Effects of past land use and landscape context on plant species composition and richness in woodlots of an agricultural landscape in Québec

Martine Larouche
Department of Geography
McGill University
Montreal, Qc
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Abstract

The forest transition occurring in developed countries, including northeastern North America and western Europe, led to an emergence of secondary forests that fueled research about past land-use legacies on biodiversity. Past land-use has been shown to lower plant species richness, especially that of forest herb species. A few studies have also considered landscape configuration around secondary forests, either in the present-day or during the early period of old field colonization. My study examines the effects of both past land-use and past landscape context on species composition and richness in a 2046 km^2 landscape dominated by agriculture in the Montérégie in southwestern Québec. Using historical topographical maps from the 1860s and 1910s, and a forest map from the 1990s, I analyzed the evolution of forest cover across the landscape and used an Affinity Propagation algorithm to cluster forest patches with similar land-use and configuration history. I then tested the effects of past land use and landscape context (surrounding forest proportion) on species composition and richness in 52 study sites using nonmetric multidimensional scaling analysis and correlations. Results show that landscape context in the past, and especially in the 1910s within a 200m buffer around study sites, is correlated with both current species composition and richness. Hence, forest patches that had a low forest cover around them in the past have a lower total, endozoochorous and anemochorous species richness and greater epizoochorous species richness than forest patches that were surrounded by a greater amount of forest in the past. As for past land use, this variable does not have a strong effect on plant species composition and richness. Other variables like soils, surficial deposits or recent forest management intensity do not affect total species richness and composition in study sites except for tree species, likely because of maple syrup production. My conclusions can be useful for forest protection and conservation by helping to prioritize forest patches to protect based on past landscape context. The results also suggest that the quality of forest patches can be enhanced by creating ecological corridors connecting patches, thereby increasing the number of surrounding seed sources.

Résumé

La transition forestière ayant lieu dans les pays développés, incluant le nord-est de l'Amérique du Nord et l'Europe de l'Ouest, a conduit à l'émergence de forêts secondaires, lesquelles ont alimenté la recherche sur les legs de l'utilisation passée des terres sur la biodiversité. Il a été démontré que l'utilisation passée du territoire peut appauvrir la richesse en espèces végétales et spécialement en herbacées forestières. Quelques études ont également considéré la configuration du paysage autour de parcelles forestières, soit à l'époque actuelle ou durant la période de colonisation des terres abandonnées. La présente étude se penche sur les effets de l'utilisation passée du territoire et du contexte paysager passé (proportion du couvert forestier environnant) sur la composition et la richesse en espèces végétales dans un paysage de 2046 km^2 dominé par l'agriculture en Montérégie, au sud-ouest du Québec. Utilisant des cartes topographiques historiques des années 1860 et 1910 et une carte forestière des années 1990, j'ai analysé l'évolution du couvert forestier sur ce territoire et utilisé l'algorithme Affinity Propagation pour regrouper les parcelles forestières ayant une histoire d'utilisation du territoire et de contexte paysager similaires. J'ai ensuite testé les effets de l'utilisation passée des terres et du contexte paysager passé sur la composition et la richesse en espèces végétales de 52 parcelles forestières en utilisant une analyse de gradation non métrique multidimensionelle ainsi que des corrélations. Les résultats montrent que le contexte paysager passé, et particulièrement dans les années 1910 à l'intérieur d'un rayon de 200 mètres autour des sites d'étude, est corrélé à la composition et à la richesse en espèces végétales actuelles de ces sites. Ainsi, des parcelles forestières ayant eu un couvert forestier faible autour d'elles dans le passé contiennent moins d'espèces végétales au total, moins d'endozoochores et d'anémochores et plus d'épizoochores que des parcelles forestières entourées d'un plus grand couvert forestier dans le passé. L'utilisation passée du territoire n'a, quant à elle, pas d'effets importants sur la composition et la richesse en espèces végétales. D'autres variables telles les sols, les dépots de surface ou l'intensité de l'aménagement forestier récent n'affectent pas la composition ni la richesse en

espèces végétales dans les sites d'étude sauf pour les espèces d'arbres, probablement en raison de la production de sirop d'érable. Les conclusions de cette étude peuvent être utiles à des fins de protection et de conservation de la forêt. Ainsi, elles pourraient aider à prioriser les parcelles forestières à protéger en se basant sur la proportion de couvert forestier autour d'elles dans le passé. Les résultats de cette étude suggèrent également que la qualité des boisés peut être améliorée en créant des corridors écologiques connectant les parcelles, augmentant par le fait même les sources de graines autour d'elles.

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Chapter 1. Literature review and research questions

1.1. Land-use history in southern Québec

The landscape of southern Québec has the longest history of human occupation in northeastern North America and has undergone major transformation since European colonization beginning in the 17th century. Little is known about land use and land cover—and especially forest—evolution at a landscape scale in this region. However, by tracing the more documented history of agriculture, which is the main land use in this region, the evolution of forest could be inferred.

Amerindian activities discernible in paleoecological records from southern Québec are rare (Muller et al. 2008). Indeed, Amerindians probably only lightly modified the land in Québec, except along the St-Lawrence River (Coates 2003), other important rivers (Muller et al. 2008; Richard 1977) and in the areas around the cities of Québec and Montreal (Coates 2003), where Amerindians practiced semi-sedentary and sedentary agriculture. Outside these areas, indigenous peoples in southern Québec were mostly nomadic hunter-gatherer (Richard 1977) who didn't modify the vegetation as much as sedentary populations. Human impacts on vegetation in Québec that are visible in pollen diagrams are therefore detected almost entirely for the period of European colonization, which started at the end of the 17th century.

The period from the end of the 18th century to the beginning of the 20th century in southern Québec was marked by widespread deforestation and the conversion of forest into agricultural land (Delcourt and Delcourt 1987; Domon and Bouchard 2007; Drushka 2003; Muller et al. 2008; Richard 1977). These disturbances started along the St-Lawrence River and progressively expanded (Richard 1977). The 19th century was marked by successive exploitation of several high-value tree species. According to wood sales recorded in notary deeds in the Haut-Saint-Laurent Regional County Municipality in southwestern Québec, from 1800 to 1809, oak sales were dominant because of naval construction. Then, between the 1820s and the 1840s, pine timber dominated the transactions because of the residential construction in the Montreal region. Finally, from the 1850s to the

1870s, hemlock and other species were exploited for the construction of the great rail networks of western North America. Wood sales started to decline in the 1860s and nearly stopped in the 1870s due to the depletion of species one after the other, which resulted from their over-exploitation and the conversion of the landscape into an extensive agricultural matrix with small remaining woodlots for owners' personal use (Domon and Bouchard 2007; Simard and Bouchard 1996).

The land-use history of Québec, especially in the southern region, is closely related to the history of agriculture (Paquette and Domon 1997) since farm area covers more than 90% of some municipal landscapes today (Ruiz and Domon 2005). At the beginning of the 20th century, almost half the population in Québec worked in agriculture (Dagenais 1959) and cultivated lands covered the largest area in the beginning of the 1920s (Latendresse 2008). Agricultural practices were traditional and family-based from 1854 to 1939, diversified and market oriented from 1939 to 1966, and specialized from 1966 to today (Morisset 1987). In the decades that followed World War II, agricultural activities diminished, constrained mostly to parts of the St-Lawrence Lowlands, due to a concentration, specialization and intensification of agriculture for dairy farms and later (in the 1970s) grain crop monocultures (Latendresse 2008; Paul-Limoges 2008; Ruiz and Domon 2005). Concurrently, population working in agriculture dropped to 25.2% in 1941 and 16.5% in 1956. Agricultural area diminished 14% from 1941 to 1956, going from 65,600 km^2 to 56,795 km^2 (Dagenais 1959).The second half of the 20th century was marked by a decrease in total farm area by 50% coupled with a 76% decrease in the total number of farms, while the mean farm size doubled (Ruiz and Domon 2005).

However, this general evolution of agriculture in Québec masks the unequal spatial distribution of such changes that epitomizes the uniqueness of Québec's agricultural history. In fact, while the decrease in the total number of farms and the increase in size happened everywhere in Québec, the variation in total farm area is clearly separated in two zones (Latendresse 2008; Ruiz and Domon 2005). The first zone is small and concentrated in the St-Lawrence Lowlands. It includes my study area. It is characterized by either an increase or a slight (25%) decrease in farm area from 1951 to 2001. The second zone, formed by regions in the periphery of the Lowlands and urban centers, encountered a moderate (25% to 50% in the peripheral regions) to strong (more than 50% in urban centers) decrease in total farm area (Ruiz and Domon 2005), presumably starting after World War II (Chatillon 1976 in Latendresse 2008). Farm abandonment was attributable to thin soil, uneven relief, less favorable climate and high distances from markets. Urbanization around cities was also responsible for the loss of agricultural and other lands (Ruiz and Domon 2005). Forest was also affected by this farm abandonment. In fact, of the 3.4 million ha decrease in farm area in the second half of the 20th century, 2 million ha was of "other lands", which include woodlots, wetlands and unusable lands (Ruiz and Domon 2005), a loss experienced in both zones. From the 1950s to the 1970s, farmland in the Lowlands peripheral regions from the second zone disappeared almost entirely. From the 1970s to the early 1990s, while farm loss continued in the second zone, the reduced number of farms in the first zone specialized, intensified and increased their cultivated area thus fragmenting or eliminating woodlots and wetlands. Today, less than 2 % of the province of Québec—34,170 km^2 (Ruiz and Domon 2005)—is under agriculture though 80 % of the total production is concentrated in the first zone (Paul-Limoges 2008). The composition of agricultural lands (cropland, artificial pasture, fallow) has also undergone major transformations, which were caused by the increased mechanization of agricultural practices, the implementation of sub-soil drainage for clay soils, and especially new agricultural policies implemented in the 1970s (Domon and Bouchard 2007; Ruiz and Domon 2009). For instance, pastures drastically decreased with the adoption of industrial pig production (Paul-Limoges 2008) and the specialization in monoculture cereals and oleaginous plants (corn, barley, soy). The number of dairy farms also dropped considerably, especially in the Vallée-du-Richelieu Regional County Municipality (RCM) (which forms the major part of my study area). These trends in the evolution of agriculture in southern Québec were accentuated from the 1990s to 2001 along with a growing contrast between the two agricultural histories in Québec corresponding to the two zones described above (Ruiz and Domon 2005).

The second part of the 20th century was also marked by a new relationship between land use types and surficial deposits (Domon and Bouchard 2007). Studies in the Haut-Saint-Laurent RCM, a region that experienced a moderate decrease in farm area accompanied by forest regrowth (zone 2), reveal that forest has regrown on morainic deposits that are no longer suitable for modern agriculture. However, before 1842, sandy soil from the morainic ridges was easier to put into farm land than clay soils from marine deposits that were heavy and poorly drained (Roy et al. 2002). It was only by the mid-19th century that lands on marine deposits also started to be cultivated before being under intensive agricultural activities today (Benjamin et al. 2005; Bouchard and Domon 1997; D'Orangeville et al. 2011; Domon and Bouchard 2007).

The increasing gap between the two agricultural trajectories in southern Québec is reflected in the recent evolution of forest cover. Forest cover showed a general tendency of deforestation in four administrative regions of Québec (Lanaudière, Centre-Du-Québec, Montérégie and Chaudière-Appalaches) from 1990 to 1999 and 1999 to 2002. The deforestation was more severe in the lowland part (zone 1) of these regions, and especially in the Montérégie during the second period, with a deforestation of 3.5% (0.39%/yr) for the first period and 2.9% (0.97%/yr) for the second (Li et al. 2003). Field investigation confirmed that losses were mainly due to land use changes (agriculture, urbanization) (Li et al. 2003; Soucy Gonthier et al. 2003). As a result, considerable differences exist in the forest cover today between the Lowlands (28.5%) (zone 1), the Appalachians (66.1%) (zone 2) and the Laurentian Plateau (91.7%) (zone 2) (Li et al. 2003).

Changes in land use, and especially in agriculture, over the last three hundred years in southern Québec have led to major modifications from the pre-settlement landscapes. For example, there have been dramatic changes in the abundance of several tree species, such as a decrease in American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*) (Brisson 2003). Also, the composition of secondary forests differs from that of precolonial forests (Bouchard and Domon 1997; Domon and Bouchard 2007; Paquette and Domon 1997; Roy et al. 2002). This has been confirmed by a low recovery of commercially valuable hardwoods (*Fraxinus americana*, *Fraxinus pennsylvanica*, *Prunus serotina*, *Acer saccharum*, *Ulmus Americana*, *Betula alleghaniensis*, *Tilia americana*, *Quercus macrocarpa*) in secondary forests of three agroforested landscapes in the Montérégie (D'Orangeville et al. 2011). Land-use change has also led to the homogenization of the agricultural landscape coupled with a simplification of territorial structures (Ruiz and Domon 2005) in areas of agricultural intensification of the St-Lawrence Lowlands (zone 1) (Schmucki et al. 2002). Along with the straightening of woodlots' boundaries, considerable property enlargement resulted in the elimination of linear and point structures used to separate the original smaller rectangular plots of land from the seigniorial system in Québec. Hence, ditches, fences, hedgerows and isolated trees have been removed from the landscape, with important ecological and agronomic consequences (Baudry et al. 2000; Ruiz and Domon 2005; Ruiz and Domon 2009).

1.2. Land-use history in the northeastern United States

The land-use history of southern Québec is unusual. Indeed, the forest transition theory proposes that developed countries around the world have experienced a shift from a drastic forest clearing related to extensive agriculture, like the one observed today in tropical countries, to a generalized forest expansion following rural exodus (Whigham 2004). The northeastern United States exemplifies this theory with a history marked by a large-scale deforestation, followed by agricultural land abandonment and forest recovery over the last three hundred years. This landscape change trajectory is therefore fundamentally different from that of Québec (except the zone 2 in southern Québec characterized by 25% to more than 50% decrease in total farm area since the 1950s).

Native Americans in the northeastern United States had a more sedentary lifestyle than Amerindians of southern Québec. Indeed, the Woodland period (2800-1000 BP) was characterized by an intensification of horticultural activity, thus increasing the area of cultivated fields and more permanent settlements mostly along floodplains of major river systems (Delcourt and Delcourt 1987; Munoz et al. 2010). Studies in southern Ontario and the northeastern United States (Almquist-Jacobson and Sanger 1995; Campbell and Campbell 1994; McAndrews 1988; Munoz et al. 2010) identified numerous pre-European settlement activities that would have potential impacts on the landscape like the use of wood, anthropogenic forest fires and field clearance for horticulture (Campbell and Campbell 1994). However, those impacts were localized where populations were most concentrated. Generally, prehistoric populations had limited lasting effect on the landscape, due to small populations, non-intensive agriculture and no grazing animals (Bellemare et al. 2002; Campbell and Campbell 1994).

During European colonization in the mid-17th century to the mid-19th century, settlers spread from coastal areas and major river valleys inland and population grew at a constant rate (Foster et al. 1998; McKibben 1995). Changes in land use then formed three contrasting phases: large-scale deforestation in the early period of European settlement, followed by widespread intensive agriculture, and rapid reforestation as settlers abandoned farms and moved west or in cities (Foster et al. 1998; Glitzenstein et al. 1990; Williams 1982).

During the phase of intensive agriculture in the first half of the 19th century that followed a massive deforestation, states like Massachusetts formed an extended matrix of open fields, with 50% to 80% of most townships supporting cultivated fields or pasture (Foster et al. 1998; Hall et al. 2002). By 1850, many areas in the northeastern United States saw their forest cover drop to less than 20% (Peterken 1996; Whitney 1996 in Vellend 2003). At that time, agriculture was dominated by extensive pasture followed in importance by diverse grain and hay cultures (Bellemare et al. 2002; Foster et al. 1998). The forest cover during this period was characterized by multiple small and isolated forest patches, which were exploited for construction material and fuel among other things (Williams 1982). Woodlots were mostly situated on lands less suitable for agriculture, like mountains, steep slopes, swamps and wetlands, and excessively well-drained sand plains (Foster et al. 1998; Hall et al. 2002).

In the second half of the 19th century, industrialization, coupled with a decline in rural densities, was the major cause of agricultural decline, and therefore land abandonment and forest recovery (Foster et al. 1998). Indeed, after the period of extensive agriculture and forest exploitation, settlers started moving to the newly opened Midwest for its productive soils or to cities (Foster et al. 1998; Hall et al. 2002). Since then, forest cover has gradually increased from 20% to 50% or as high as 80% in some places (Hermy and Verheyen 2007) so that current landscapes resemble those prior to 1800. For instance, New Hampshire is now 90% forested, Vermont went from 35% forest in 1850 to 80% today and similar trends were observed in Connecticut, Rhôde Island (McKibben 1995), Massachusetts (Bellemare et al. 2002), New York (Flinn and Honnay 2004; Glitzenstein et al. 1990), and Wisconsin (Rhemtulla et al. 2009). However, the composition of post agricultural forests and thus their ecological value are not comparable to primary forests (Benjamin et al. 2005; Brisson 2003; Rhemtulla et al. 2009).

As with southern Québec, the forest history of the northeastern United States is linked to its agricultural history. Abandonment of agricultural lands and industrialization led to a change in agricultural production on remaining lands by favouring products that could be transported to urban centers, like vegetables and milk (Black 1959 in Foster et al. 1998; Russel 1982 in Hall et al. 2002). In return, marginal farmlands with more relief and at higher elevation, like those observed in Massachusetts, were the first to be abandoned to reforestation before the rest of the state underwent the same transformation. Hence, those uplands became highly wooded through the 20th century (80% to 90% forest) while lowlands still gained forest but kept a significant area in intensively cultivated lands and urban areas (Foster et al. 1998).

Despite the natural reforestation starting in the second half of the 19th century, forest-cutting activities were continued in the region though their intensity and size evolved through time. From the end of the 19th century to 1985 in central Massachusetts, young hardwoods were harvested for diverse wood products like fuel, railroad ties, poles and posts while white pine were cut for boxes, barrels, and crates (Fisher 1933 in Foster et al. 1998). From 1985 to 1995, older forests were selectively logged for commercially valuable trees. This can be explained by the height and age of the forest during these periods. Indeed, from the end of the 18th century to the mid-20th century, forests were mostly composed of small and young trees probably because of extended logging, but became taller and older in more recent times as forest growth exceeded logging (Foster et al. 1998).

1.3. Impact of past land use on vegetation

Previous studies show that past land-use occurrence (Bellemare et al. 2002; Vellend et al. 2007), types (Flinn and Marks 2007; Stover and Marks 1998), and intensity (Brown and Boutin 2009; Dupouey et al. 2002) all significantly affect present-day plant diversity as well as secondary forest regeneration patterns (D'Orangeville et al. 2011; Flinn and Marks 2007).

Direct and indirect effects of past land use on vegetation are profound and can persist for decades to millennia (Bellemare et al. 2002; Dupouey et al. 2002; Vellend 2003, 2004b; Vellend et al. 2006). Direct effects include the local elimination of plants and diaspores affecting the structure of forest plant communities (Hermy and Verheyen 2007; Jacquemyn and Brys 2008) whereas indirect effects are related to the alteration of environmental conditions, like soil properties (Dupouey et al. 2002; Hermy and Verheyen 2007). Past land use can have a stronger effect on secondary forests than environmental conditions and other disturbances (Bellemare et al. 2002; de Blois et al. 2001; Motzkin et al. 1996).

Direct effects of past land use are related to its type and duration. For example, forests on former pastures, which were unplowed, are more likely to have a plant composition similar to old-growth forests because of on-site persistence of forest herb species (Glitzenstein et al. 1990; Koerner et al. 1997; Vellend 2004b; Wulf

2004). When the field is abandoned to vegetation regrowth, both on-site resprouting from relict populations and colonization by seed dispersal from surrounding sources contribute to the site's species richness (Williams 1982). Conversely, forests grown on former croplands, which have often been plowed, are expected to have lower plant diversity than previously because plowing hampers seed persistence in the soil (Glitzenstein et al. 1990; Singleton et al. 2001; Vellend 2004b; Williams 1982; Wulf 2004). Previously plowed sites may also have fewer interior forest species and more edge species, given that in general, seed production of forest plant species is lower than for plant species of open habitats and their large seeds are not persistent in the soil (Bierzychudek 1982; Bossuyt and Hermy 2001; Brown and Oosterhuist 1981).

