/veg	3	5	2	1.4349	mucilaginous	3
<i>Lysimachia ciliata</i>	native	p.forb	120	seed/veg	2	4	2	0.062	aerenchym	3
<i>Lysimachia nummularia</i>	exotic	p.forb	20	veg	3	4	2	-1.7204	aerenchym	3
<i>Lysimachia terrestris</i>	native	p.forb	60	seed/veg	1	5	1	-0.5942	aerenchym	3
<i>Lysimachia thyrsoiflora</i>	native	p.forb	80	seed/veg	2	5	2	-0.2995	aerenchym	3
<i>Lythrum salicaria</i>	exotic	p.forb	100	veg	1	5	3	-2.8134	mucilaginous	3
<i>Maianthemum canadense</i>	native	p.forb	22	veg	3	2	1	2.1972	nutrient.envelope	1
<i>Maianthemum racemosum</i>	native	p.forb	90	veg	3	2	1	3.4242	nutrient.envelope	1
<i>Maianthemum stellatum</i>	native	p.forb	50	veg	2	3	1	2.7892	nutrient.envelope	1
<i>Matteuccia struthiopteris</i>	native	fern	230	veg	3	3	3	-4.6052	no.specialization	3
<i>Medicago lupulina</i>	exotic	a.forb	30	seed	1	2	3	0.5341	nutrient.seed	1
<i>Medicago sativa</i>	exotic	p.forb	50	seed	1	1	3	0.693	nutrient.seed	1
<i>Melilotus albus</i>	exotic	a.forb	150	seed	1	2	3	0.7747	nutrient.seed	1
<i>Mentha arvensis</i>	native	p.forb	60	seed/veg	2	4	3	-1.6094	no.specialization	3
<i>Mentha xpiperita</i>	exotic	p.forb	90	seed/veg	1	5	3	-2.3106	no.specialization	3
<i>Mimulus ringens</i>	native	p.forb	100	seed/veg	2	5	3	-3.5066	mucilaginous	3
<i>Monotropa uniflora</i>	native	p.forb	30	seed	3	2	2	-5.4436	no.specialization	3
<i>Muhlenbergia frondosa</i>	native	graminoid	120	seed/veg	3	4	3	-1.1962	wing	3
<i>Myosotis laxa</i>	native	p.forb	50	seed	1	5	3	-1.743	appendages	2
<i>Myosotis scorpioides</i>	exotic	p.forb	60	seed/veg	2	5	3	0.7009	appendages	2
<i>Myosotis stricta</i>	exotic	a.forb	20	seed	2	1	3	-1.8338	appendages	2
<i>Nabalus altissimus</i>	native	p.forb	200	seed/veg	3	2	2	0.4047	hairs	1
<i>Oenothera parviflora</i>	native	a.forb	95	seed	1	2	3	-0.6733	no.specialization	3

species code	origin	lifespan	height	reproduction	shade	wetness	seedBk	seedWg	diaspore morphology	buoyancy
<i>Onoclea sensibilis</i>	native	fern	150	seed/veg	3	4	1	-4.6052	no.specialization	3
<i>Origanum vulgare</i>	exotic	p.forb	70	seed	2	1	3	-2.3026	no.specialization	3
<i>Osmorhiza claytonii</i>	native	p.forb	100	seed	3	2	2	2.3144	appendages	1
<i>Osmunda regalis</i>	native	fern	300	veg	3	5	1	-4.6052	no.specialization	3
<i>Oxalis stricta</i>	exotic	p.forb	25	veg	1	2	2	-1.6451	no.specialization	1
<i>Pastinaca sativa</i>	exotic	a.forb	100	seed	1	1	1	1.0986	wing	2
<i>Penthorum sedoides</i>	native	p.forb	60	veg	2	5	3	-4.5974	no.specialization	3
<i>Persicaria amphibia</i>	native	p.forb	120	veg	1	5	1	0.8961	no.specialization	3
<i>Persicaria pensylvanica</i>	native	a.forb	100	seed	1	4	3	1.8145	no.specialization	1
<i>Phalaris arundinacea</i>	native	graminoid	230	veg	1	4	3	-0.1707	wing	3
<i>Phleum pratense</i>	exotic	graminoid	150	seed/veg	2	2	2	-0.9419	wing	2
<i>Phragmites australis subsp. australis</i>	exotic	graminoid	500	veg	1	4	1	-2.3026	hairs	3
<i>Phryma leptostachya</i>	native	p.forb	100	seed	3	2	1	1.6094	appendages	1
<i>Physalis alkekengi</i>	exotic	p.forb	100	seed	1	1	3	0.47	nutrient.envelope	1
<i>Physostegia virginiana</i>	native	p.forb	80	veg	1	4	1	0.9555	no.specialization	1