Site colonization as well as species recruitment and establishment are also indirectly affected by past land use. First, past land use alters soil physical and chemical properties by increasing soil pH, phosphorus, carbon and nitrogen content and decreasing organic matter and litter (Bossuyt et al. 1999; Dupouey et al. 2002; Fraterrigo et al. 2005; Honnay et al. 1999; Koerner et al. 1997; Peterken and Game 1984). Given that rare species usually show specific requirements in terms of soil acidity (either acidic or basic soils), their recruitment may be limited in post-cultivated fields, compared to species with no habitat requirement (Jacquemyn et al. 2003). Moreover, Bellemare et al. (2002) observed a lower frequency of less nutrient-demanding forest herbs in secondary forests than primary forests. Second, forest herb species, which are poor competitors, experience high competition with ruderal species and woody taxa (Bellemare et al. 2002) that flourish in the first phase of vegetation regrowth after land abandonment, a phenomenon amplified by the increased soil phosphate content resulting from past cultivation that boosts ground vegetation growth (Honnay et al. 1999; Kucera 1952; Peterken and Game 1984). Third, past land use plays a role in homogenizing patch habitat, with nutrients being more evenly distributed in areas with intense agriculture history compared to primary forests (Fraterrigo et al. 2005). In addition, forest herb species' seedlings have high rates of mortality and are associated with specific features in forests like treefall pits and mounds, fallen logs, and canopy gaps, which are not seen in formerly plowed field until centuries later (reviewed in Singleton et al. 2001). Another indirect impact of past land use on post-agricultural forest is the presence of exotic earthworms brought by European colonizers to agricultural fields in North America (Hale et al. 2005). Earthworms create a major species recruitment limitation since they heavily impact forest floor characteristics, eliminating organic horizons, decreasing surface-soil organic matter storage, and increasing rates of litter disappearance (Bohlen et al. 2004; Surez et al. 2006).

Although species richness can increase substantially with time since abandonment (Flinn and Honnay 2004; Flinn and Vellend 2005; Jamoneau et al. 2011), in particular due to the increasing microenvironmental heterogeneity of the site (Jacquemyn et al. 2001), primary forests usually have higher species richness than post-agricultural forests (Flinn and Vellend 2005; Hermy and Verheyen 2007; Vellend 2004b). However, the latter are richer in ruderal species, including exotic taxa (Bossuyt et al. 1999; Brown and Boutin 2009). Genetic diversity can also be lower in secondary forests than in primary forests because of a reduced population size (Vellend 2004b). Species composition in secondary forests is therefore homogenized and impoverished. Changes in the composition of forest communities can also be irreversible (Jacquemyn and Brys 2008; Vellend et al. 2007; Williams 1982).

1.4. Impact of landscape configuration on vegetation

Island biogeographic theory (MacArthur and Wilson 1967) and metapopulation theory (Gilpin and Hanski 1991; Vellend 2004a) address the critical role of patch isolation in population dynamics, which can also be applied to scattered semi-natural habitats in an agricultural matrix. As with islands, species richness in dispersed remnants may be a function of area, isolation, shape, time, and habitat diversity (Peterken and Game 1984). Indeed, the reduction of diversity in secondary forests compared to primary forests can be due to both environmental limitations and dispersal limitation (Öster et al. 2007; Verheyen and Hermy 2001), though the latter likely overrides the former (Bossuyt et al. 1999; Honnay et al. 2005; Öster et al. 2009; Peterken and Game 1984; Vellend 2003, 2004b; Williams 1982). Environmental limitation is the capacity of a species to establish on a site, which is partly dependent on past land use, while the dispersal limitation includes the amount and configuration of seed sources available in the landscape (Vellend 2003) together with individual species' colonization rates and dispersal capacities (Jacquemyn et al. 2003).

Present landscape configuration and its effect on species colonization of an old field is the object of multiple studies in the northeastern United States and Europe (Bossuyt et al. 1999; Butaye et al. 2001; D'Orangeville et al. 2011; Dzwonko 1993; Singleton et al. 2001; Vellend 2003; Verheyen and Hermy 2001) though fewer have looked at the influence of past landscape configuration on secondary natural habitats. For instance, species diversity, density and richness is positively correlated with past (1900 and 1950) connectivity in semi-natural grasslands in Sweden (Lindborg and Eriksson 2004) because plants are known to respond slowly to habitat fragmentation (Cousins et al. 2007). Individual forest interior species, mostly dispersed by birds and ants, were also shown to be affected by past connectivity (Grashof-Bokdam 1997).

Metrics used to define landscape configuration include the distance from the target recent forest patch to neighbouring ancient forest patches (Bossuyt et al. 1999; Brunet et al. 2000; Dzwonko 1993; Flinn and Honnay 2004; Singleton et al. 2001), the area or proportion of surrounding forest patches (Brown and Boutin 2009; Vellend 2003), or both metrics (D'Orangeville et al. 2011; Jamoneau et al. 2011; Lindborg 2007).

The proximity to ancient forest patches, which are the main source of diaspores of typical forest herb species, and the modes of species dispersal from ancient to recent forest patches can affect species richness and composition of recent forest fragments (Dzwonko 1993; Grashof-Bokdam 1997; Verheyen et al. 2003a). The probability of seed occurrence in a recent forest patch typically declines logarithmically with distance from the parent plant living in the surrounding ancient forest patches (reviewed in Williams 1982 and Bellemare et al. 2002).

Generally, dispersal distance decreases from dispersal by seed ingestion (endozoochores and ornithochores), to seed adhesion (epizoochores), to wind (anemochores), to ants (myrmecochores) to no specific dispersal mechanism (barochores) (Jacquemyn and Brys 2008; Williams 1982). However, anemochores have also been shown to be the best dispersers as seeds can travel through cultivated areas easily (D'Orangeville et al. 2011). Forest herb species are generally slow dispersers as they are typically myrmerochores and barochores (Bellemare et al. 2002; Honnay et al. 1999; Vellend et al. 2003). For instance, the scale of ant-dispersion of seeds is only a few meters (Vellend et al. 2003). The low colonization capacity of many forest herb species is also directly related to their life-history traits: large seeds, no dispersal mechanism, low fecundity, specific germination conditions, clonal growth, and no persistent seed bank (Bellemare et al. 2002; Hermy and Verheyen 2007; Verheyen et al. 2003b; Whigham 2004). Thus, forest herb species are less common in secondary forest stands (Bellemare et al. 2002; Brunet et al. 2000; D'Orangeville et al. 2011; Dzwonko 1993; Flinn and Vellend 2005; Peterken and Game 1984). A time lag of several centuries can exist between the abandonment of a patch and its colonization by most herbaceous species, even the rapid colonizers (Bellemare et al. 2002; Bossuyt et al. 1999; Honnay et al. 2005; Vellend 2003). However, forests more than two kilometers away from ancient forests may never achieve a complete recovery of herbaceous plant species composition (Honnay et al. 2005).

In some cases, area has been shown to be a better metric than distance in influencing the colonization of a patch by plant species, though it depends on the radii selected (D'Orangeville et al. 2011; Vellend 2003). Moreover, the kind of forest considered for this metric matters. Indeed, a meta-analysis of studies conducted in Europe and North America showed that the proportion of ancient forest in a landscape significantly explains the relative diversity of ancient forest herbs in recent forest, regardless of the proportion or age of recent forest in the landscape (Vellend 2003).

Impacts of landscape configuration on plant species composition and richness in remnant forests are comparable to those induced by past land use. Severe reduction or local extinction of populations of forest plant species happen with the slow colonization rates of forest herb species and a decreasing and unprotected primary forest cover (Bellemare et al. 2002; Jacquemyn et al. 2003). Indeed, there is clear evidence of an extinction debt that can persist for more than a century after forest fragmentation. An extinction debt is the phase before the potential complete disappearance of some species after fragmentation and isolation (Vellend et al. 2006). Vellend (2003) suggested that when ancient forest cover in a landscape is below 10-15%, no matter the recent forest cover, patch occupancy for a slow colonizer in a recent forest is low and takes considerably more time to reach equilibrium than in a landscape with a greater proportion of ancient forest. It can take as much as 240 to 800 years to reach equilibrium when the proportion of ancient forest is less than 5%. However, for a rapid colonizer, both the proportion of ancient forest and recent forest in the landscape affect the species' patch occupancy in a recent forest, especially if below 10%. Parallel to the reduction or local extinction of some species, the overall value of the recent forest can be affected by landscape configuration. For example, a low commercial value hardwood regeneration was observed in post-agricultural stands in the Montérégie due to a colonization restricted by the amount of surrounding forests (D'Orangeville et al. 2011). Finally, one of the major impacts of increasing spatial isolation is the decrease in genetic variation among populations through genetic drift, increased inbreeding and reduced gene flow between populations (Honnay et al. 2005). Nevertheless, the impacts of landscape configuration on vegetation are still difficult to measure and isolate from those linked to abiotic conditions, human and natural disturbances, and their relative influence can be landscape-dependent (De Blois et al. 2002b).

1.5. Research questions and rationale

In this study, I analyze historical forest and landscape change in the Montérégie, in southwestern Québec, Canada, and the effects of this change on plant diversity in remnant woodlots. This landscape has a land-use history going back to the end of the 17th century and is today an agricultural matrix with scattered forest patches forming less than 20% of the total area.

I address two specific questions:

(1) How has the forest cover changed from the 1860s to the 1990s?

(2) What are the effects of past land use and landscape context on current plant species composition and richness?

To answer the first question, I reconstructed forest cover at three dates: 1860s, 1910s, and 1990s. Then, I analyzed both the evolution of forest in the landscape as a whole and by individual forest patches using a novel clustering algorithm: Affinity Propagation. To assess the effects of past land use and landscape context, I conducted field sampling to measure current plant species richness in forest patches with different land-use history and level of past neighbouring landscape context.

Although several local studies have been conducted in southern Québec using different historical documents to reconstruct the vegetation and land-use changes since the 19th century (Bouchard and Domon 1997; Domon and Bouchard 2007; Paquette and Domon 1997; Roy et al. 2002), none of them have considered the regional scale. Moreover, the impacts of anthropogenic disturbances are less known for the northern hardwood forest zone of Eastern Canada than for this same zone in the northeastern United States and similar vegetation zones of Fennoscandia (Boucher et al. 2006).

My research thus provides one of the first regional landscape ecology studies (2000 km^2) in southwestern Québec. This study also constitutes an important example of a region that does not follow the global forest transition theory evident in other developed countries. In addition, this landscape, which is in one of Canada's most densely populated regions, is also one of the richest areas of biodiversity in the country. Hence, an assessment of the impact of past land use and landscape context on the present-day plant diversity in this area is critical to managing the territory (Haines-Young 2005 in Ruiz and Domon 2009; Domon and Bouchard 2007) and restore biodiversity (Foster et al. 2003).

Chapter 2. Methodology

This chapter is divided into two distinct parts corresponding to the two research questions. To the question *How has the forest cover changed from the 1860s to the 1990s?,* I first explain how I analyzed the landscape as a whole in terms of forest cover extent and configuration. Then, I describe the Forest Patch Change Trajectory analysis focusing on individual forest patches in this landscape. To the question *What are the effects of past land use and landscape context on current plant species composition and richness?*, I first describe the field work including the choice of sites and the sampling design. I subsequently detail three statistical analyses used to link historical variables to plant composition and richness: nonmetric multidimensional scaling analysis, Spearman's rank correlations, and Kruskal-Wallis test with Multiple Comparisons post-hoc test.

2.1. Study area

2.1.1. Setting

This study was conducted in the Montérégie region (lat: 45° 26' 3", long: -73° 9' 2"), a rural agro-forested landscape southeast of Montreal, Québec, Canada (Figure 1). The study area is 2046 km^2 with approximately 270,000 inhabitants (estimated based on population density in the Montérégie) (Institut de la Statistique du Québec 2013). It is bordered by the St-Lawrence River to the northwest and the Yamaska River to the east; the Richelieu River flows across the area from south to north. The study area includes the entire Vallée-Du-Richelieu Regional County Municipality (RCM), which is a 586.6 km^2 terrestrial area of 114,322 inhabitants (Institut de la Statistique du Québec 2013). Other RCMs partly included in the study area are: Marguerite-D'Youville, Les Maskoutains, Pierre-De Saurel, Rouville, Le Haut-Richelieu, Roussillon, and Longueuil (Figure 1).

The average temperature in the study area (Sainte-Madeleine meteorological station, 45°37’N, 73°08’W) is -10.6 in January and 20.4 in July and the average precipitation is 1000.2 mm annually (snow and rain). With its 2055 degree-days (above 5°C, 1971-2000 data, Environment Canada, 2010), the study area is located in the most productive agricultural region in Québec. It is part of the Northern hardwoods forest type, at the transition between the deciduous and boreal vegetation zones (Boucher et al. 2006), and more specifically in the sugar maple-hickory ecozone (Grandtner 1966). The species characterizing this ecozone are *Acer saccharum, Carya Cordiformis*, *Tilia Americana* and *Fagus Grandifolia* (Institut de recherche et de développement en agroenvironnement 2008). Only 371 km^2 of the study area is covered by forest, less than 20% of the total area (including water bodies) (Ministère des Ressources naturelles et de la Faune 2003). The majority of the region is covered by agriculture with urban areas in the southwestern part.

The geology of the study area consists of Paleozoic sedimentary rocks of the Appalachian orogeny forming the flatland, and Mesosoic intrusive rocks forming the four Monteregian Hills which break the continuity of the flatland: Mt Saint-Hilaire, Mt Rougemont, Mt Saint-Bruno and Mt Saint-Gregoire (Figure 1). Marine surface deposits formed by the post-glacial Champlain Sea lie on the bedrock over much of the study area, whereas post glacial alluvial deposits from the Champlain Sea beaches are located on its eastern and western limits (Earth Sciences Information Centre 2010). Ice contact sand and gravel, till, and veneer cover the Monteregian hills. When controlling for drainage, soils in the study area are among the most suitable soils for agriculture in Québec. On the marine deposits, they consist of humic gleysol and melanic brunisol. However, humo-ferrique podzols located on the alluvial deposits are less suitable for agriculture (Institut de recherche et de développement en agroenvironnement 2008).

The Richelieu River, which runs through the center of the study area, was a major transportation route for Amerindians and later for European colonists, who established seignories on both sides of the river from 1672 to 1750. Agricultural development was prosperous in the valley, given the favorable climate and soils, along with access to the Richelieu River for transporting goods and the proximity of the urban market of Montreal. The original subsistence farming rapidly gave way to commercial wheat production around 1750, hay around 1860 and milk around 1930 (Beauregard 1970). Shifts in agricultural production were engendered by major historic events: the British Conquest (1750), the Canadian Confederation of Canada (1867) and the Great Crash (1929) (Beauregard 1970). Starting around 1860, a long period of rural exodus resulted in a severe decrease in the number of farms. Concurrently, the urban population of the valley increased rapidly (Beauregard 1970). Indeed, the population of Chambly increased from 957 inhabitants in 1901 to 25,571 in 2011 while the population of Beloeil increased from 550 to 20,783 inhabitants over the same period (Statistics Canada 2013; The Atlas of Canada 1974) (Figure 1). Since the 1970s, soybean and corn have dominated the agricultural lands of the study area (La Financière agricole du Québec 2008). In Montérégie today, 29.4% of farms are dedicated to these monocultures (Marois 2007; Paul-Limoges 2008), forming respectively 57 % and 59 % of the total Québec soy crop and corn crop area (Montminy 2010).

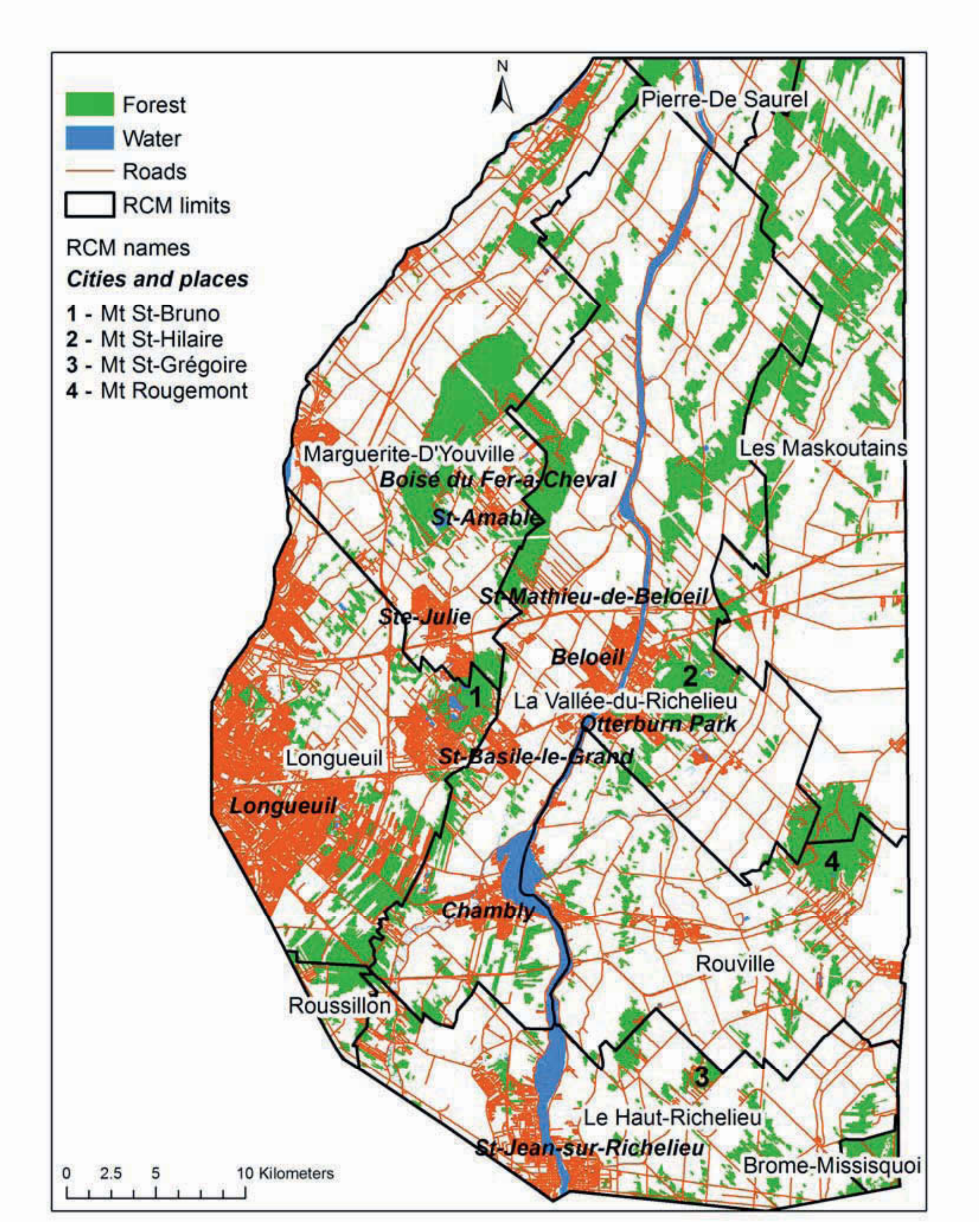

Figure 1: Study area showing Regional County Municipality (RCM) administrative divisions, some cities and places mentioned in the text.

2.2. Forest cover change analysis

Changes in the extent and spatial configuration of forest from the 1860s to the 1990s were assessed with analyses of forest cover change through time at the landscape level and at the patch level using specific trajectories of change (Ruiz and Domon 2009). The goal of the latter analysis was to represent and synthesize in a visually eloquent way the evolution of the forest cover in the study area during this period. Trajectories were determined from a dataset of points representing each forest patch in the landscape. The software ArcGIS 10 and FRAGSTATS (McGarigal et al. 2002) were used to create and add variables to the points while the Affinity Propagation algorithm (Frey and Dueck 2007) was used to perform the trajectory analysis.

2.2.1. Historical data

I used historical topographic maps and modern forest maps to reconstruct land cover for four time periods: the 1860s, the 1910s, the 1970s, and the 1990s (Table 1). Historical maps for the 1930s were also initially digitized but ultimately only used to guide forest plant sampling (section 2.3.1.).

My 1860s forest map was derived from two hand drawn topographic maps, from 1864 and 1867, covering respectively the left and the right bank of the Richelieu River (Table 1) (Appendix I). These maps delineate wooded areas in the Vallée-du-Richelieu RCM and surroundings (1 to 15 km around the RCM) as well as roads, houses and rivers. Three areas forming less than 20% of the study area are erased from the maps by what appears to be water damage or normal wear and tear and were therefore removed from further analyses. Maps were georeferenced using the road network of the Système d'Information Ecoforestière (SIEF) (Ministère des Ressources naturelles et de la Faune 2003). Mean residual errors were relatively high (for example, the two maps overlapped on their northern part – this part has thus been removed from the study area) likely because of inaccuracies in the historical maps and the difficulty in georeferencing using a modern road network. The resolution of the resulting digitized maps is therefore coarse and the limits of features are not precise. The thresholds that the mapmakers used to distinguish a wooded area from other land covers are not known for these maps.

The 1910s and the 1970s forest maps were derived from National Topographical System historical map series from the Bibliothèque et Archives Nationales du Québec (Table 1). Three maps at a scale of 1:63,360 were required to cover the entire study area for the 1910s. Full coverage was not available for the 1970s, but I was able to map about 60% of the study area using 10 maps at a scale of 1:25,000. 1970s maps were chosen because they correspond to a critical period in the mechanization of agriculture (section 1.1.).

Historical maps from the 1930s and 1950s (Table 1) were also available, and I initially digitized historical topographic maps from the 1930s to guide my forest patch sampling as this date broadly corresponds to a key plant colonization period (section 2.3.1.). However, I subsequently decided to use neither the 1930s maps nor the 1950s maps for trajectory analysis and statistical analysis as they seemed to have been created by lightly editing the 1910s series of maps and the former thus seemed more reliable.

I used the SIEF (Ministère des Ressources naturelles et de la Faune 2003) map to represent the 1990s.

As with the 1860s maps, the resolution of the 1910s maps is coarse. Indeed, before the use of air photos in 1922 (Sebert 1970), cartographers used aneroid observations, clinometers and ground surveys to draw topographic maps, which can result in interpretation errors. In terms of delimiting forest patches, even if "considerable attention was given to woods as an important military feature" (Sebert 1970), there was no agreement on a standard definition of wooded area at this time. However, in 1923, the National Topographic Series was introduced by the Board of Topographical Surveys and Maps (called National Topographical System after 1950), along with standardized definitions of land cover (Floyd 1969). A wooded area was defined as "an area at least 35 per cent covered by perennial vegetation of a minimum height of 2 m” (Natural Resources Canada 2008). According to the SIEF classification, tree height between 2 and 4 m corresponds to trees from 0 to 20 years old. Hence, I consider that topographic maps from the 1930s, the 1970s and potentially the 1910s show even the youngest stands, which is comparable to the SIEF’s 1990s maps.

When digitizing the 1860s and the 1910s maps, orchards and vineyards (absent from the 1860s topographical maps) were excluded, but plantations and all other forest cover (except isolated trees) were retained. Given the maps’ georeferencing-driven error higher than 5 meters, I chose a resolution of 5m when transforming maps in a raster format. This thus prevented me to digitize features of this dimension. For example, railways, streams and channels, all 5m-width maximum, did not affect the digitization of forest patches they bisected. However, roads and rivers of more than 10m width (15m in average for the region) were taken into account in the digitization of forest patches they bisected in order to keep the fragmentation they generate (Trombulak and Frissell 2000) (Figure 2). The same modifications concerning linear features were brought to the SIEF’s map of the 1990s.

Table 1: Historical data for forest cover reconstruction.

Period	Date	Source	Resolution	Number
1860s	1864, 1867	National Archives Canada	unknown	Microfiche NMC16666, Microfiche NMC16665
1910s	1914, 1918 (2)	Bibliothèque et Archives Nationales du Québec, historical NTS	1: 63,360	G 3400 s63 C37 31-H-11 1918 CAR, G 3400 s63 C37 31-H-14 1918 CAR, G 3400 s63 C37 31-H-06 1914 CAR
1930s	1934, 1935, 1936	Bibliothèque et Archives Nationales du Québec, historical NTS	1: 63,360	G 3400 s63 C37 31-H-11 1936 CAR, G 3400 s63 C37 31-H-14 1934 CAR, G 3400 s63 C37 31-H-06 1935 CAR
1970s	1970 (3) 1971 (4) 1966 (3)	Bibliothèque et Archives Nationales du Québec, discontinued NTS	1: 25,000	G 3400 s25 C37 31-H-11-b 1971 CAR, G 3400 s25 C37 31-H-11-f 1966 CAR, G 3400 s25 C37 31-H-11-d 1971 CAR, G 3400 s25 C37 31-H-11-c 1966 CAR, G 3400 s25 C37 31-H-11-e 1971 CAR, G 3400 s25 C37 31-H-11-g 1970 CAR, G 3400 s25 C37 31-H-06-f 1966 CAR, G 3400 s25 C37 31-H-06-e 1971 CAR, G 3400 s25 C37 31-H-06-g 1970 CAR, G 3400 s25 C37 31-H-14-b 1970 CAR
1990s	1991 to 2003	Système d'Information Ecoforestière, 3rd inventory	1: 20,000	31h14so, 31h14se, 31h11so, 31h11se, 31h11no, 31h11ne, 31h06so, 31h06se, 31h06no, 31h06ne

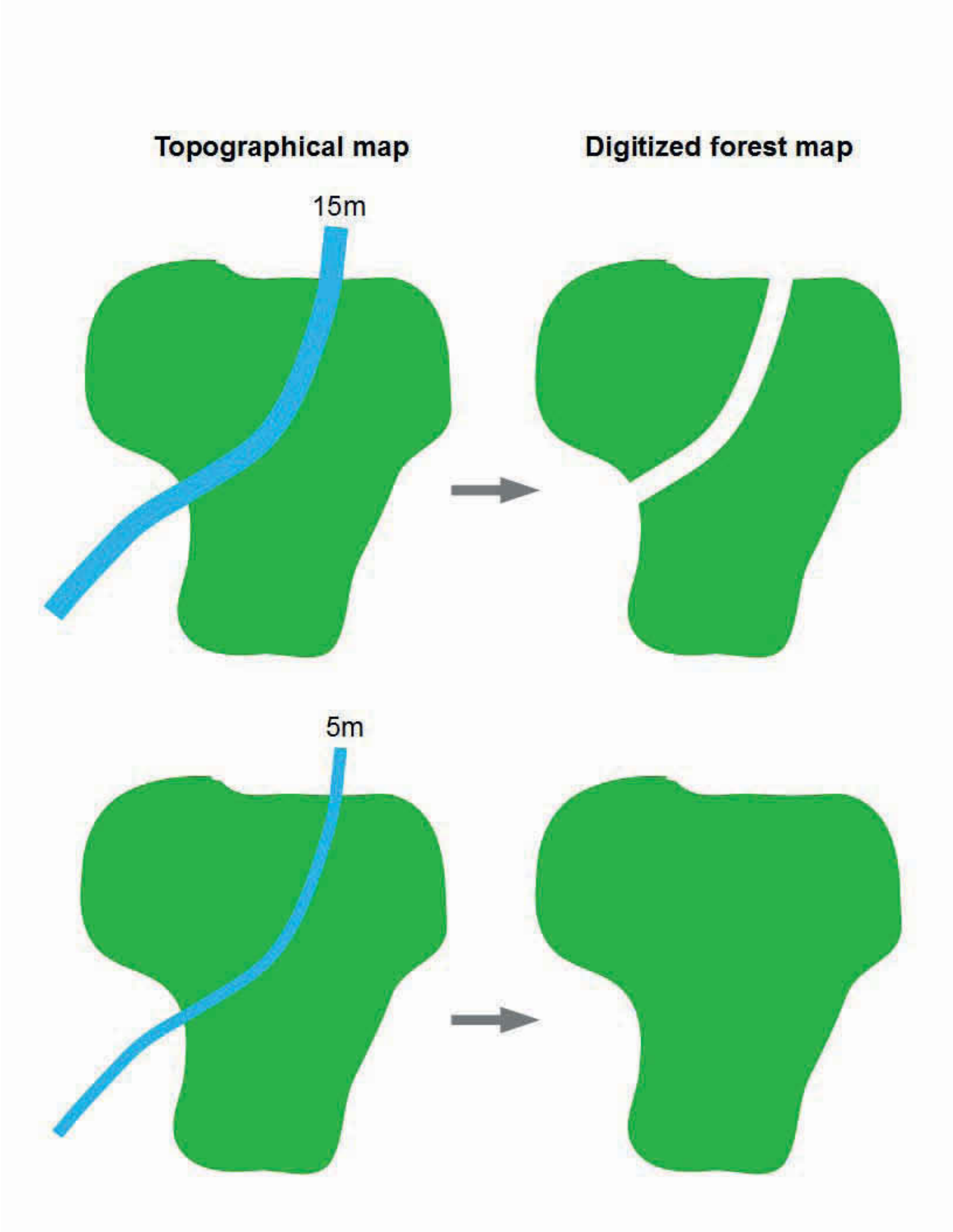

Figure 2: Digitizing threshold for linear features. Forest patches bisected by linear features greater than 10m in width (mostly roads and rivers) were digitized as two separate patches. However, when linear features bisecting a forest patch were less than 5m-width (mostly railways, streams and channels), this forest patch was digitized as one single patch.

2.2.2. Landscape-scale forest cover change

To analyze forest cover change, I converted the 1860s, the 1910s, and the 1990s maps into 5m-resolution raster maps (ArcGRID format), and calculated a series of metrics at the class level (forest) using FRAGSTATS software (McGarigal et al. 2002). Metrics at the class level describe the forest cover as a whole to better understand its amount and spatial configuration. Metrics from the following categories were calculated: area and edge (*class area, percentage of the landscape, total edge, patch area distribution*), shape (*fractal dimension index distribution, perimeter-area ratio distribution, shape index distribution, related circumscribing circle distribution*), core area (*total core area, core area percentage of the landscape, number of disjunct core areas, core area distribution, disjunct core area distribution, core area index distribution*), and aggregation (*landscape shape index, number of patches, euclidean nearest neighbor distance distribution, proximity index distribution*) (McGarigal et al. 2002). Since the analysis used the same study area for all maps (i.e. the 1860s' map extent), the value of each metric was not relativized to allow comparisons between the maps.

2.2.3. Forest Patch Change Trajectory Analysis (Affinity Propagation)

To conduct the Forest Patch Change Trajectory analysis, I assigned a point to each forest patch at each time period, so that the entire forest cover was represented. Points were created with *Feature to point* in ArcGIS 10, and represent the centroid of the polygon. In cases where the centroid was located outside the polygon, the algorithm automatically moved it inside. To avoid duplicates for the same forest patch, I removed points when they were within 200 meters from a point in the preceding time period. Points were then manually added or removed to properly represent small patches close together or large patches. As such, when a forest patch was maintained through time, only one point was used. However, when a forest patch became fragmented, points were created for each fragment produced. Thus, one patch could contain more than one point.

Each point was given attributes of the patch it pertained to for each of the four time periods. Attributes were patch metrics (patch area and proximity index) calculated with FRAGSTATS (McGarigal et al. 2002). The analysis was run for both the entire study area (1860s, 1910s, and 1990s only) and the reduced study area as covered by the 1970s'map (using all four time periods).

The point dataset was analyzed using an Affinity Propagation algorithm (Frey and Dueck 2007) in R (R Development Core Team 2011). Affinity Propagation groups similar datapoints into clusters and identifies one exemplar that best represents each cluster formed. This new algorithm was originally used for many purposes such as detecting exemplars of face images or identifying easily accessible cities by commercial airlines (Frey and Dueck 2007).The algorithm bases its calculations on measures of similarity between pairs of data points using negative Euclidian distances. It is an iterative process that runs until a set of exemplars arises with the points clustering around each exemplar. The Affinity Propagation algorithm has been adapted to the use of landscape metrics, which have different scales and are often correlated. This transformation of the algorithm, including a scaling of the metrics and their ordination using a Principal Component Analysis (PCA) (Figure 3), was developed by Cardille and Lambois (2009) for the 1992 US National Land Cover Dataset. In this study, the authors found a set of 17 distinct exemplar landscapes that best represent the land uses and land covers of the continental United States. Choosing the right number of clusters depends on: the overall net similarity of the model, which is the model's fitness; the complexity of each cluster, estimated using a regression tree (Figure 4); and the mapping visual limitation.

I chose to report six trajectories of forest patch change for the 1714 points representing forest patches in the study area for a better visual interpretation and because points clustered more distinctly with six than with more or less groups. Trajectories were determined using the logged area (to lower the weight of the landscape's biggest patch) and the logged proximity index, within a 500-meter radius around each forest patch.

To verify if the creation of trajectories with the Affinity Propagation algorithm was robust, I also analyzed a second series of points derived from the first one but modified by the addition of the 1970s map layer. The number of points is smaller because the area not covered by the 1970s map was removed from the analysis. The 1430 points were also grouped into six trajectories.

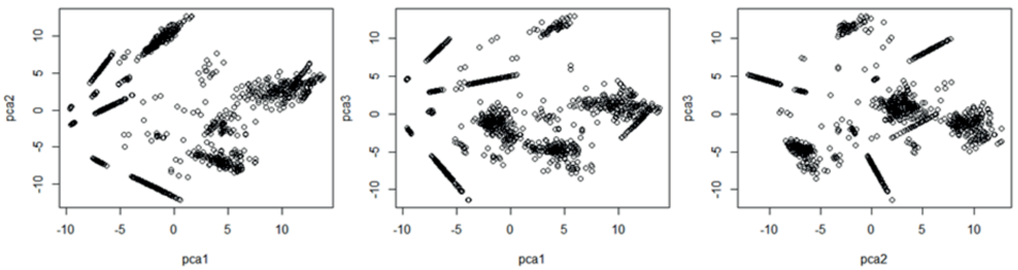

Figure 3: Principal Component Analysis on the datapoint matrix prior to its use for Affinity Propagation algorithm (Axes 1, 2, and 3).

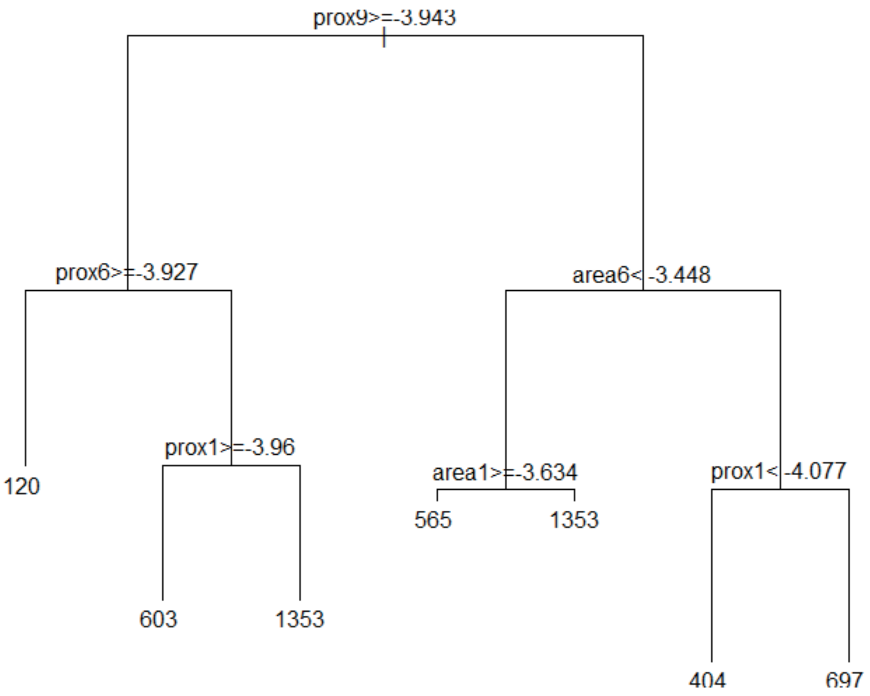

Figure 4: Regression tree used to show the importance of different variables for clustering results. prox9: Proximity index in the 1990s; prox6: Proximity index in the 1860s; prox1: Proximity index in the 1910s; area1: Area in the 1910s; area6: Area in the 1860s.

2.3. Analysis of historical legacies on forest plant composition and richness

In this section, I first explain the choice of study sites and the sampling design. Then, I describe the statistical tests that were used to analyze plant species composition and plant species richness separately against a set of environmental and historical variables.

2.3.1. Forest plant sampling

A total of 52 forest stands were sampled between June and August 2011 (Figure 5). I delimited stand boundaries based on the 1990s' SIEF map forest polygons corresponding to homogenous forest stands (Ministère des Ressources naturelles et de la Faune 2003). I selected stands to sample based on size, age, and land-use history.

From the SIEF map, I chose medium size forest stands (3 to 27 hectares) greater than 75 years old (verified in the field by counting growth rings in tree cores) in order to avoid any early-successional forest. All of them contain *Acer saccharum* in their stand type description to reduce the inter-patch heterogeneity.

Stands were also chosen according to a preliminary analysis of the past land use and landscape configuration within a 200m-radius. The past land use, determined at the stand level using the 1860s digitized map, was given the value of "cleared (C)" (17 stands) or "forest (F)" (35 stands) according to the proportion of the stand overlaying forest polygons in the 1860s map. If less than 30% of the target stand overlaid forest in the 1860s, this stand was considered to have been under agriculture (pasture or cropland). If more than 30% of the target stand was forested in the 1860s, it was classified as forest (F). The "cleared" category on the 1860s map likely corresponds to land under agriculture or grazing given the study area history (section 2.1.1.). I chose these thresholds to compensate for the 1860s' map coarse resolution.

A landscape configuration variable was calculated within a 200m buffer around each target stand using the 1930s and 1990s digitized maps. I chose this buffer size because when a forest stand is situated further than 200 meters from the nearest forest stands, the probability of colonization of forest herb species, which are isolation sensitive, is very low (Butaye et al. 2001). Two metrics were used to measure landscape configuration: the area of forest surrounding the target stand in a 200m buffer, and the average distance from the edges of the target stand to neighbouring forest stands. Those landscape characteristics influence seed dispersal and thus plant diversity (section 1.4.). The FRAGSTATS *Proximity index* metric at the stand level already combines these variables into one formula (McGarigal et al. 2002). Because I wanted to know the distribution of both metrics and to verify the accuracy of their calculation, however, I used the same formula but calculated each metric separately using *Analysis Tools* in ArcGIS for the area and *Conefor Inputs extension* for ArcGIS (Jenness 2011) for distances:

$$\text{Proximity Index}=\sum_{s=1}^{n}\left(\frac{\text{aijs}}{\text{hijs}^2}\right)$$

where *aijs* is the area (m^2) of stand *ijs* within specified neighborhôod (200m) of stand *ij*, and *hij*s is the distance (m) between stand *ijs* and stand *ij*, based on the nearest stand edge-to-edge distance (McGarigal et al. 2002).

To avoid a division by zero, a target forest stand adjacent to another type of forest stand (in the same forest patch) has been given an edge-to-edge distance of 1 meter. The values of the *Proximity Index* ranged from 0 to 100, the latter being the highest level of connectivity for a given stand ($100\%/1m^2$). For both the 1930s and 1990s, I assigned the category “connected (C)” to stands with index values of more than 60, while I classified as “isolated (I)” stands whose index values were less than 30. “Semi-connected” stands had a value ranging from more than 30 to less than 60. To simplify categories of forest history, only stands from the categories “C” and “I” were retained along with a few stands at the upper or the lower ends of the “semi-connected” category.

Finally, I combined the 1860s land use with the 1930s and 1990s landscape configuration to create unique land-use history categories (Table 2). Every forest stand was classified into one of these categories; only categories containing 8 or more stands were retained. There were not enough stands per category to allow their random selection. Hence, every stand (8 and more) of each category was retained for sampling. However, some stands were eliminated from the analysis when their access was forbidden or when they did not contain *Acer* species (contrarily to the map description).

For each forest stand chosen for the study, I surveyed the vegetation at least 50 meters from the forest edge to prevent the "edge effect" on species composition (Brown and Boutin 2009; Matlack 1994).

A nested plot design was adopted to sample sites because it makes collecting accurate species data more efficient (Stohlgren 2007). I thus delimited three 10m x 10m plots, randomly distributed, per forest stand (Bellemare et al. 2002), each containing two 4m quadrats at opposite corners of the plot. Each quadrat was then divided into 4 adjacent rectangles of 1mx4m (Figure 6). In the 10mx10m plot, I identified all tree species (DBH≥5cm) and measured diameter at breast height (DBH). The percent cover of saplings (1cm≤DBH<5cm) and shrub species was estimated in the two 4m quadrats while that of seedlings (DBH<1cm) and herb species was estimated in the eight 1mx4m rectangles (Benjamin et al. 2005; D'Orangeville et al. 2011; Ministère des Ressources Naturelles et de la Faune 1994). Individuals were counted for saplings and seedlings in order to measure their density. Percent cover was estimated using Braun-Blanquet percent cover classes (75-100; 50-75; 25-50; 5-25; 1-5; <1; <<1) (Mueller-Dombois and Ellenberg 1974). Plants were identified to the species level when possible and to the genus level when their differential features (flowers, fruits) were either faded or not yet existent. Spring ephemerals, non-vascular plants and graminoids were excluded, due to identification complexity. The nomenclature from Gleason and Cronquist (1963) was followed for all species.

The dispersal mode for each species was based on Brown and Boutin (2009) and other relevant literature. Species were classified as anemochores (wind), hydrochores (water), epizoochores (fur), barochores (gravity), ballistichores (explosively), endozoochores (animal ingestion), or myrmerochores (ants) (Aubin et al. 2009). A habitat specification was also assigned to each species using Gleason and Cronquist (1963) and other relevant literature. Species were classified as forest specialists or generalists (Appendix II).

During summer 2011, I sampled a total of 177 species, including 119 herbaceous species, 28 shrub species and 32 tree species (sapling, seedling, and tree). I was unable to identify three herbaceous species, but since they were clearly different species, I kept them in the analysis to maintain the plots' richness. Grass and moss species were not identified but their presence was noted. Twelve species were identified to the genus level when either the species were known to be hard to differentiate from each other like *Carex*, *Sphagnum*, *Crataegus*, *Viola*, and *Amelanchier*, or when the specimen was too hard to identify like a species of *Ribes*.