<i>Pilosella piloselloides</i>	exotic	p.forb	100	veg	1	1	1	-2.031	hairs	2
<i>Plantago major</i>	exotic	p.forb	50	seed/veg	1	2	3	-1.7278	mucilaginous	1
<i>Plantago rugelii</i>	exotic	p.forb	20	seed	1	3	3	-0.6931	mucilaginous	1
<i>Poa compressa</i>	exotic	graminoid	50	seed/veg	1	2	3	-1.6632	wing	2
<i>Poa nemoralis</i>	exotic	graminoid	80	seed/veg	2	2	1	-1.6094	wing	2
<i>Poa palustris</i>	native	graminoid	120	seed/veg	2	4	1	-1.4326	wing	3
<i>Poa pratensis</i>	exotic	graminoid	90	veg	1	2	3	-1.1199	wing	3
<i>Polygonatum pubescens</i>	native	p.forb	90	veg	3	1	1	3.163	nutrient.envelope	1
<i>Potentilla anserina</i>	native	p.forb	20	seed/veg	1	4	2	-0.1054	no.specialization	3
<i>Potentilla argentea</i>	exotic	p.forb	50	seed/veg	1	2	3	-2.4651	no.specialization	1
<i>Potentilla recta</i>	exotic	p.forb	70	seed/veg	1	1	2	-1.204	no.specialization	3
<i>Prunella vulgaris</i>	exotic	p.forb	70	veg	1	3	3	-0.3873	mucilaginous	2
<i>Pteridium aquilinum</i>	native	fern	100	veg	2	2	3	-4.6052	no.specialization	3
<i>Pycnanthemum virginianum</i>	native	p.forb	120	seed/veg	1	4	1	-1.9576	no.specialization	1
<i>Pyrola elliptica</i>	native	p.forb	25	veg	3	2	1	-4.6052	no.specialization	3
<i>Ranunculus abortivus</i>	native	p.forb	60	seed	3	3	2	-1.0642	aerenchym	2

species code	origin	lifespan	height	reproduction	shade	wetness	seedBk	seedWg	diaspore morphology	buoyancy
<i>Ranunculus acris</i>	exotic	p.forb	100	veg	1	3	2	0.47	aerenchym	2
<i>Ranunculus repens</i>	exotic	p.forb	30	veg	2	3	2	0.8755	aerenchym	3
<i>Rorippa amphibia</i>	exotic	p.forb	90	seed/veg	1	5	3	-2.4304	mucilaginous	3
<i>Rubus pubescens</i>	native	p.forb	50	veg	3	4	3	0.9163	nutrient.envelope	1
<i>Rumex verticillatus</i>	native	p.forb	150	seed	1	5	3	0.5481	wing	3
<i>Sagittaria latifolia</i>	native	p.forb	140	seed	1	5	1	1.9123	aerenchym	3
<i>Sanguinaria canadensis</i>	native	p.forb	30	veg	3	2	2	2.4432	nutrient.envelope	1
<i>Sanicula marilandica</i>	native	p.forb	130	seed	2	2	1	1.6152	appendages	1
<i>Saponaria officinalis</i>	exotic	p.forb	60	seed/veg	2	2	1	0.5956	no.specialization	2
<i>Schedonorus arundinaceus</i>	exotic	graminoid	200	seed/veg	1	2	2	0.8755	wing	1
<i>Schoenoplectus acutus</i>	native	graminoid	130	seed/veg	1	5	3	0.1519	appendages	3
<i>Scirpus atrocinctus</i>	native	graminoid	150	veg	2	5	2	-3.2189	aerenchym	3
<i>Scirpus cyperinus</i>	native	graminoid	150	seed/veg	2	5	3	-4.3742	aerenchym	3
<i>Scutellaria lateriflora</i>	native	p.forb	70	seed/veg	2	5	1	-1.1907	aerenchym	3
<i>Silene latifolia</i>	exotic	a.forb	100	seed/veg	1	1	3	-0.3401	no.specialization	1
<i>Silene vulgaris</i>	exotic	p.forb	45	veg	1	1	3	-0.3355	no.specialization	1
<i>Sisyrinchium montanum</i>	native	p.forb	45	veg	1	3	1	-0.1744	no.specialization	1
<i>Sium suave</i>	native	p.forb	200	seed	1	5	2	0	aerenchym	3
<i>Smilax herbacea</i>	native	p.forb	500	seed	3	3	1	3.6089	nutrient.envelope	2
<i>Solanum dulcamara</i>	exotic	p.forb	300	seed/veg	1	3	1	0.4371	nutrient.envelope	1
<i>Solidago altissima</i>	native	p.forb	200	veg	2	2	3	-2.4079	hairs	1
<i>Solidago caesia</i>	native	p.forb	100	veg	2	2	2	-0.4341	hairs	1