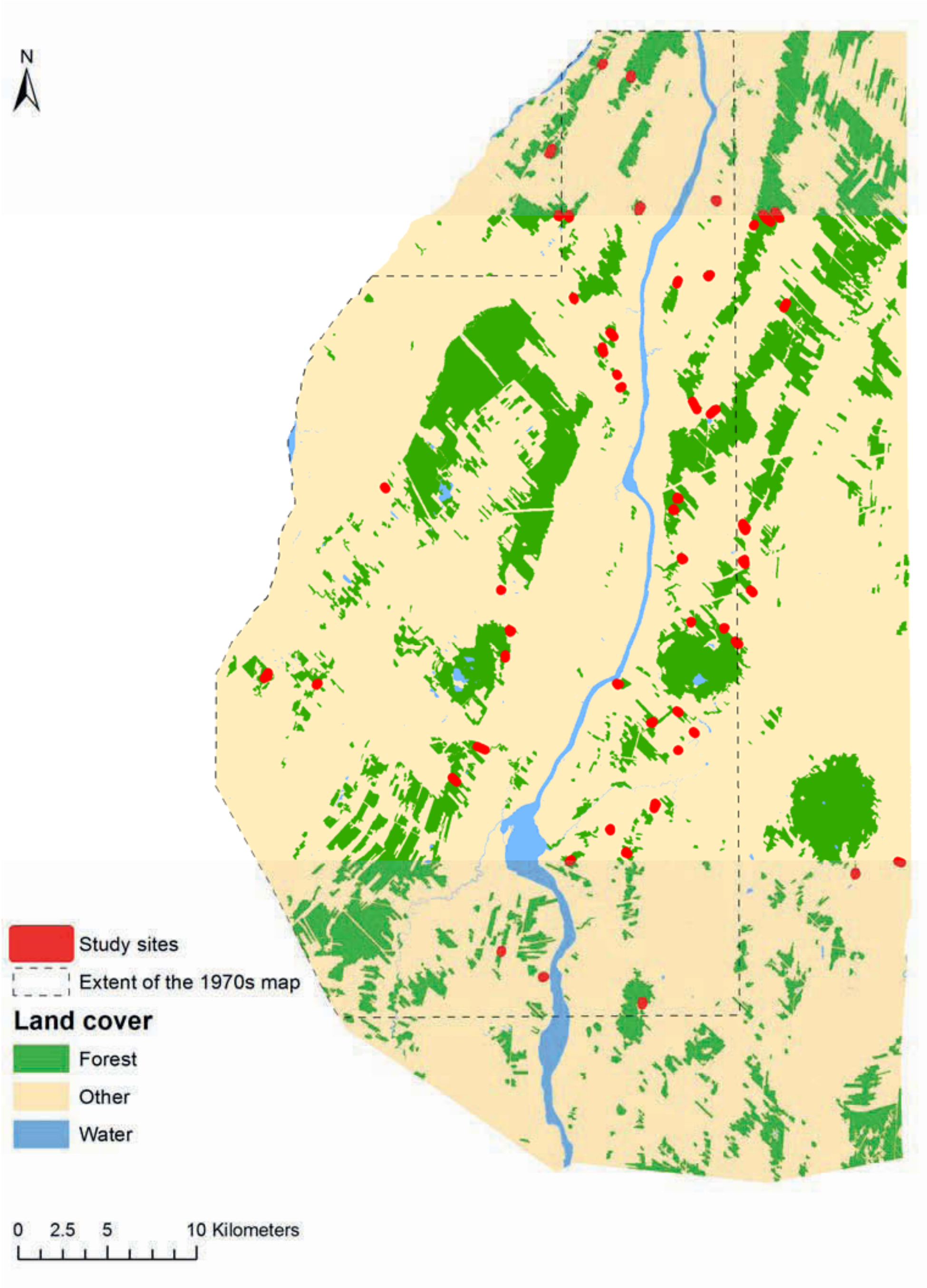

Figure 5: The 52 study sites sampled in summer 2011.

Table 2: Categories of study sites according to the land use in the 1860s and the landscape configuration in the 1930s and 1990s.

Category	Number of study sites	1860s	1930s	1990s
CII	8	cleared	isolated	isolated
CCI	9	cleared	connected	isolated
FII	9	forest	isolated	isolated
FCC	10	forest	connected	connected
FCI	8	forest	connected	isolated
FIC	8	forest	isolated	connected

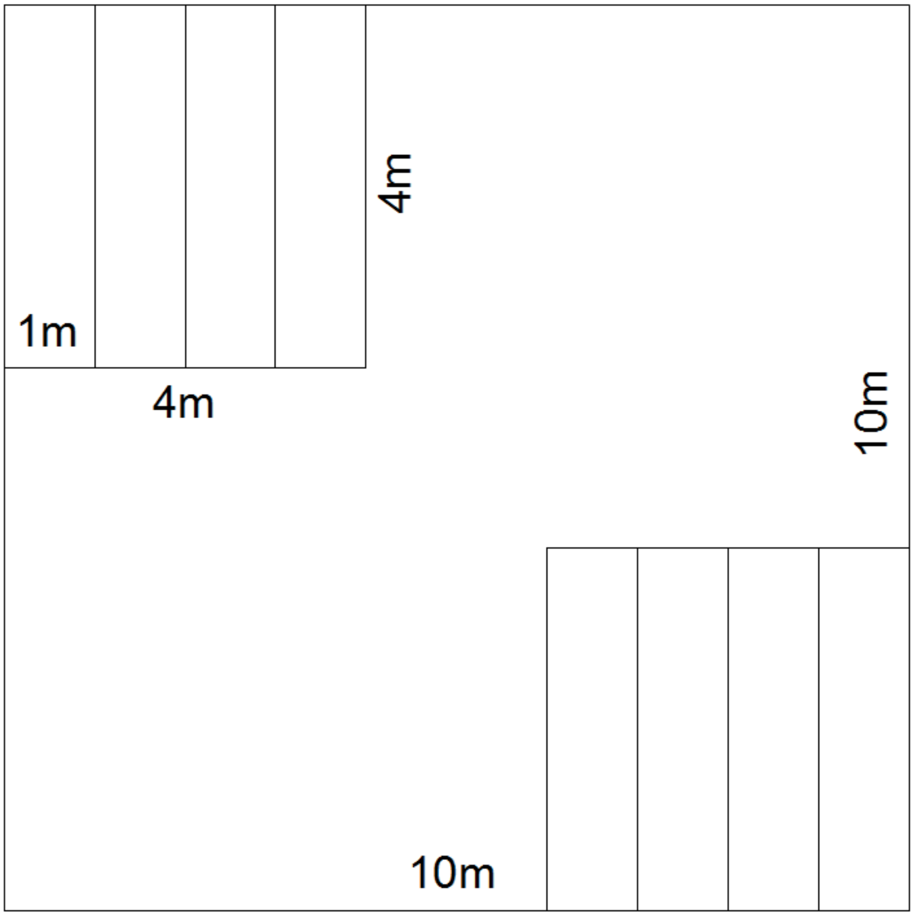

Figure 6: Nested plot sampling design. Diameter at breast height (DBH) of all tree species (DBH≥5cm) was measured in the 10x10m plot. The percent cover of saplings (1cm≤DBH<5cm) and shrub species (non-tree wooded species) was estimated in the two 4m quadrats while that of seedlings (DBH<1cm) and herb species was estimated in the eight 1mx4m rectangles.

2.3.2. Non Metric Multidimensional Scaling Ordination Analysis

To assess the effect of past land use and landscape context on species composition, I performed a nonmetric multidimensional scaling analysis (NMDS), an ordination technique appropriate for assessing patterns in nonnormal data sets, like plant species data measured in the field (McCune and Grace 2002). This iterative optimization method offers multiple advantages for ecological community data sets and is thus increasingly used by ecologists (Brown and Boutin 2009; Chandy et al. 2009; Jamoneau et al. 2011; McCune and Grace 2002; Nelson et al. 2009; Rhemtulla et al. 2009). Response variables included relative basal area of trees (Cottam and Curtis 1956), and the percent cover of shrubs, saplings, and herbs. For seedlings, density was calculated with count data following Cottam and Curtis (1956) (Table 3).

For herbs, shrubs and saplings, I replaced cover class data with the middle-class value in order to keep the quantitative format of the data (87.5%, 62.5%, 37.5%, 15%, 2.5%, 0.1% and 0.05%) (Mueller-Dombois and Ellenberg 1974). Basal area, cover and density measures taken in subplots were then averaged to the stand level in order to prevent autocorrelation in the NMDS analysis (McCune and Grace 2002; Stohlgren 2007). The following independent variables were then related to ordination results using correlations for ranked or numerical variables and overlays for categorical variables: soil order and drainage; surficial deposit; canopy cover; forest patch change trajectory, management intensity; past land use intensity; and landscape context in the 1860s, the 1910s, and the 1990s (Table 3). Landscape context in the 1970s was excluded from this analysis because 12 study sites fell outside the extent of the 1970s maps (Figure 5). The soil order (brunisolic, gleysolic, podzolic, regosolic), drainage (good, imperfect, bad, moderate), and surficial deposits (fluviatile, marine, morainic, glacial, lacustrine, colluvial, glacio-fluvial, not defined) were obtained using 1:20,000 soil maps (Ministère de l'Agriculture des Pêcheries et de l'Alimentation du Québec 1998-2006). Surficial deposits were also determined with the use of a 1:1,000,000 000 map (Earth Sciences Information Centre 2010) and were classified into clay or coarse deposits (which includes sand and gravel). Canopy cover was measured with a convex densiometer as an estimation of overstory density in percent. The forest patch change trajectory was calculated in section 2.2.3. and each study site was given the trajectory of the forest patch in which it was located. Management intensity was estimated by the presence on site of: cleaning/removal of dead wood; stumps; trails; ditches; traces of furrows from past plowing; and taps and tubes for maple syrup production. Features were noted in the field and each was given the same weight because their intensity was hard to estimate. Management features were then summed for each plot and averaged at the site level to provide a measure of intensity of past and present management practices. Species richness was calculated for all species, species by life-form, and woody species. It was also calculated for forest specialists, generalists, anemochores, hydrochores, epizoochores, barochores, ballistichores, endozoochores, and myrmerochores as the number of species per site falling into each category (total and herbaceous). I analyzed correlations between species richness by life-form (i.e. number of species in each life-form category), dispersal type and habitat preference and the NMDS axes, to help identify the ecological gradients structuring the ordination.

To make study sites more comparable between each other, a triangle was drawn joining the three sampled plots in each site, and this triangle (instead of the entire 1990s forest stand) was overlaid on the 1860s map to determine past land use. Landscape configuration was also calculated for these smaller triangles but only included the proportion of forest within 200m, 500m, and 1000m buffers. Isolation metrics based on area are better predictors of patch colonization by species than isolation metrics based on distance (Tischendorf et al. 2003). Hence, I replaced “landscape configuration” by “landscape context”. Landscape configuration is defined as “the particular spatial arrangement of habitat at a given point in time” (Villard et al. 1999), and therefore implies the use of metrics showing both the area and the isolation of a patch (Bélisle et al. 2001; Honnay et al. 2005; Lindborg 2007). Landscape context rather refers to the area of a habitat type or landscape composition (Haynes et al. 2007; Kleijn and van Langevelde 2006; Steffan-Dewenter 2003; Steffan-Dewenter et al. 2002; Thies et al. 2003).

Unlike in the pre-fieldwork analysis, past land use was not characterized as either "cleared" or "forest" based on the 1860s map. Instead, I included the past land use in the 1860s, 1910s, and 1970s, which was, for three sites, confirmed by the presence of furrows in sample plots. I created a ranked variable named "Past land-use intensity" with a value ranging from 1 to 7. Values were based on the amount of the triangle-shaped study site cleared in the 1860s, 1910s, or 1990s (Table 4). The higher the rank, the longer a forest stand was cleared.

Response variables were organized in a main matrix while explanatory variables (environmental and spatial), dispersal and species richness data formed a secondary matrix (Table 3). Separate ordinations were run for the entire dataset, species by life-form and woody species only. Correlations of individual species and each of the environmental, dispersal and species richness variables to the ordination axes were performed in order to identify which species and variables would follow these gradients. For forest patch change trajectories, soil order and drainage, and surficial deposits, which are categorical variables, I used Multiresponse Permutation Procedure (MRPP) in PC-ORD using Sorensen distance to test whether data grouped by forest patch change trajectories or surficial deposit type were significantly different (Brown and Boutin 2009). I also used stand scores on Axis 1 to run a Kruskal-Wallis test in order to test the difference in means between groups of forest patch change trajectories and surficial deposits because it doesn't require normal distributions and equal variances. A Multiple Comparisons post hoc test was added to identify which pairs of groups have significant different means. I did the same tests using species scores on Axis 1 to see if species were grouped according to their dispersal vector.

The NMDS ordination used a main matrix of 52 sites against 221 species (includes different life-forms) and the Sorensen (Bray-Curtis) distance measure (Brown and Boutin 2009) was employed to calculate the dissimilarity matrix. A random starting configuration using the time of the day and 250 runs with real data were used to assess the dimensionality of the ordination. A three-dimensional solution was obtained after 249 randomized runs (p=0.004). It was retained because the Monte Carlo test results and the scree plot (Appendix III) showed that the reduction in stress from three to four dimensions was little compared to that between two and three dimensions.

The NMDS ordination for tree species used a main matrix of 52 sites against 30 species with a dissimilarity matrix calculated with the Sorensen (Bray-Curtis) distance measure. The same setup values than the NMDS with all taxa were used for this ordination (random starting configuration: the time of the day; 250 runs with real data) to assess the dimensionality of the ordination. A three-dimensional solution was obtained after 249 randomized runs (p=0.004).

2.3.3. Correlations and Kruskal-Wallis test

While an NMDS analysis was performed to seek the impact of landscape context on the species composition in study sites, Spearman's rank correlations were used to evaluate its impact on current species richness. I used this non parametric method because species data were not normally distributed. Plant species richness, previously calculated for the NMDS, included total species, species by life-form, woody species, species by habitat preference (total and herbaceous only), and species by dispersal type (total and herbaceous only). The explanatory variables were the same numerical variables as in the NMDS analysis: canopy cover, management, past land-use intensity, and landscape context in the 1860s, 1910s, and 1990s. A Kruskal-Wallis test was then used to test the difference in species richness means between groups of study sites having different forest patch change trajectories, soil order and drainage, and surficial deposits. A Multiple Comparisons post hoc test was added to identify which pairs of groups had significant different means.

Table 3: Variables used in the NMDS ordination of sample sites based on species composition.

Dependant	Explanatory-quantitative	Explanatory-categorical	Correlated-species richness
Herb (% cover)	Canopy cover	Soil order	Total
Tree (basal area)	Management intensity	Soil drainage	Woody
Shrub (% cover)	Past land-use intensity	Surficial deposit	By life-form (herb, shrub, tree, sapling, seedling)
Sapling (% cover)	Landscape context in the 1860s (200m, 500m, and 1000m buffers)	Forest Patch Change Trajectory	By habitat preference (forest specialist, generalist)
Seedling (density)	Landscape context in the 1910s (200m, 500m, and 1000m buffers)		By dispersal type (anemochores, hydrochores, epizoochores, barochores, ballistichores, endozoochores, and myrmerochores)
	Landscape context in the 1990s (200m, 500m, and 1000m buffers)		

Table 4: Past land-use intensity rank value determined by the number of plots per site that were cleared in the 1860s, the 1910s, and the 1970s.

Number of plots cleared in the 1860s, the 1910s, and the 1970s	**Past land-use intensity**
No plots cleared at any dates	1
One plot cleared at one date	2
Two plots cleared at one date	3
Three plots cleared at one date	4
Three plots cleared at one date and one plot cleared at another date	5
Three plots cleared at one date and two plots cleared at another date	6
Three plots cleared at one date and three plots cleared at another date	7

Chapter 3. Results

3.1. Forest change from the 1860s to the 1990s

3.1.1. The relative stability of forest cover

Forest cover in the study area was remarkably stable through time, though gradual deforestation and increased fragmentation was observed. The forest cover in the study area decreased 36% from the 1860s to the 1990s, going from almost 30% of the landscape to less than 20% (Figure 7 and Table 5). This decrease was faster between the 1860s and the 1910s, with a loss rate of 204 ha/yr compared to a loss rate of 86 ha/yr between the 1910s and the 1990s. The forest cover also became more fragmented, with the number of forest patches increasing by almost 70% between 1860s and 1990s. This increase occurred primarily between the 1860s and the 1910s, with a decrease of 15% in the number of patches between the 1910s and the 1990s. Although the number of patches significantly increased during the whole period, their mean size decreased by 60%. The irregularity of patches and the amount of edge in the landscape also amplified during this period. The total length of edge in the landscape increased by more than 50% in 130 years, influencing the landscape shape index which increased by almost 100% during this period. In terms of patch convolutedness, four parameters calculated in FRAGSTATS (*shape index, fractal dimension index, perimeter-area ratio, related circumscribing circle*) converged on the same conclusion: on average, forest patches tended to become more irregular, convoluted, elongated and linear from the 1860s to the 1990s. Along with the growing fragmentation and complexity of forest patches, the total core area in the landscape (area within 50 meters of the patch boundary) decreased by almost 50% while the number of disjunct core areas increased by 200%. Patches in the 1990s thus had less contiguous core area than in the 1860s and the mean area per disjunct core went from around 80 hectares to 14 hectares during this period. Although the overall forest area decreased between the 1860s and the 1990s and the fragmentation augmented, the proximity to neighbouring forest patches (within a 500-meter radius) increased in time (from 234m in the 1860s to 156m in the 1990s), with the greatest change occurring between the 1860s and the 1910s.

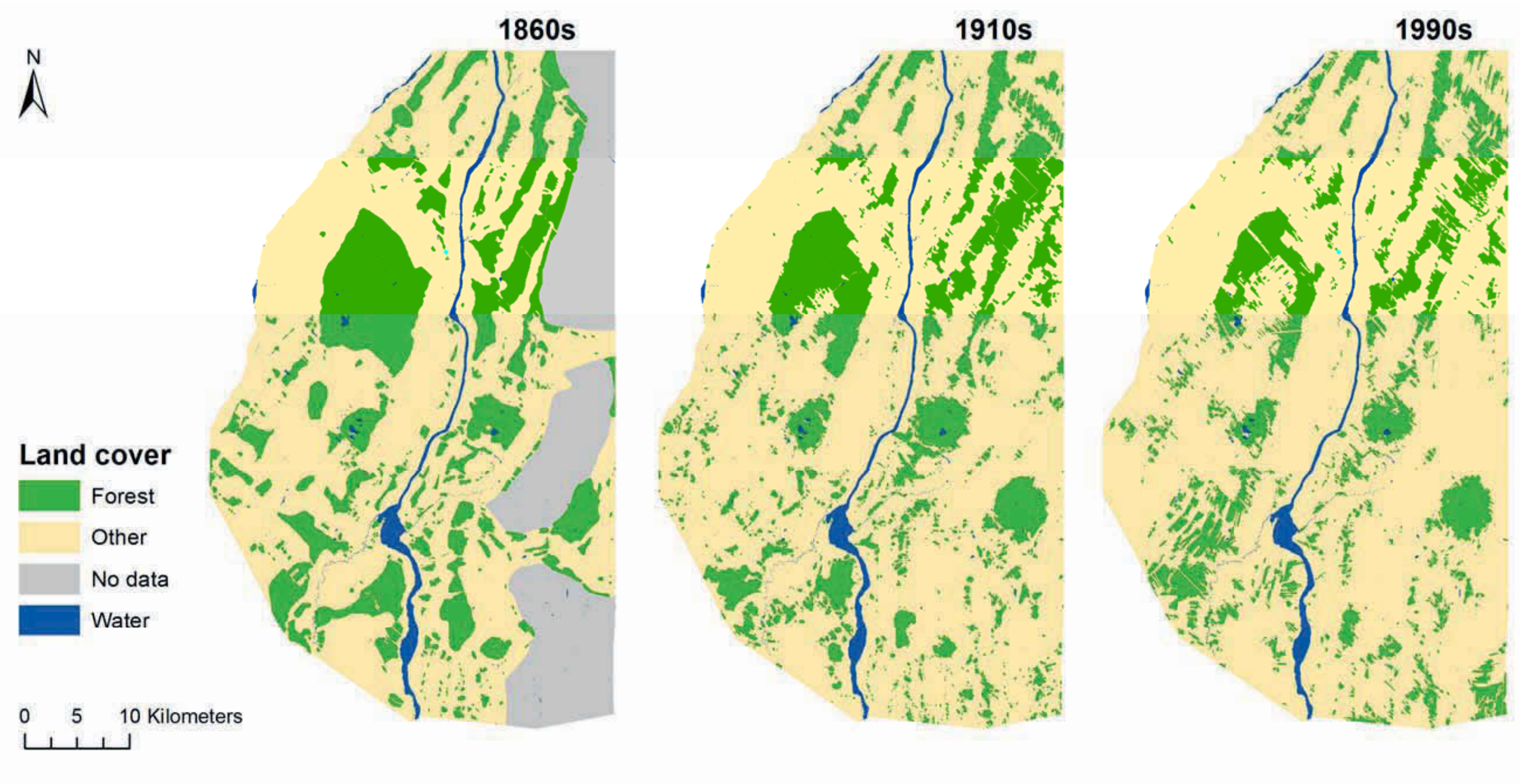

Figure 7: Forest cover in the study area in the 1860s, the 1910s, and the 1990s, based on historical topographic (1860s, 1910s) and forest (1990s) maps.