<i>Solidago canadensis</i>	native	p.forb	150	veg	1	2	2	-2.3168	hairs	1
<i>Solidago flexicaulis</i>	native	p.forb	100	veg	3	2	2	-0.4341	hairs	1
<i>Solidago gigantea</i>	native	p.forb	300	veg	1	4	2	-0.4341	hairs	1
<i>Solidago nemoralis</i>	native	p.forb	80	veg	1	1	2	-0.7987	hairs	1
<i>Solidago rugosa</i>	native	p.forb	200	veg	1	3	2	-0.7907	hairs	1
<i>Sonchus arvensis</i>	exotic	p.forb	120	seed/veg	1	2	2	-0.7133	hairs	2
<i>Sonchus asper</i>	exotic	a.forb	80	seed	1	2	3	-1.273	hairs	2
<i>Sparganium eurycarpum</i>	native	p.forb	150	seed/veg	2	5	1	5.7331	aerenchym	3
<i>Spartina pectinata</i>	native	graminoid	250	veg	1	4	1	-0.3427	wing	3

species code	origin	lifespan	height	reproduction	shade	wetness	seedBk	seedWg	diaspore morphology	buoyancy
<i>Stachys hispida</i>	native	p.forb	100	seed	2	4	3	-0.078	no.specialization	3
<i>Stachys pilosa</i>	native	p.forb	120	seed/veg	2	4	3	0.182	no.specialization	3
<i>Symphotrichum cordifolium</i>	native	p.forb	100	veg	1	1	1	-1.4839	hairs	2
<i>Symphotrichum lanceolatum</i>	native	p.forb	250	veg	2	4	2	-1.8152	hairs	2
<i>Symphotrichum lateriflorum</i>	native	p.forb	150	seed/veg	2	3	1	-0.503	hairs	2
<i>Symphotrichum novae-angliae</i>	native	p.forb	150	seed/veg	1	4	1	-0.4161	hairs	2
<i>Tanacetum vulgare</i>	exotic	p.forb	100	seed/veg	1	2	2	-1.6094	no.specialization	1
<i>Taraxacum officinale</i>	exotic	p.forb	50	seed	1	2	3	-0.2153	hairs	2
<i>Teucrium canadense</i>	native	p.forb	60	seed/veg	2	4	1	0.5585	no.specialization	3
<i>Thalictrum dioicum</i>	native	p.forb	60	veg	3	2	1	0.7669	appendages	2
<i>Thalictrum pubescens</i>	native	p.forb	250	veg	2	4	1	0.5176	appendages	2
<i>Thelypteris palustris</i>	native	fern	70	seed/veg	1	4	2	-4.6052	no.specialization	3
<i>Tragopogon pratensis</i>	exotic	a.forb	100	seed	1	1	1	1.5686	hairs	1
<i>Trifolium arvense</i>	exotic	a.forb	40	seed	1	1	3	-0.9163	appendages	1
<i>Trifolium aureum</i>	exotic	a.forb	50	seed	1	1	2	-1.204	nutrient.seed	1
<i>Trifolium pratense</i>	exotic	p.forb	40	seed	1	2	3	0.5106	nutrient.seed	1
<i>Trifolium repens</i>	exotic	p.forb	40	veg	1	2	3	-0.4509	nutrient.seed	1
<i>Trillium erectum</i>	native	p.forb	40	seed/veg	3	2	1	0.7885	nutrient.envelope	1
<i>Trillium grandiflorum</i>	native	p.forb	45	seed/veg	3	2	1	2.1805	nutrient.envelope	1
<i>Trillium undulatum</i>	native	p.forb	60	seed/veg	3	2	1	1.6385	nutrient.envelope	1
<i>Tussilago farfara</i>	exotic	p.forb	20	veg	1	2	1	-1.204	hairs	2
<i>Typha latifolia</i>	native	p.forb	270	veg	1	5	2	-2.8134	hairs	2
<i>Uvularia grandiflora</i>	native	p.forb	75	veg	3	1	1	1.6136	nutrient.envelope	1
<i>Valeriana officinalis</i>	exotic	p.forb	150	veg	1	2	1	-0.0102	hairs	2
<i>Verbena urticifolia</i>	native	p.forb	160	seed	3	3	3	-0.6931	no.specialization	2
<i>Veronica anagallis-aquatica</i>	native	p.forb	30	seed/veg	1	5	3	-2.6679	mucilaginous	3
<i>Veronica scutellata</i>	native	p.forb	30	seed/veg	1	5	3	-1.5799	mucilaginous	1
<i>Vicia cracca</i>	exotic	p.forb	200	seed/veg	1	1	2	2.4281	nutrient.seed	1
<i>Viola pubescens</i>	native	p.forb	15	veg	3	2	2	0.6821	nutrient.envelope	2
<i>Viola sp.</i>	native	p.forb	10	seed/veg	3	2	2	0	nutrient.envelope	2