Table 5: Evolution of the forest cover from the 1860s to the 1990s using FRAGSTATS metrics at the class (forest) level.

Fragstats metric	Name	Units	1860	1910	1990	% change 1860-1910	% change 1910-1990	% change 1860-1990
CA	Forest area	hectares	46951.78	36716.96	29817.22	-21.80	-18.79	-36.49
PLAND	Percentage of the landscape in forest	percent	28.03	21.92	17.80	-6.11	-4.12	-10.23
NP	Number of patches	none	421.00	823.00	705.00	95.49	-14.34	67.46
TE	Total edge	meters	1716620.00	2140500.00	2669760.00	24.69	24.73	55.52
LSI	Landscape Shape Index	none[1]	19.80	27.93	38.65	41.01	38.39	95.15
AREA_MN	Mean patch size	hectares	111.52	44.61	42.29	-60.00	-5.20	-62.08
AREA_MD	Median patch size	hectares	12.10	4.72	7.25	-60.95	53.41	-40.10
AREA_RA	Range in patch size (max - min)	hectares	10666.12	5378.61	2608.47	-49.57	-51.50	-75.54
SHAPE_MN	Mean shape index	none[2]	1.45	1.43	1.83	-1.45	28.40	26.54
FRAC_MN	Mean fractal dimension index	none[3]	1.06	1.06	1.10	0.10	3.38	3.48
PARA_MN	Mean perimeter-area ratio	none	195.50	358.34	800.00	83.30	123.25	309.20
CIRCLE_MN	Mean related circumscribing circle	none[4]	0.56	0.51	0.62	-8.33	21.29	11.18
TCA	Total core area	hectares	40730.46	29269.53	20997.74	-28.14	-28.26	-48.45
CPLAND	Core area percent of landscape	percent	24.32	17.48	12.54	-6.84	-4.94	-11.78
NDCA	Number of disjunct* core areas	none	507.00	1011.00	1519.00	99.41	50.25	199.61
CORE_MN	Mean core area per patch	hectares	96.75	35.56	29.78	-63.24	-16.25	-69.21
CORE_MD	Median core area per patch	hectares	5.16	1.16	1.67	-77.48	43.87	-67.60
DCORE_MN	Mean area per disjunct* core	hectares	80.34	28.95	13.82	-63.96	-52.25	-82.79
DCORE_MD	Median area per disjunct* core	hectares	3.07	0.58	0.04	-81.04	-92.70	-98.62
CAI_MN	Mean core area index	percent	45.37	28.43	27.11	-16.94	-1.32	-18.26
CAI_MD	Median core area index	percent	46.03	24.11	22.97	-21.92	-1.15	-23.06
PROX_MN	Mean proximity index	none[5]	3386.61	6481.27	7033.01	91.38	8.51	107.67
ENN_MN	Mean Euclidean nearest neighbor distance	meters	234.04	203.78	156.08	-12.93	-23.41	-33.31

(Table 5 continued)

*** Disjunct core area**: core area (> 50m from the edge) in a patch can be either joint or disjunct depending on the variation in the width of the patch

1 **LSI** ≥ 1, increases without limit as landscape shape becomes more irregular and/or as the length of edge of the corresponding patch type in the landscape increases.

LSI = 1 when the landscape consists of a single square patch of the corresponding type

2 **SHAPE** ≥ 1, without limit.

SHAPE = 1 when the patch is square and increases without limit as patch shape becomes more irregular

3 **1 ≤** FRAC ≤ 2

A fractal dimension greater than 1 for a 2-dimensional patch indicates a departure from Euclidean geometry (i.e., an increase in shape complexity). FRAC approaches 1 for shapes with very simple perimeters such as squares, and approaches 2 for shapes with highly convoluted, plane-filling perimeters.

4 **0 ≤** CIRCLE < 1

CIRCLE = 0 for square patches and approaches 1 for elongated, linear patches one cell wide.

5 **PROX** ≥ 0.

PROX = 0 if a patch has no neighbors of the same patch type within the specified search radius. PROX increases as the neighborhôod (defined by the specified search radius) is increasingly occupied by patches of the same type and as those patches become closer and more contiguous (or less fragmented) in distribution. The upper limit of PROX is affected by the search radius (here 500 meters) and the minimum distance between patches.

3.1.2. Six local trajectories

The Affinity Propagation algorithm resulted in six clusters exhibiting different trajectories of forest patch change from the 1860s to the 1910s (Figure 8 and Figure 9) based on the evolution of patch area and proximity index measures (Figure 10).

The six trajectories can be grouped by three characteristics: stability, clearing and reforestation. 22% of the points pertain to the first trajectory, *Stability or Gradual Shrinking*, in which forest patches were among the biggest and the most connected of the landscape in the 1860s, 1910s, and 1990s. Since the forest cover has generally decreased during this period, these patches decreased in size as well. Patches with this trajectory are scattered throughout the landscape and include the boisé du Fer-à-cheval and the monteregian hills.

A total clearing of forest patches was observed in two trajectories. The first one, *Early Clearing,* includes 17% of points, and is characterized by small patches that were poorly connected in the 1860s, and disappeared completely by the 1910s. They were present across the whole landscape but concentrated along the Richelieu River, and in the municipality of Longueuil. The second trajectory (14% of points), *Recent Clearing,* has patches that were medium sized and connected in the 1860s and the 1910s, but become absent in the 1990s map. The interior part of the boisé du Fer-à-cheval held the highest concentration of points from this trajectory.

The last three trajectories show small scale reforestation. The first one, *Early Reforestation,* with 14% of points, shows reforestation starting in the 1910s. Patches were thus nonexistent in the 1860s, and appeared as medium sized forest patches with a medium connection in the 1910s and were still in place in the 1990s. They are scattered throughout the landscape. 21% of points pertain to the trajectory *Temporary Reforestation*. Small and poorly connected forest patches were created in the 1910s then cleared in the 1990s. Points having this trajectory were found primarily in Longueuil and in the southern part of the monteregian hills. The last trajectory (12% of points), *Recent Reforestation* shows medium sized and medium connected forest patches that only appeared in the 1990s. Points showing this trajectory are mostly concentrated on the edges of the municipality of Longueuil.

When using the 1970s maps and a smaller study area, the trajectories obtained are very similar to those of the previous analysis using the larger data set.

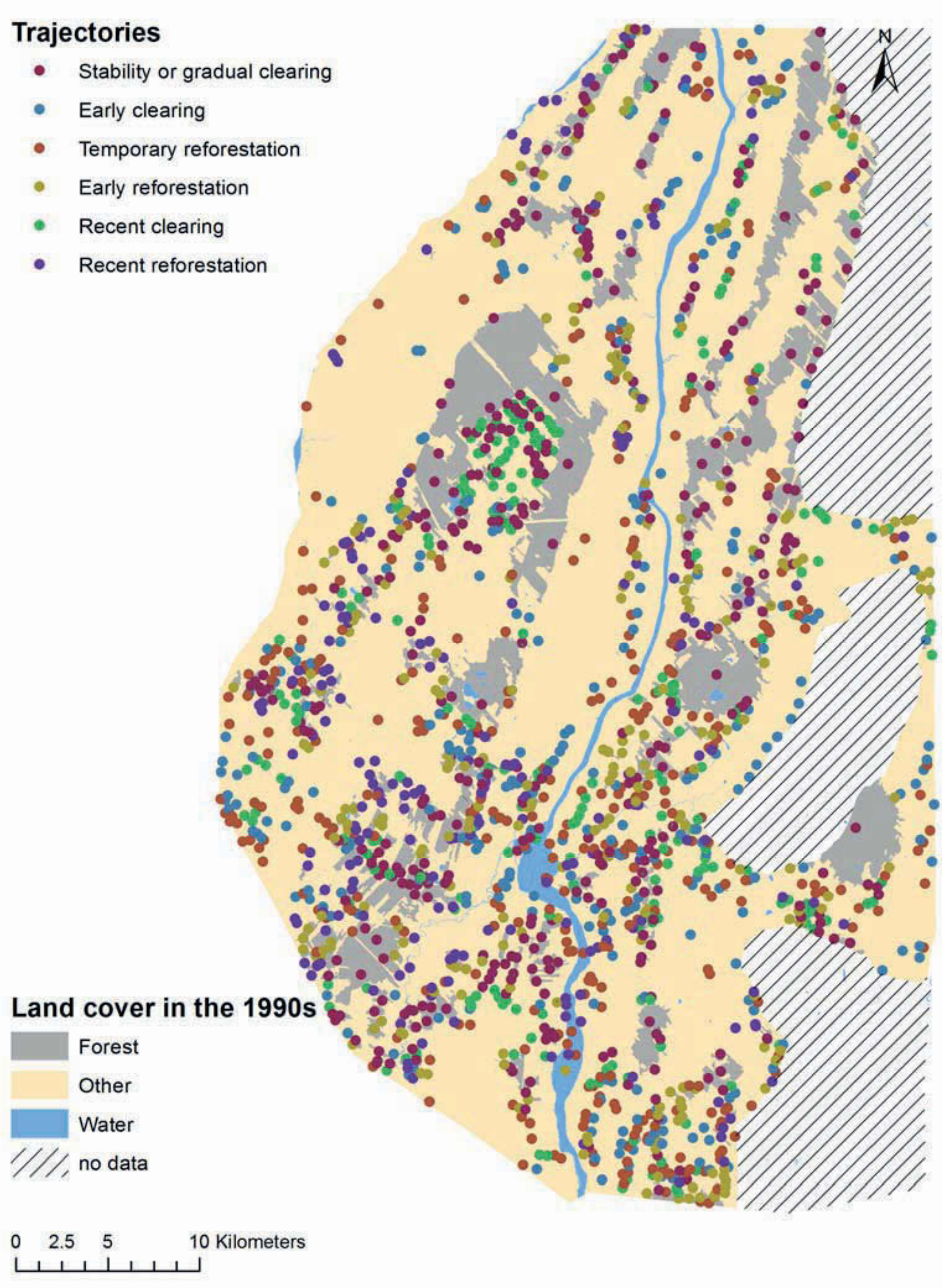

Figure 8: Six trajectories of forest patch change through time, using measures of patch area (log) and proximity index (log) from the 1860s, 1910s, and 1990s forest maps. Trajectories were obtained with Affinity Propagation algorithm (Frey and Dueck, 2007) modified for landscape ecology studies (Cardille and Lambois, 2007).

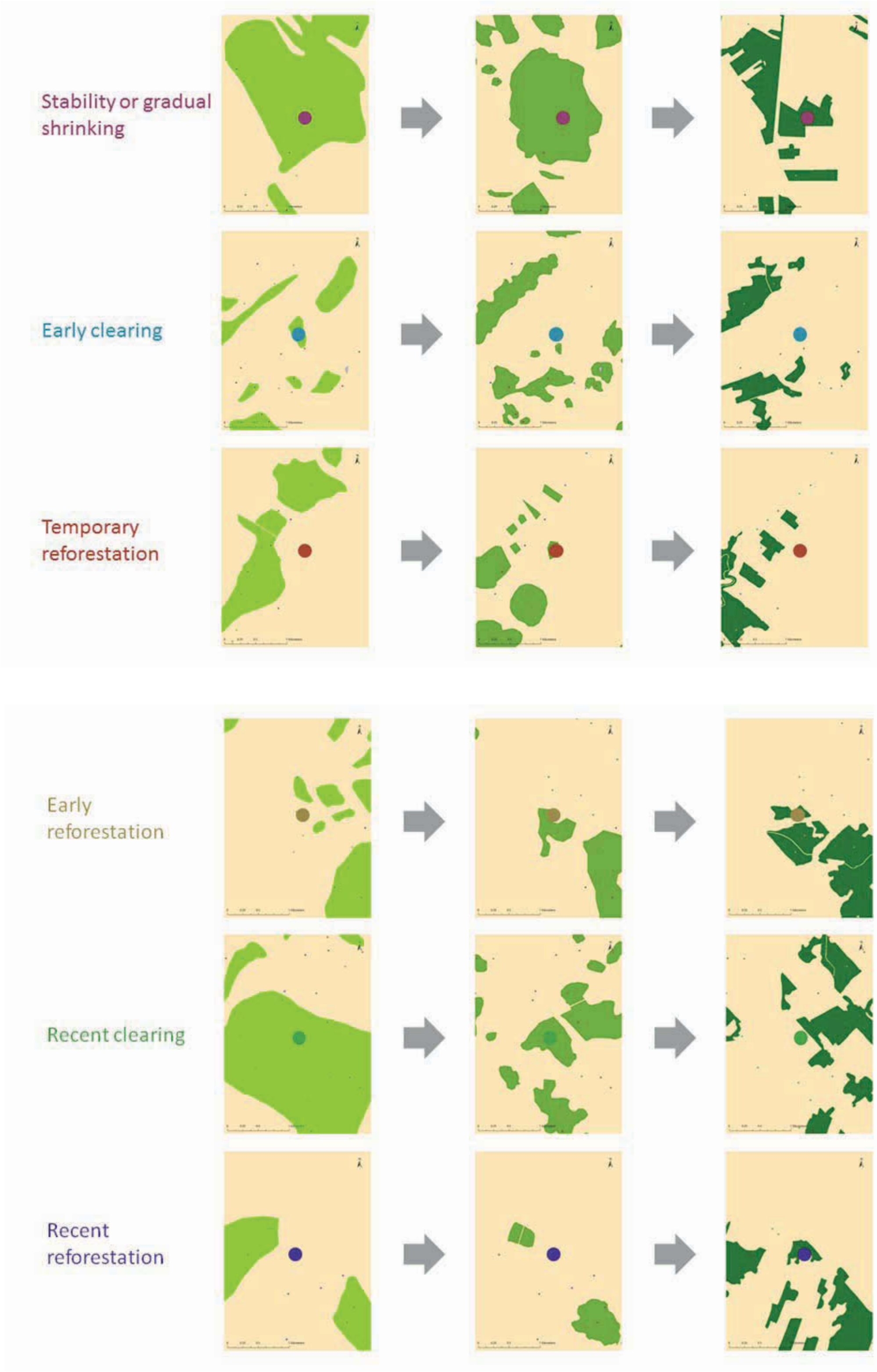

Figure 9: Examples of the six forest patch change trajectories created with Affinity Propagation algorithm.

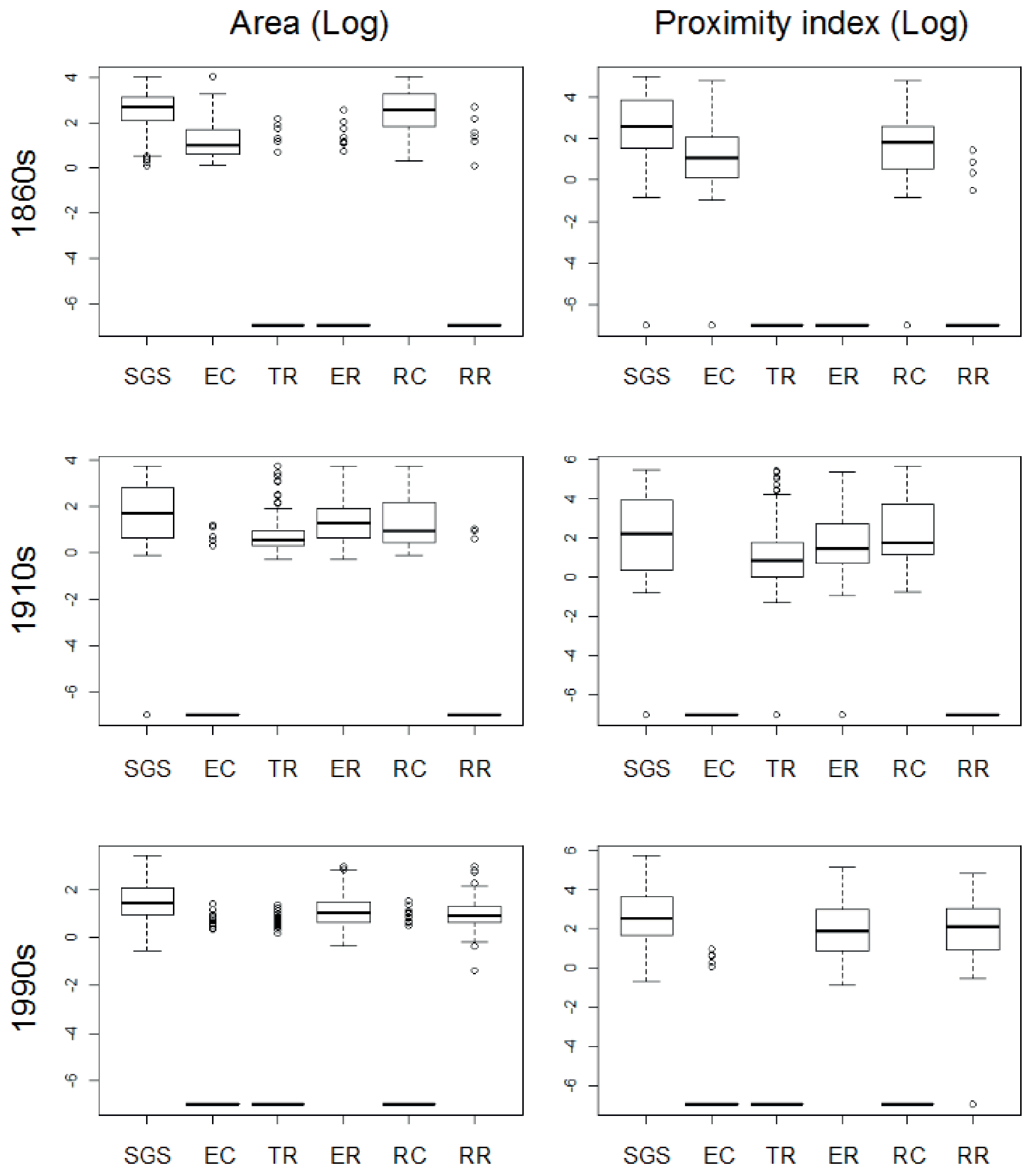

Figure 10: Boxplots showing the distribution of points in forest patch change trajectories according to log [area] and log [proximity index] of the forest patches they pertain to. SGS: Stability or Gradual Shrinking; EC: Early Clearing; TR: Temporary Reforestation; ER: Early Reforestation; RC: Recent Clearing; RR: Recent Reforestation. Units on the Y axis are the values of each clustering variable (Area (Log) and Proximity Index (Log)) for the six different cluster.

3.2. Changes in species composition and richness

During summer 2011, I sampled a total of 177 species, including 117 herbaceous species, 28 shrub species and 32 tree species (sapling, seedling, and tree). 72(41%) are anemochores, 56(32%) endozoochores, 12(7%) epizoochores, 12(7%) of unknown dispersal vector, 9(5%) barrochores, 7(4%) myrmerochores, 7(4%) ballistichores, and 2(1%) hydrozoochores. In terms of habitat preference, 96(54%) species are characteristic of forest habitat, 74(42%) are open-habitat species, and the habitat preference for 7(4%) species is undefined. Including all life-forms, 13(6%) species occupy more than 38(70%) study sites, 27(12%) species occupy 26 and more (50%) study sites, 106(48%) species occupy less than 6(10%) study sites, and 58(26%) species occupy less than 3(5%) study sites. The most common species (more than 70% of study sites) are *Athyrium filix-femina, Arisaema triphyllum, Dryopteris intermedia, Maianthemum canadense, Carex sp., Acer saccharum* (tree, sapling and seedling), *Fraxinus sp.* (seedling), *Acer rubrum* (tree and seedling), and *Fagus grandifolia* (tree and seedling). The following sections explore the factors correlated with this species composition and richness.

3.2.1. Species composition differs between two forest patch change trajectories

3.2.1.1. Species composition (all strata)

38(73%) study sites have the *Stability or Gradual Shrinking* trajectory, 13(25%) have the *Early reforestation* trajectory*,* and one (2%) has the *Recent reforestation* trajectory. The first two forest patch change trajectories have different species composition. Forest patch change trajectories group study sites on a gradient parallel to Axis 1 in the NMDS using all species data (Figure 11). Sites on the left end of the gradient (Axis 1) pertain to *Early Reforestation* patches while sites on the right end of the gradient represent the trajectory *Stability or Gradual Shrinking*. While the two groups are not significantly different based on the MRPP test, they are distinct based on a Kruskal-Wallis test using stands' NMDS scores on Axis 1 (chi-squared = 8.0157, df = 2, p-value = 0.01817; Kruskal-

Wallis multiple comparisons: observed diff=12.410931, critical diff=11.65711, $p \leq 0.05$) (Figure 12).

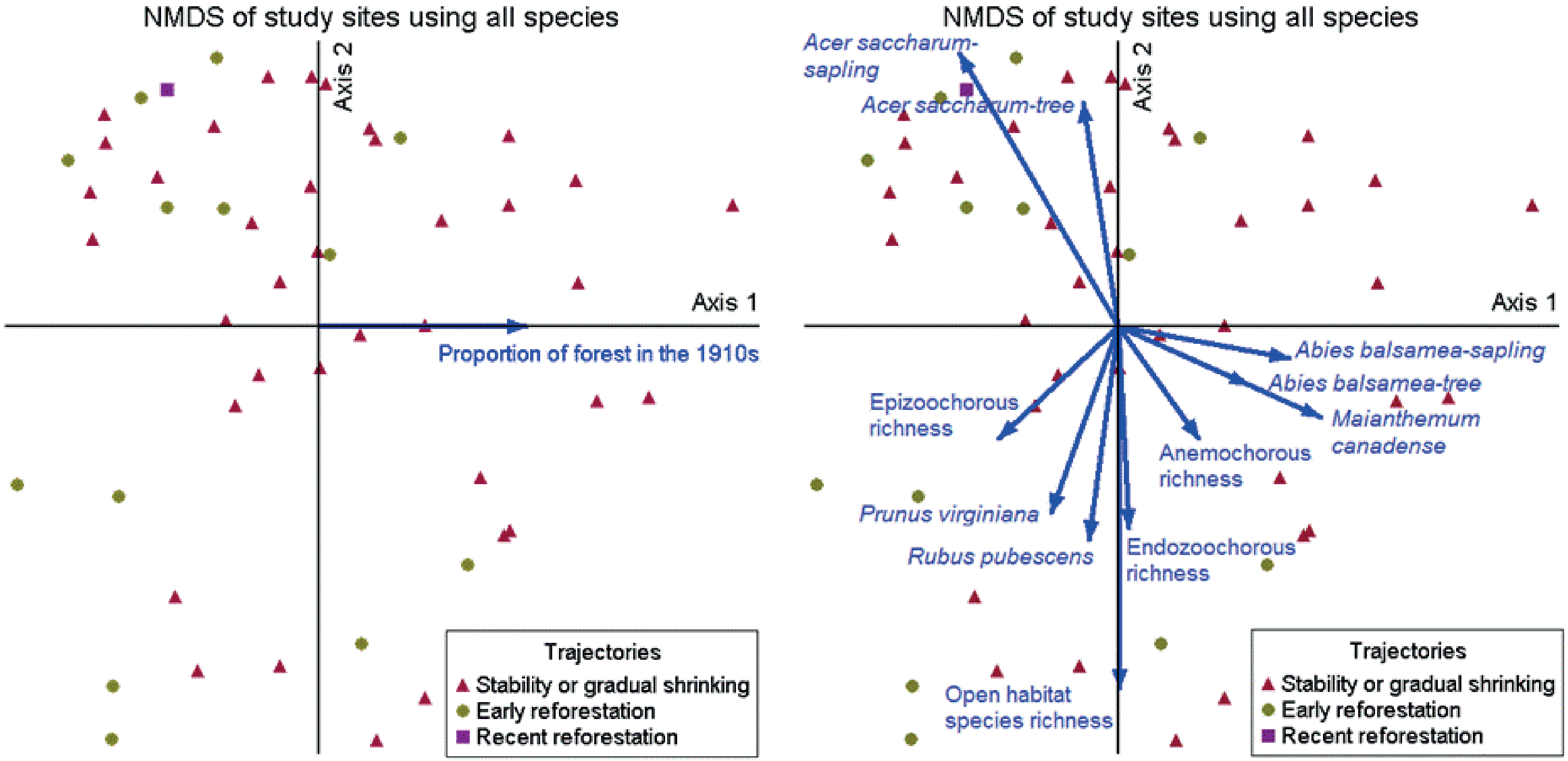

Figure 11: Non-metric Multidimensional Scaling analysis (NMDS) of sample sites based on total species composition. The final solution reached stability after 348 iterations with a final instability of 0.00000 and a stress of 15.09. The proportion of variance represented by each orthogonal axis, based on the r^2 between the distance in the ordination space and the distance in the original space, is 0.201 for Axis 1, 0.142 for Axis 2 and 0.417 for Axis 3 for a cumulative variance of 0.759. The overlays are drawn according to a correlation cut-off of $r^2 = 0.200$. The color and symbols represent the forest patch change trajectory of the stand where the study site was established. The other trajectories (*Early Clearing, Early Reforestation, Temporary Reforestation*) are not included in the graph since study sites pertain to only three different trajectories.

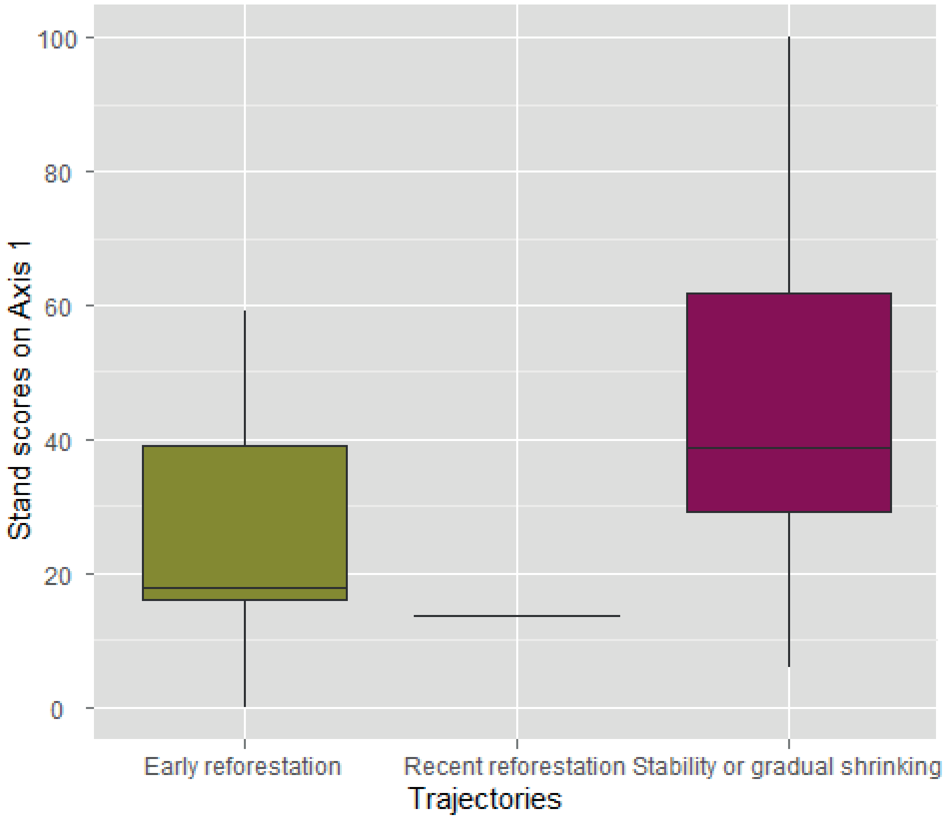

Figure 12: Stand scores on Axis 1 of the NMDS of study sites using all species, grouped by forest patch change trajectories. Kruskal-Wallis test : chi-squared = 8.0157, df = 2, p-value = 0.01817; Kruskal-Wallis multiple comparisons: observed diff= 12.410931, critical diff= 11.65711, p≤0.,05.

3.2.1.2. Endozoochorous species composition

Forest patch change trajectories also group study sites according to their endozoochorous herbaceous species richness. Indeed, *Stability or Gradual Shrinking* patches are richer in herbaceous species dispersed by animal ingestion than *Early Reforestation* patches (Kruskal-Wallis test: chi-squared = 7.1425, df = 2, p-value = 0.02812; multiple comparison post-hoc test: observed diff=12.90385, critical diff=11.65711, $p \leq 0.05$) (Figure 13).

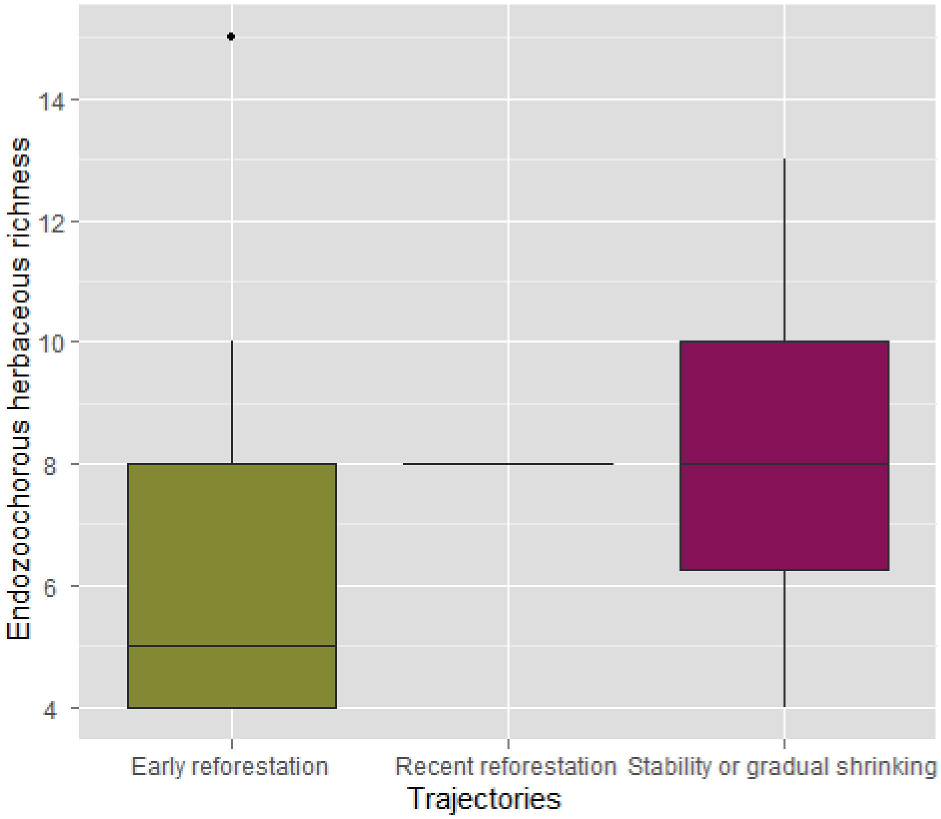

Figure 13: Endozoochorous herbaceous species richness per site, grouped by forest patch change trajectories. Kruskal-Wallis test: chi-squared = 7.1425, df = 2, p-value = 0.02812; Multiple comparison post-hoc test: observed diff= 12.90385, critical diff= 11.65711, $p \leq 0.05$.

3.2.2. Landscape context in the 1910s controls species composition and richness

3.2.2.1. Species composition (all strata)

Non-metric multidimensional scaling analysis suggests that the landscape context in the 1910s within a 200-meter buffer around study sites is the variable that best explains the variation in species composition (r^2=0.318 on Axis 1) among sample plots when considering all taxa (Figure 11) (Appendix IV). Similar but weaker results were obtained when using 500m and 1000m buffers (r^2 of 0.297 and 0.286, respectively). The connectivity of the forest in the 1990s also partly explains the species composition (r^2 = 0.268, 0.211 and 0.229 for 200, 500 and 1000-meter buffers respectively). As for the landscape context in the 1860s, it explains less than 20% of the variation in species composition (r^2=0.122, 0.170 and 0.183 for 200, 500 and 1000-meter buffers). Nevertheless, all landscape context variables influence species composition in the same direction on the same axis (Axis 1).

Several individual species explain a bigger part of the ordination than others, as shown by a greater correlation coefficient against the ordination axes. The gradient created by the past landscape context variables on Axis 1 is correlated with the abundance of five species in a moderate way. *Maianthemum canadense* has the strongest positive correlation with Axis 1 (r^2=0.347), followed by *Abies balsamea* in a sapling form (r^2=0.284) and in a tree form (r^2=0.223). *Acer saccharum* in a sapling form is negatively correlated with Axis 1 (r^2=-0.320), and positively correlated with Axis 3 (r^2=0.363).

3.2.2.2. Total species richness

The landscape context in the 1860s, the 1910s and the 1990s within three different buffers (200 meters, 500 meters and 1000 meters) showed a moderate but significant correlation with species richness (Table 6). The best correlation was found for the landscape context in the 1910s in a 200-meter buffer against total species richness (rhô=0.38; p=0.005) followed by herbaceous species richness (rhô=0.37; p=0.01). Thus, the higher the proportion of forest around a study site was in the 1910s, the greater species richness was found on site. A positive correlation with all species and herbaceous species richness was also found when using the landscape context in the 1860s within all buffers. As for herbaceous species only, they were correlated with the landscape context in the 1910s within a 500-meter buffer (rhô=0.29; p=0.04), and the landscape context within a 200-meter buffer in the 1990s (rhô=0.31; p=0.03). When considering species adapted to forest habitat, a moderate positive correlation with past landscape context was also observed meaning that a greater number of forest specialists were found in study sites that had more forest around them in the past.

Table 6: Spearman's rank correlations between past landscape context around sample sites and species richness according to their life-form and habitat preference.

	Species richness											
	Total		**Herb**		**Tree**		**Woody**		**Total forest specialist**		**Herb forest specialist**	
Proportion of forest	rho	p-value	rho	p-value	rho	p-value	rho	p-value	rho	p-value	rho	p-value
1860s-200m	**0,32**	**0,02**	**0,30**	**0,03**	0,10	0,50	0,24	0,09	**0,28**	**0,04**	**0,33**	**0,02**
1860s-500m	**0,35**	**0,01**	**0,36**	**0,01**	0,12	0,39	0,23	0,09	**0,32**	**0,02**	**0,39**	**0,00**
1860s-1000m	**0,29**	**0,03**	**0,31**	**0,02**	0,11	0,42	0,20	0,16	**0,30**	**0,03**	**0,37**	**0,01**
1910s-200m	**0,38**	**0,01**	**0,37**	**0,01**	**0,28**	**0,04**	**0,30**	**0,03**	**0,40**	**0,00**	**0,43**	**0,00**
1910s-500m	0,25	0,07	**0,29**	**0,04**	0,10	0,49	0,14	0,33	0,25	0,07	**0,36**	**0,01**
1910s-1000m	0,11	0,43	0,15	0,30	0,00	1,00	0,05	0,72	0,16	0,27	0,25	0,07
1990s-200m	0,25	0,08	**0,31**	**0,03**	-0,06	0,69	0,11	0,43	**0,32**	**0,02**	**0,40**	**0,00**
1990s-500m	0,14	0,32	0,20	0,15	-0,06	0,67	0,04	0,77	0,23	0,10	**0,35**	**0,01**
1990s-1000m	0,07	0,62	0,14	0,34	-0,06	0,67	-0,01	0,97	0,17	0,22	**0,31**	**0,03**

3.2.2.3. Understory woody species are more affected by past landscape context than herbaceous species

When running an NMDS ordination with understory herbaceous species only, past landscape context variables have a weaker effect on species composition than with all species together (r^2=0.168 with Axis 1 for the landscape context in a 200-meter in the 1910s). However, when adding the shrub species to the herbaceous species matrix, the effect increases (r^2=0.200 for the landscape context in a 200-meter in the 1910s). The sapling species composition is also more influenced by past landscape context variables than that of herbaceous species. A similar result is obtained when ordinating sapling and herbaceous species together (r^2=0.232 for the landscape context in a 200-meter in the 1910s). Finally, when using only all woody species together in the same matrix (shrub, sapling, seedling, tree), the results are similar to those of the total-species ordination (r^2=0.237 for the landscape context in a 200-meter in the 1910s).

3.2.2.4. Epizoochorous species are more represented in historically isolated forests

The richness of epizoochorous species (dispersed by fur adhesion) is negatively correlated with Axis 1 (r^2=-0.128) in the NMDS analysis of study sites using total species (Figure 11). Thus, epizoochorous species tend to be more represented in study sites that were isolated in the past.

This is verified by Spearman's rank correlation: the landscape context in the 1910s within the 200m, the 500m and the 1000m buffers is negatively correlated with all epizoochorous species and herbaceous epizoochorous species (Table 7). Thus, the more isolated a study site was in the 1910s, the more epizoochorous species were inventoried in it.

To be noted is the separation of epizoochorous species and anemochorous (wind-dispersed) species into two significantly different groups (Kruskal-Wallis test: chi-squared = 24.3722, df = 7， p=0.0009798 and Kruskal-Wallis multiple comparison test: observed diff= 74.960670, critical diff=61.36, $p \leq 0.05$) on Axis 1, which is correlated to past landscape context variables.

3.2.2.5. Anemochorous and endozoochorous species are more represented in historically connected forests

While herbaceous species dispersed by wind (anemochorous) follow mostly the gradient on Axis 3 in the NMDS analysis of all species and are weakly correlated with Axis 1 and thus the past landscape context variables (r^2=-0.224 on Axis 3 and r^2=0.164 on Axis 1) (Figure 11), total and herbaceous anemochorous species richness is still correlated with past landscape context variables when using Spearman's rank correlation (Table 7). This test indicates moderate positive correlations between the landscape context within a 200m buffer in the 1910s and all anemochorous taxa (rhô=0.51, p=0.0001) and anemochorous herbaceous species (rhô=0.50, p=0.0002). Other significant correlations were found with the landscape context in the 1860s, the 1910s and the 1990s. Therefore, the more connected a studied forest was in the past, the more wind-dispersed species were found on site.

Species ingested by birds or mammals (endozoochorous) are also positively correlated with past landscape context variables. The landscape context in the 1860s, the 1910s, and the 1990s for some or all buffers are weakly to moderately correlated with both all and herbaceous endozoochorous taxa (Table 7).

Table 7: Spearman's rank correlations between past landscape context around sample sites and species richness according to their dispersal type.

	Species richness									
	Total and herb epizoochorous		**Total anemochorous**		**Herb anemochorous**		**Total endozoochorous**		**Herb endozoochorous**	
Proportion of forest	rho	p-value	rho	p-value	rho	p-value	rho	p-value	rho	p-value
1860s-200m	-0,02	0,89	**0,31**	**0,02**	**0,30**	**0,03**	**0,31**	**0,03**	**0,34**	**0,01**
1860s-500m	-0,06	0,66	**0,35**	**0,01**	**0,38**	**0,01**	**0,35**	**0,01**	**0,42**	**0,00**
1860s-1000m	-0,15	0,29	**0,35**	**0,01**	**0,34**	**0,01**	**0,30**	**0,03**	**0,41**	**0,00**
1910s-200m	**-0,27**	**0,05**	**0,51**	**0,00**	**0,50**	**0,00**	**0,31**	**0,03**	**0,41**	**0,00**
1910s-500m	**-0,30**	**0,03**	**0,36**	**0,01**	**0,43**	**0,00**	0,26	0,07	**0,37**	**0,01**
1910s-1000m	**-0,36**	**0,01**	0,25	0,07	**0,32**	**0,02**	0,13	0,36	0,25	0,07
1990s-200m	-0,03	0,82	**0,27**	**0,05**	0,33	0,02	**0,29**	**0,04**	**0,39**	**0,00**
1990s-500m	-0,11	0,44	0,17	0,22	0,25	0,07	0,23	0,10	**0,38**	**0,01**
1990s-1000m	-0,23	0,10	0,12	0,40	0,21	0,14	0,18	0,20	**0,33**	**0,02**

3.2.3. Past land use does not influence species composition and richness

3.2.3.1. Species composition

Past land use intensity, which is a ranked variable applied as a numerical variable, does not have a strong correlation with Axis 1 in the NMDS of study sites using total species composition (r^2=-0.117), herbaceous species composition (r^2=-0.051), tree species composition (r^2=0.004) or woody species composition (r^2=-0.065).

3.2.3.2. Only species related to particular ecological traits react to past land-use intensity

Weak to moderate Spearman's rank correlations with the past land-use intensity were found when considering species richness according to habitat preference or vector of dispersal (Table 8). The richness of herbaceous species adapted to forest habitat is negatively correlated with past land-use intensity (rhô=-0.30, p=0.03), which means that the richer a study site is in forest herbaceous species, the less likely it was cleared in the past. Like with past landscape context variables, epizoochorous species are positively correlated to the past land-use intensity, as opposed to anemochorous and endozoochorous species, which are negatively correlated. To be noted is the moderate to strong correlation between the past landscape context variables and the past land-use intensity, from rhô =-0.74 (p=5.485e-10) with the landscape context in the 1860s within a 200-meter buffer, to rhô =-0.42 (p=0.002) with the landscape context in the 1990s within a 1000-meter buffer.

Table 8: Spearman's rank correlations between management intensity (intensity of past and present management practices measured as a sum of features present on site like cleaning/removal of dead wood, stumps, trails, ditches, traces of furrows from past plowing, and taps and tubes for maple syrup production), past land-use intensity and species richness according to their life-form, habitat preferences, and dispersal type.

	Species richness											
	Shrub		**Total generalist**		**Herb generalist**		**Herb forest specialist**		**Total anemochorous**		**Herb anemochorous**	
	rho	p-value	rho	p-value	rho	p-value	rho	p-value	rho	p-value	rho	p-value
Management intensity	**-0,29**	**0,04**	**-0,38**	**0,01**	**-0,30**	**0,03**	0,06	0,66	-0,20	0,15	-0,09	0,50
Past land-use intensity	-0,12	0,39	0,06	0,70	-0,01	0,95	**-0,30**	**0,03**	**-0,30**	**0,03**	**-0,29**	**0,04**

3.2.4. The management regime influences tree species composition and species richness related to habitat preference

3.2.4.1. Tree species composition

When analyzing the tree species separately in an NMDS, the model differs from that with all taxa. Past landscape context is no longer a predictor of the variation in tree species composition (r^2 = -0.005 with Axis 1), while the management regime explains 37% of the variation (r^2=0.373) (Figure 14). Two species were found to be driving the gradient on Axis 1. *Acer saccharum* is strongly correlated with Axis 1 (r^2=0.800) while *Acer rubrum*, which is also weakly and negatively correlated with Axis 1 (r^2=-0.200), is mostly correlated to Axis 2 (r^2=0.649). With Spearman's rank correlation, a weaker but significant negative correlation was also found for shrub species richness (rhô=-0.29, p=0.04). Thus, the more managed the forest is, the more *Acer saccharum* and the less *Acer rubrum* and shrub species should be found on site.

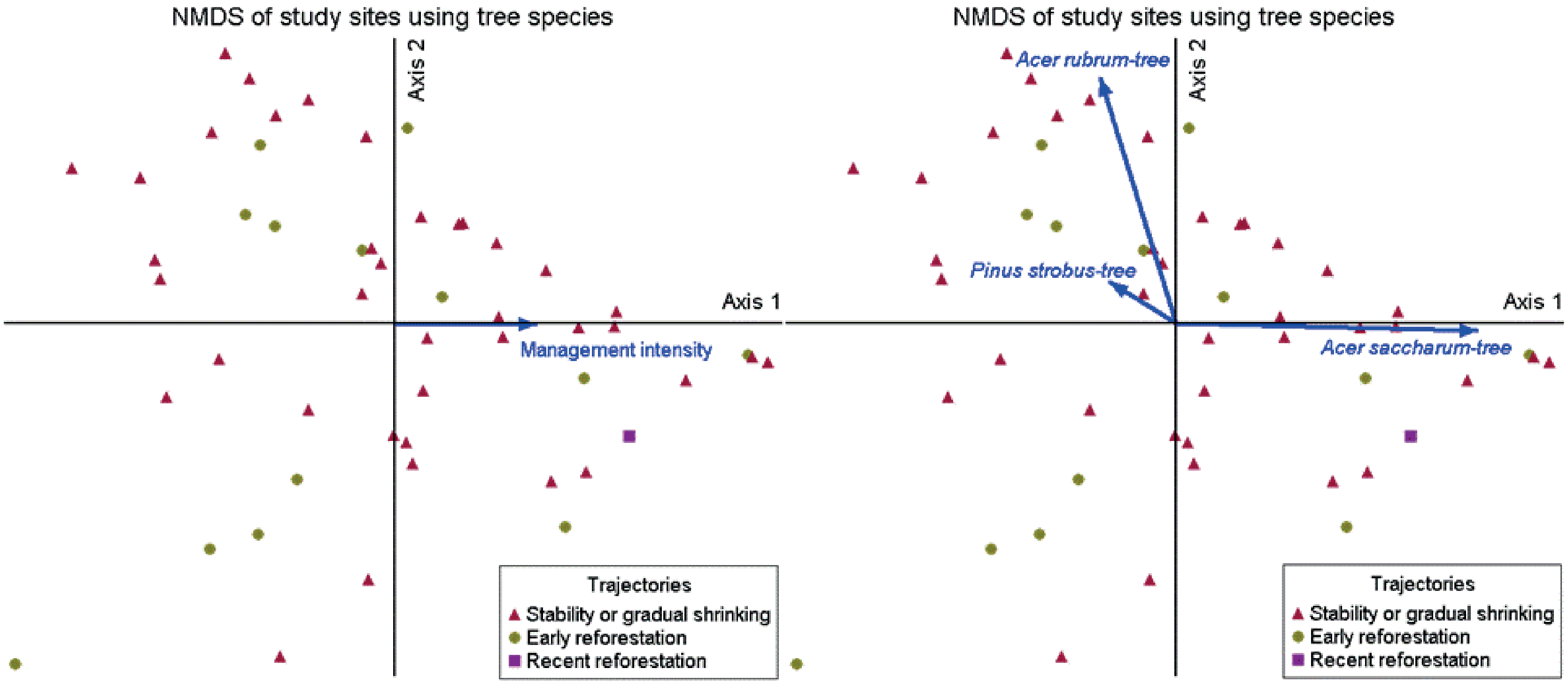

Figure 14: Non-metric Multidimensional Scaling analysis (NMDS) of study sites using only their tree species composition. The final solution reached stability after 395 iterations with a final instability of 0.00000 and a stress of 13.48. The proportion of variance represented by each axis, which are orthogonal, is of 0.314 for Axis 1, 0.287 for Axis 2 and 0.222 for Axis 3 for a cumulative variance of 0.823. The overlays are drawn according to a correlation cut-off of r^2 =0.200. The color and symbols represent the forest patch change trajectory of the patch where the sample sites were located.

3.2.4.2. Species richness according to habitat preference

The richness in generalist species is negatively correlated with the management regime (intensity of past and present management practices measured as a sum of features present on site like cleaning/removal of dead wood, stumps, trails, ditches, traces of furrows from past plowing, and taps and tubes for maple syrup production), be it with total generalist species richness (rhô=-0.38, p=0.005) or herbaceous generalist species richness (rhô=-0.30, p=0.03) (Table 8). Hence, the more intensively managed a forest is, the less open habitat or generalist species are found on site.

3.2.5. Soils, recent surficial deposits, and canopy openness have no effect on species composition and richness

Soil order (brunisolic, gleysolic, podzolic, regosolic) did not group species in distinct clusters (Kruskal-Wallis test: chi-squared = 5.1922, df = 4, p-value = 0.2681) nor did soil drainage (good, imperfect, bad, moderate) (Kruskal-Wallis test: chi-squared = 3.3995, df = 4, p-value = 0.4933). Species composition and richness were not different between recent surficial deposits either, be it at a fine scale (Kruskal-Wallis test: chi-squared = 9.4308, df = 7, p-value = 0.2232 when using fluviatile, marine, morainic, glacial, lacustrine, colluvial, glacio-fluvial, and not defined deposits) or a larger scale (Kruskal-Wallis test: chi-squared = 0.0731, df = 1, p-value = 0.7868 when using clay vs coarse deposits). Finally, canopy cover was not correlated with species composition or richness (Axis 1: r^2=-0.043, Axis 2: r^2=0.006, Axis 3: r^2=-0.106).

The strong gradient observed on Axis 3 of the NMDS with all taxa is not driven by any of these explanatory variables but is rather clearly correlated to open-habitat/generalist species richness (r^2=-0.640 for herbaceous generalists; r^2=-0.614 for total generalists) (Figure 11). Several species are correlated with Axis 3 and follow this gradient of habitat preference. *Acer saccharum* (sapling and tree) have the opposite direction then generalist species while *Rubus pubescens*, *Prunus* *virginiana*, *Carex sp*., *Scutteleria lateriflora* and *Acer rubrum* (tree) lean towards the open habitat end of Axis 3.

Chapter 4. Discussion

4.1. A contrast with northeastern North America

The overall evolution of forest cover at the landscape scale in the study area suggests that forests have decreased in total area and become more fragmented, and that the remaining fragments have decreased in size while increasing in shape complexity.

This pattern contrasts with the general trajectory observed in much of northeastern North America, including elsewhere in the province of Québec, and western Europe, where large-scale deforestation and subsequent land abandonment was followed by extensive forest recovery between the second half of the 19th century and the first half of the 20th century (Bellemare et al. 2002; Foster et al. 1998; Hermy and Verheyen 2007; McKibben 1995). I suggest four hypotheses to explain the differing trend in my study area: climate and soils favouring agriculture, specialization in livestock/grain production, cultural and political factors, and urban spread.

The first possible explanation lies in better abiotic conditions. While less than 2 % of Québec's territory is under agricultural land use today, 80% of agricultural production is concentrated in the St-Lawrence Lowlands ecoregion—and particularly around Montreal (Paul-Limoges 2008). This region also possesses the best soils for agriculture in Québec and the most favourable climatic conditions. Hence, while 8000 km^2 of agricultural lands were abandoned to fallow in Québec by the middle of the 1990s, especially in marginal regions like the Gaspesie, Bas-Saint-Laurent, and Abitibi (Labrecque 1999 in Vouligny and Gariepy 2008), agricultural area along the strip of land adjacent to the St-Lawrence River has been stable or increasing since the 1950s (Ruiz and Domon 2005).

The agricultural sector in Québec, despite the decline observed in marginal regions (section 1.1.), is an important part of the province's economy; within Canada, Québec and Ontario have the highest number of people working in agriculture and food processing (Montminy 2010). Livestock production occupies a large place in Québec's agriculture and provides around 60% of total agricultural income (Ministère de l'Agriculture des Pêcheries et de l'Alimentation du Québec 2012). In the Montérégie, the average number of animals per farm (including pigs, cattle and calves, and chickens) is higher than in the rest of the province, except for dairy cows, and the region produces 33.8% of Québec's total swine production. This region, which is "Québec's garden" (Marois 2007), is also the biggest producer of grain corn and soy in the province (Paul-Limoges 2008). The East-Montérégie alone, where the study area is situated, accounts for 20% of Québec's total agricultural income and 14.7% of the total number of farms (Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec 2005 in Marois 2007). A feedback loop engendering the expansion of cropland at the expense of forest patches can be associated with this production in the province, particularly in the Montérégie. Industrial farms wanting to increase their livestock need to put more land into agriculture in order to dispose of the extra manure produced. The latter is thus used to fertilise high nitrogen-demanding crops, like grain corn and soy (Li et al. 2003; Paul-Limoges 2008). Moreover, these crops constitute the main ingredients used in cattle feeding (Paul-Limoges 2008). As a result, the area attributed to large monocultures, and to a greater extent grain-corn production, has increased noticeably in Québec between 1971 and 2001 (Paul-Limoges 2008). Grain-corn is particularly favoured because of its higher nutritional value, its greater productivity, and above all, its high absorption of fertilizing materials (Paul-Limoges 2008).

Cultural and political factors could also explain the persistent and growing hold of agriculture in this part of the Montérégie. From the second half of the 19th century to the beginning of the 20th century, the Catholic Church, with its nationalist and agricultural ideology that dominated society, especially in rural areas, had a major role in encouraging the spread of agriculture across the land. Two strategies were put forward in order to protect French-Canadian culture (ancestors' heritage, language, religion) against English Protestants from the rest of Canada and the United States: increasing birth rate and controlling the land. The Church also fought against capitalism, urbanization and emigration among other things

(Morisset 1987). Multiple laws dating back to 1818 aimed at promoting, protecting and structuring agriculture in Québec (Glenn 1980). The decline observed in most of Québec's agricultural regions (Ruiz and Domon 2005) and uncontrolled urban spreading (Montminy 2010) after World War II coupled with a stagnation in demand for milk and more expensive grain supplies led to a shift from milk production to grain crops (Domon et al. 1993). This was favoured by the first grain self-supply policy in 1972 (Union des Producteurs Agricoles 1973 in Domon et al. 1993) and strengthened by the René Levesque government, which was elected in 1976 and promoted self-sufficiency in food by helping the agricultural sector financially (Domon et al. 1993; Fréchette 1985; Glenn 1980; Morisset 1987; Paul-Limoges 2008). The government pursued three objectives: increasing drained areas (for rapid snow run-off thus allowing earlier spring sowing to increase the growing season) (Conseil des productions végétales du Québec 1984 in Domon et al.1993), acquiring better grain storage infrastructure, and creating an income stabilization insurance plan. For the two first objectives, subsidy programmes and assistance measures were created by the government to help producers both financially and technically (Domon et al. 1993). The 1978 *Loi sur la protection du territoire agricole* was a turning point in the management of agricultural lands in Québec. This law decreed the application of a special jurisdiction on a delineated agricultural zone. Areas under this new zoning, comprising the St-Lawrence Lowlands, are called *Régions agricoles désignées*, and are subject to a freeze on non-agricultural activities. In other terms it is forbidden, except with a special authorization, to use a plot for any activity other than agriculture or an *érablière* (defined as a stand suitable for maple syrup production) (Glenn 1980). For regions whose main economic activity was agriculture, like around the Richelieu River, this law accelerated the ongoing increase in agricultural areas (Fréchette 1985) like observed indirectly in my results, through the decrease in forest cover and increase in fragmentation between the 1910s and the 1990s. For example, today 86% of the area of the Vallée-du-Richelieu RCM is defined as permanent agricultural zone and this RCM is among those with the biggest number of farms in Québec (Marois 2007;

Montminy 2010). The law, along with technological advances, favoured the expansion and the prosperity of commercial farms over smaller family farms by consolidating their area under cultivation (Fréchette 1985; Montminy 2010; Paul-Limoges 2008). In other words, the government, by means of minimum prices, tariff barriers, quotas, supply management and other measures, favoured the persistence of three particular large-scale productions in Québec: milk, swine, and grain-corn (by association with swine), which are all highly represented in my study area (Paul-Limoges 2008). Both the Catholic Church and the government aimed towards the protection and the valorization of agriculture in Québec, which could have fuelled the ongoing deforestation in the study area (Li et al. 2003).

A law released in 2002, the *Règlement sur les Exploitations Agricoles*, lowered the impact of the 1978 law on agricultural zoning by restricting the increase of lands under cultivation in degraded catchments (modification added in 2004)—like the Richelieu region—mainly to lower phosphorus run-off in rivers (Éditeur officiel du Québec 2012). This new law protects forest woodlots to a certain extent only, since they can still be cleared for other purposes. One of these purposes is residential construction. More recently, urban spread is another threat to the forest (Li et al. 2003) and arises in several municipalities in the study area that are within the Montreal Census Metropolitan Region (CMA) like Beloeil, Sainte-Julie, Saint-Amable, Saint-Basile-le-Grand, and to a lesser extent, Saint-Mathieu-de-Beloeil and Otterburn Park. Outside the CMA, Saint-Jean-sur-Richelieu is also subject to the phenomenon (Figure 1). Urban spread occurring in these municipalities have been assessed by measuring the total area of agricultural land subject to a dezoning request for residential purposes (Montminy 2010). Moreover, even if Regional County Municipalities (RCM) administrations set goals to protect and sustainably manage the forest, municipalities still hold regulatory power on their territory (Rouffignat 1995 in Montminy 2010). For instance, in order to increase the total property tax, which is a municipality's main income, municipalities compete to attract industries and businesses in their territory, thus increasing urban spread (Montminy 2010). Before 2002, agriculture was the main threat to the forest, whereas the un-zoning for urban development has prevailed since 2002 (personal communication, Stephanos Bitzakidis, MDDEFP, 2012). However, the un-zoning and urban expansion were likely also happening in the 1990s (Li et al. 2003). This is observed in my results when looking at forest patch change trajectories (section 3.2.1.).

Few North American landscapes east of the Corn Belt (Hart 1986) show the same overall change in forest cover towards increasing fragmentation as does my study area. Two exceptions, though at a finer scale (30 and 41 km^2, respectively), are the case of Wellesley Township in southern Ontario and Huntington County in the Haut St-Laurent RCM. With fine-textured soils similar to those of my study area, the Wellesley Township has a history of early colonization and a strong and persistent agricultural tradition. The number of forest fragments, forming 18% of the landscape, slightly increased from the 1930s to the 1970s while mean patch size decreased (Moss and Davis 1994). In southwestern Québec, Domon al. (1993) showed that from 1979 to 1987 in the Huntington County, the remaining cultivated area—after a phase of general farm abandonment on morainic deposits—kept expanding at the expense of woodlands. My study area is thus one of the only large-scale (2000 km^2) landscapes in northeastern North America that has been cleared in the 19th and 20th centuries and has not yet experienced agricultural land abandonment. Unlike in other regions of Québec, like Gaspésie, Côte-Nord, Saguenay-Lac-Saint-Jean, Charlevoix, the backcountry of Bas-Saint-Laurent and Chaudière-Appalaches, Laurentides, Outaouais, Abitibi-Témiscamingue, Estrie and the south of Centre-du-Québec (Labrecque 1999 in Vouligny and Geriepy 2008; Ruiz and Domon 2005) and in the United States, like New Hampshire, Vermont, Connecticut, Rhôde Island (McKibben 1995), Massachusetts (Bellemare et al. 2002), New York (Flinn and Honnay 2004; Glitzenstein et al. 1990), and Wisconsin (Rhemtulla et al. 2009), my study area does not follow the forest transition theory expected in developed countries. This stipulates that an extensive forest recovery took place in these countries after people moved to cities and abandoned lands not suitable for modern agriculture (Mather 1992).

While the overall pattern of forest cover evolution at the landscape scale in my study area reflects the reality, some cautions should be applied. First, as the methods for making the 1860s maps are unknown, the threshold used by authors to delineate woodlots could have been more conservative than that used in the 1910s and the 1990s maps. Thus, the 95% increase in the number of patches from the 1860s to the 1990s is likely overestimated. In terms of the increase in the average patch complexity, an overestimation is again conceivable. Indeed, the contour of a patch is function of its actual shape, but also of the map's resolution. For the 1860s and the 1910s maps, smooth contours may result from a patch shape closer to a square and/or the author's choice to simplify feature's shape. For the 1990s maps, irregular contours are more likely to resemble reality because the representation of forest cover is the maps' main objective. Despite over or underestimation of some metrics' values, it is likely that my study area has undergone a gradual decrease in forest cover and increase in fragmentation from the 1860s to the 1990s. Moreover, given the already low forest cover in the 1860s (around 30%) and the suitability of the landscape for forest, this trend probably started before the 1860s.

The habitat loss and fragmentation in the study area can have multiple ecological consequences. First, as forest cover decreases, the extinction rate of species increases. With only 18% of the landscape covered by forest in the 1990s—and a smaller percentage of ancient forest—we can expect an abrupt decline in patch occupancy of herb species; moreover, it could take centuries for slow colonizers to reach equilibrium (Vellend 2003) (section 1.4.). Several studies have concluded that species survival is more likely ensured when its breeding habitat covers more than 20%-30% of the landscape, no matter the level of fragmentation. Below this level, fragmentation effects on species extinction probability is expected (reviewed in Fahrig 1997 and 2003). Habitat loss affects species richness and genetic diversity, and population abundance, distribution and growth rate (reviewed in Fahrig 2003) among others. As for fragmentation, its effects on biodiversity are usually weaker than those from habitat loss when the latter is held constant (Fahrig 2003). A negative effect of fragmentation per se is due to a growing number of increasingly smaller patches, as observed in the study area, which results in the incapacity of small habitats to sustain local populations of species that are not able to colonize neighbouring patches (Fahrig 2003). Moreover, agricultural landscapes can be hostile for animals like birds, which are seed dispersers, as natural habitat disappears in favour of fields and edge environments where species are more vulnerable to predators and their movements are constrained (Bélisle et al. 2001). Other negative effects would result from the isolation of habitat remnants, their shape and the structure of the surrounding matrix habitat (Ewers and Didham 2006; Kupfer et al. 2006). Recent studies warn that the matrix should be analyzed as much as the habitat remnants because, despite the parallel with the island biogeography theory, the matrix is not a homogenous barrier to species and includes gradients of suitability for species dispersal or habitat (Kupfer et al. 2006; Laurance 2008).

4.2. Drivers of six local trajectories

The trajectories of *Early Clearing*, *Temporary Clearing* and *Early Reforestation* all reflect the first round of massive deforestation that occurred in the study area from French colonization in the 18th century to the beginning of the 1920s, the period of maximal agricultural cover (Latendresse 2008). Indeed, when Europeans settled the St-Lawrence valley, they started by clearing large areas of forest to create as much cropland as they could (Drushka 2003). They cut the best trees for construction uses and burned the rest to sow diverse crops like wheat, oat, barley and turnip (Coates 2003; Paul-Limoges 2008). Wood was also used for fences and fuel (Drushka 2003). A good example of the large scale deforestation is a report from Gédéon de Catalogne in the first half of the 18th century where he notes that the St-Lawrence north shore in the Batiscan Seignory was totally devoid of trees (Coates 2003). Another account from a German officer in Batiscan and Saint-Anne Seignories in 1776 and 1777 reveals the bare aspect of the landscape, deploring the methods of colonists who would burn every tree to exploit arable land, including around their houses, gradually moving the forest line further back in the land (Coates 2003) where sites were less suitable for agriculture (Drushka

2003). In fact, forest had little value and was even feared by colonists because of wild livestock predators and Iroquois attacks (Drushka 2003). Both the 1860s and the 1910s are comprised in that period of massive deforestation for extensive agriculture. In the case of forest patches with the *Early Clearing* trajectory, which are concentrated along the Richelieu River and Longueuil, the hypothesis of extensification of agriculture with the elimination of small woodlots and the creation of vast cleared lands in the 1910s is confirmed. The same scenario is applied also for the 1860s, with the *Temporary Reforestation* and *Early Reforestation* trajectories, since forest patches of these trajectories were cleared in this period. Forest patches with a *Temporary Reforestation* trajectory are concentrated around the monteregian hills, meaning that in the 1860s, forest was cleared even on lands having a slope, likely for pastures.

The *Temporary Reforestation* happening in the 1910s (and followed by re-clearing by the 1990s) can either be a real trend or an artefact due to biases in the historical data sources as explained in section 4.1. Forest patches with this trajectory and concentrated around Mt Saint-Hilaire might have been subsequently cleared because of residential development around the mountain (Mt Saint-Hilaire and Otterburn Park). The same explanation stands for the presence of patches with a *Temporary Reforestation* trajectory in Longueuil.

The trajectory of *Stability or Gradual Shrinking* includes the biggest and the most connected forest patches in the landscape in the 1860s, 1910s, and 1990s. Patches with this trajectory are mostly situated on post glacial alluvial deposits from the Champlain Sea beaches, like the boisé du Fer-à-cheval, and ice contact sand and gravel, till, and veneer on the monteregian hills (Earth Sciences Information Centre 2010). Those deposits were likely not suitable for agriculture, even during the period of extensification in the 1860s and the 1910s. Moreover, some patches are situated on wetlands (mostly marshes, sometimes wooded bogs) (Canards Illimités Canada 2007), like the southwestern or very northwestern parts of the study area, and have thus always likely been rejected for agriculture. However, one big patch of *Stability and Gradual Shrinking* trajectory in the southwest of the study area was greatly fragmented in the 1910s, likely for pasture establishment, before growing back in the 1990s. This can result from the fact that yields would be too low for the cost of making this wetland cultivable today. (Domon et al. 1993).

The two trajectories that reflect recent changes occurring in the 1990s'—*Recent Reforestation* and *Recent Clearing*—result from two different phenomena. *Recent Reforestation* patches are mostly concentrated on the edge of the city of Longueuil. Lands in this area are mostly wetlands and are forested likely because they are not suitable for modern agriculture or their cultivation would not be cost effective (Domon et al. 1993). Once reforested, they became protected by clause 22 of the *Loi sur la Qualité de l'Environnement of the MDDEFP* which was passed in 1993 and stipulates that any development in a wetland requires authorization (Ministère du Développement durable 2012b). *Recent clearing* patches are mostly concentrated in the middle of the boisé du Fer-à-cheval forest. This horseshoe-shaped forest patch is linked to the creation of the municipality of Saint-Amable. In the 1910s, about 75 families were scattered on this territory. The parish of Saint-Amable was then officialised in the *Gazette officielle du Québec* in 1921 (Gazette officielle du Québec 1921). Some forest fragmentation already appearing in the 1910s map in this area was likely the consequence of this settlement. The drastic decrease in size and the fragmentation in small woodlots only occur on the 1990s map, likely due to the expansion of Saint-Amable and the creation of new agricultural lands on sand deposits for potato production (MRC de Marguerite-D'Youville 2010).

An important ecological consequence of habitat fragmentation on natural ecosystems is the nonrandom distribution of those forest patches. In fact, habitat remnants are found in areas usually not suitable for agriculture and thus correspond to lands with steep slope, poor soils, at higher elevations or partially inundated. Their species composition is therefore different from that of the lost habitats (Cogbill et al. 2002; D'Orangeville et al. 2011; Flinn and Vellend 2005; Laurance 2008). Indeed, an interview conducted in a 41km^2 County in Haut-

Saint-Laurent RCM, southwestern Québec, indicated that woodlots remaining in the landscape were considered as residual farmlands. Almost half of landowners interviewed said that the first reason why they kept their woodland was because the soil underneath was not suitable for cultivation whereas over a third mentioned that yields would be too low for the cost of putting this land in crops (Domon et al. 1993). In my study area, this spatial pattern of woodlots is also observed, but only for the large forest patches, like the boisé du Fer-à-cheval, the monteregian hills or the northeast of the study area. Their location broadly corresponds to the limits of post glacial alluvial deposits from the Champlain Sea beaches and the ice contact sand and gravel, till, and veneer deposited on the monteregian hills (Earth Sciences Information Centre 2010), and podzolic soils (Ministère de l'Agriculture des Pêcheries et de l'Alimentation du Québec 1998-2006). However, given the elongated shape of these forest patches (except the monteregian hills), parallel to the Richelieu River and colonial roads, their distribution on the landscape is also attributed to the seigniorial system (woodlots were left at the back ends of each rectangular lots). Since alluvial deposits also follow the course of the river, it is hard to establish which factor—physical or historical—better explains the spatial distribution of these large forest patches. However, the seigniorial system is likely the only variable underlying the spatial configuration of smaller forest fragments in this landscape.

4.3. Past landscape context has the strongest correlation to species richness

Results suggest that past landscape context, especially in the 1910s, influences both species composition and species richness. Past landscape context variables form one (Axis 1) of the two main gradients that ordinate study sites according to their total species composition in the NMDS.

The best correlation with Axis 1 was found for landscape context around study sites in the 1910s, within a 200m buffer. Similar results were found in the northeastern Netherlands where of the three buffers used to measure the area of forest habitat around study sites at time of abandonment (100m, 500m, and

1000m), the 100m buffer was the one under which most effects with different species richness measures were found. Moreover, species occurrence largely increased when the amount of forest habitat within this buffer increased (Grashof-Bokdam 1997). It has also been shown that annual plant species are unable to colonize suitable sites more than 100m away from a woodland (Primack and Miao 1992) and 200m for isolation-sensitive forest species (Butaye et al. 2001). My results show that correlations with Axis 1 also exist for the landscape context within 500 and 1000m buffer around study sites though they are weaker than the 200m buffer. This can be explained by the non-independence of the three variables, given that bigger buffers include the value of the smaller buffers.

It could be hypothesized that the area of a patch would better explain the species composition and richness of a site than its connectivity to neighbouring forest. For instance, in a landscape in the northeastern Netherlands, area had more frequent and higher significance than connectivity (measured as the amount of forest habitat around each studied woodlot at the time of abandonment, within 100, 500, and 100m buffers) in affecting species richness (Grashof-Bokdam 1997). However, connectivity was significant when authors considered the occurrence of ten individual species, a result also obtained by Ouborg (1993). Simberloff and Gotelli (1984) found that multiple small natural habitats, even after 80 to 100 years of isolation, contained more species that one big natural habitat of the same cumulative area, which contradicts the species-area relationship theory postulating that large areas would contain more species than small ones (reviewed in Connor and McCoy 1979). Moreover, when area matters, it is explained by a higher likelihood that a larger patch contains greater habitat diversity, and thus this heterogeneity engenders greater plant diversity (van Ruremonde and Kalkhoven 1991). In this study, since I consider the amount of forest within 200m, 500m, and 1000m buffers around study sites (triangular shape formed by three sampled plots in a forest stand), both the area of the stand and that of its surroundings are included. Hence, the bias linked to using only the area or the connectivity is removed.

Since gradients are created by species cover/density data, we expect a certain set of species to have more influence than others. *Maianthemum canadense,* which is the species most correlated with study sites that were more connected in the 1910s (r^2=0.347 with Axis 1), is characteristic of moist woods (Gleason and Cronquist 1963; Singleton et al. 2001) and is dispersed by mammal or bird ingestion (endozoochore) (Brown and Boutin 2009). *Abies balsamea*, a late successional species common in moist woods and swamps (Gleason and Cronquist 1963) and wind dispersed (Gachet et al. 2007), is also one of the taxa leading this gradient, both in its sapling (r^2=0.284) and tree form (r^2=0.223). *Maianthemum canadense* is a common forest species and a rapid colonizer that can be very abundant in post-agricultural forests (Singleton et al. 2001; Vellend 2003) so its greater abundance in highly connected study site in the 1910s is not explained by a dispersal limitation. However another study focusing on the effect of overstorey composition and age on common understorey species revealed that *Maianthemum canadense* demonstrated an association with secondary conifer (white-pine stands) forests (Whitney and Foster 1988). In my study, six sites had *Pinus strobus* individuals, though only four of them had more than 70% forest proportion within a 200m buffer around them in the 1910s. The occurrence of the other coniferous species (*Picea rubens, Tsuga Canadensis, Abies balsamea*) is not correlated with past surrounding forest proportion. *Abies balsamea* however, might have a dispersal limitation as its large seeds tend to disperse closer to the parent trees than other coniferous species like *Picea glauca* or *Thuja occidentalis* (Asselin et al. 2001), with a mean seed dispersal distance from 25-60m (Frank 1990) and as much as 115m (Asselin et al. 2001). *Abies balsamea* is most common on cool, wet-mesic sites, and on strongly to moderately acid soils. On poorly drained clay soils, like on most of the study area, this species can thus be a climax type (Johnston 1986).

Rare species (present in less than 5% of study sites (McCune and Grace 2002)) are also more likely to be found on sites that had a high proportion of forest around them in the 1910s. For example, the threatened species *Panax quinquefolius* was found in one of my sample sites which had 100% forest cover within a 200m buffer around it. Two tree species likely of being designated as Threatened or Vulnerable, *Carya ovata* and *Juglans cinerea*, were found in sites with a large range of surrounding proportion of forest and in secondary stands (presence of furrows) though their dispersal limitation in fragmented landscapes has been shown elsewhere (Hanson et al. 1990; Hewitt and Kellman 2002). Six other species are classified as Vulnerable to Harvesting and were found in one or more study sites, often among the more connected ones: *Matteuccia struthiopteris*, *Sanguinaria Canadensis*, *Uvularia grandiflora*, *Cardamine diphylla*, *Asarum canadense*, *Adiantum pedatum* (Ministère du Développement durable 2012a). The first one is threatened by harvesting only while the five others, whose survival is not jeopardized at the moment, become rarer as their natural habitat, consisting of rich humid sugar maple stands of southern Québec, is degraded or destroyed.

One reason why forests that were more connected in the past have a different species composition and higher species richness today might result from the tradeoff between immigration and extinction of species, the core of metapopulation theory (Gilpin and Hanski 1991; Vellend 2004a). While immigration is mostly affected by isolation, extinction is likely more dependent on area (Jacquemyn et al. 2003). It is important to mention that few species react to both isolation and area, but more likely to one or the other (Grashof-Bokdam 1997; Ouborg 1993). The balance between immigration and extinction and the resulting supersaturation vs relaxation (removal) of species could explain why, in our study area, ancient forests that were isolated for decades contain less species than recently fragmented ancient forest patches of the same area that likely have not yet experienced local extinction of species (Peterken and Game 1984). The latter authors' results did not verify these conclusions though they found that recent woods that were adjacent to ancient woods at some point in the past were richer than recent woods that have been isolated from ancient woods by at least 10m of non-forest habitat since before 1820.

Although several studies have confirmed the effect of isolation (past and/or recent) on species richness and composition in secondary forest patches (Bossuyt et al. 1999; Butaye et al. 2001; Dzwonko 1993; Grashof-Bokdam 1997; Grashof-Bokdam and Geertsema 1998; Scanlan 1981; Vellend 2003; Verheyen and Hermy 2001), few studies have considered ancient forests fragments, like 35 of my study sites (forested since the 1860s), to address that issue. Three studies though can be compared to my study because they identified ancient (or of unknown history) forest remnants with different degrees of past isolation. Islands of forest created artificially by the filling of a reservoir in 1954 on the Savannah River were sampled in 1991 to assess if distance to the mainland affected woody species richness and composition. Some islands were logged prior to the creation of the reservoir and their woody species richness was found to be negatively correlated with distance from the mainland whereas previously unlogged islands didn't show any correlation between the two variables (Kadmon and Pulliam 1993). The degree of isolation of unlogged islands did, however, affect woody species composition, which was poorer in species dispersed over short distances (Kadmon and Pulliam 1995). This study thus confirms the imbalance between local extinction and immigration that occurs in ancient forest fragments when they become isolated. Further empirical evidence of this phenomenon was found in the western Carpathian foothills. Dzwonko and Loster (1988) compared two series of remnant forest patches with different histories: the first continuously isolated (measured as the area of adjacent forest) from before 1845 until 1986 and highly disturbed by humans, and the second more connected in 1845 than in 1986 and less disturbed than the first group. Results showed that the first group contained fewer species than the second one even though its soils were richer, likely due to the local extinction of species not replaced by new colonizers. One last study yielding results similar to ours found lower current woody species richness in forest fragments more isolated (distance to the closest mainland) and having less forest within 500m around them in 1941 than other forest fragments. Although these fragments did not originate from old agricultural fields, they can't be considered as ancient or primary per se because they were logged and burned in the late 19th century (McEuen and Curran 2006). Other habitat fragments like semi-natural grasslands also demonstrated an extinction debt after their connectivity decreased (Helm et al. 2006; Lindborg and Eriksson 2004). Other studies on the other hand have found no effects of isolation on species richness (Mikk and Mander 1995).

4.4. Past land use is not strongly correlated with plant species composition and richness

The forest patch change trajectory of study sites revealed a different composition between *Early Reforestation* patches (the left end of Axis 1) and *Stability or Gradual Shrinking* patches (right end of Axis 1). Hence, this could suggest an influence of past land-use on today's species composition since the *Early Reforestation* trajectory represents sites that were cleared in the 1860s and the *Stability or Gradual Shrinking* trajectory includes forest patches that have never been cleared since this date. A similar result is obtained when land use in the 1860s' is used as a binary variable (cleared vs not cleared; results not shown), which suggests that the result in fact would reflect a dichotomy between younger forest and older forest. However, all studied stands are more than 75 years old according to the 1990s forestry map (Ministère des Ressources naturelles et de la Faune 2003) and there is no significant relationship between the forest patch change trajectory and the stand's age structure (even-aged vs uneven-aged) (results not shown). Moreover, when looking at the DBH distribution of tree species, 12 out of 13 study sites included in *Early Reforestation* forest patches have trees with a DBH greater than 40cm which would likely indicate older trees. For sites included in *Stability or Gradual Shrinking* forest patches, 31 out of 38 also contain trees over that DBH. Likewise, the two trajectories do not differ according to the average DBH of a site (and average relative basal area) (results not shown). Hence, both trajectories represent forests of similar age, likely due to complete or partial clearing of primary forest in *Stability or Gradual Shrinking* patches.

Past land-use intensity was negatively correlated with herbaceous species adapted to forest habitat (rhô=-0.30, p=0.03), which means the longer a stand was cleared, the fewer forest herb species are found today. This is consistent with results obtained from studies looking at past land use in northeastern North America and Europe. Forest interior species are poor colonizers and are adapted to stable ecosystems with natural small-scale disturbance typical of primary or ancient forest (Bellemare et al. 2002; Dupouey et al. 2002; Peterken and Game 1984; Singleton et al. 2001) so either a dispersal or a recruitment limitation—or even both—limit the presence of forest herb species in recent or secondary forests (Verheyen and Hermy 2001). Ancient forests in my study are not different from recent forest in terms of management intensity (results not shown) though the fact that ancient forest have not been entirely cleared in the past make their ecosystem more stable than recent forest. Depending on the nature of the past land use, the presence/absence and the abundance of typical forest species in secondary forests is variable (Wulf 2004). In my study, endozoochorous and anemochorous species are negatively correlated whereas epizoochorous species are positively correlated with past land-use intensity. This result resembles that obtained with forest patch change trajectories (*Early Reforestation* patches have fewer species dispersed by animal ingestion than patches with the *Stability or Gradual Shrinking* trajectory) and especially with past landscape context variables (section 4.3.). Interestingly, past land-use intensity and all past landscape context variables are moderately to strongly correlated (ex. rhô =-0.63, p=`5.576e-07` with the landscape context in the 1910s within a 200-meter buffer). This could be partly explained by the inclusion of the area of the forest patch in which study sites are situated in the calculation of surrounding forest proportion. However, results of the NMDS are not affected by the removal of the 20 sites having been entirely or almost entirely cleared in the past (past land-use intensity rank: 4 to 7) (Table 4) (results not shown). Hence, I conclude that because previously partially or totally cleared stands were also often isolated in the past, results showing an effect of past land-use on species composition and richness should be attributed to species' dispersal capacity depending on landscape context rather than to site limitations due to past land use.

This could also mean that the effects of past land-use on species composition and richness are weaker than those of past landscape context in my study area. Though several studies have reported that species richness is greater in ancient forest than recent forests no matter the age of the latter (Dzwonko and Loster 1992; Flinn and Vellend 2005; Hermy and Verheyen 2007; Peterken and Game 1984; Vellend 2004a), Bellemare et al. (2002) showed that recent forests older than 60 years old have similar forest herb species richness as ancient forests. Moreover, recent forests older than 33 years old (Peterken and Game 1984) and 100 years (Peterken and Game 1984; Scanlan 1981) in England have been found to reach equilibrium between colonization and extinction because their species richness is independent of stand age. Two reasons were suggested to explain that rapid equilibrium: some species were already present on site (former semi-natural habitat or pre-existing hedges) and some woodland species are rapid colonizers. Indeed, hedgerows and ancient parcel margins can contain relict populations of forest species (Corbit et al. 1999; Flinn and Honnay 2004; Fritz and Merriam 1993; Verheyen et al. 2003a), which can survive in these linear habitats providing a low management intensity (Corbit et al. 1999) and certain environmental conditions and low-intensity adjacent land uses (de Blois et al. 2002a; Fritz and Merriam 1996). When a hedge is present in a new wood, 10 or 20 woodland species are likely to be spread from there (Peterken and Game 1984). However, colonization of all species is not complete within a time period of 33 or even 100 years, but it might not affect the total species richness as early colonists gradually become extinct (Peterken and Game 1984). Another hypothesis explaining why past land use is not a good explanatory variable in this study could stem from the type of soil modifications created by past agriculture. In New York, soils were not greatly improved because they were not really suitable for agriculture. As a result, soils from former cultivated or pastured fields are physically and chemically similar to undisturbed soils after 70–100 years (Flinn and Honnay 2004), though the spatial distribution of their nutrients can be homogenized (Fraterrigo et al.

2005). Hence, I suggest that the weak signal from past land use may also be due to its early occurrence—before the 1910s for 17 study sites (only 4 sites were entirely cleared in the 1910s)—reducing the intensity of its legacies on soils.

4.5. Tree species composition is sensitive to management regime

Past landscape context affects species composition and richness more than management regime in the study area. I first explain the extent of the management in this region and mention its unverified or limited impact in other studies. I then explain why it mostly affects tree species composition.

Forests sampled in this study are all private (94% of the monteregian territory is private) and are managed to some extent for small scale production of timber, firewood, and maple syrup (Nature-Action Québec et la Fondation du Mont St-Bruno 2005). Most woodlots are likely not intensively managed. For instance, interviews with landowners conducted in 1987 in the Haut-Saint-Laurent RCM, southwest of the study area, revealed that only 7% of them sold wood products. Moreover, after agricultural reasons, conservation for wildlife and the environment in general was evoked more often than economic reasons like timber production or maple syrup production to explain why they kept their woodlands (Domon et al. 1993).

The effects of management practices can be low compared to past land-use or landscape context. Selective cutting, which occurs in the study area, as well as windstorms have been shown to have a limited impact on ground layer vegetation (reviewed in Bellemare et al. 2002). Moreover, results obtained by Aubin et al. (2007) suggest that understorey species in woodlots of the Haut St-Laurent and Outaouais regions in southern Québec are generally resilient to different types of human disturbance (harvesting by single-tree selection, maple syrup production, abandoned pasture). The effect of management intensity on biodiversity remains unclear (Hermy and Verheyen 2007), unpredictable (Decocq et al. 2004) and can be hard to isolate from other variables. Dzwonko and Loster (1988), comparing two groups of ancient woodlands, found that small ancient woodlands isolated for a longer time and more anthropogenically disturbed (grazing, trampling, rubbish dumping) than woodlands of the other group contain fewer species in total, fewer herbaceous species, tree and shrub dyszoochores (seeds gathered by an animal for its reserves and sometimes forgotten), herb endozoochores, and myrmerochores, but more non-woodland species and flying tree anemochores despite their location on richer soils. However, they did not isolate the effect of each variable—isolation and disturbance—thus we cannot determine the importance of management intensity on species composition and richness.

In the NMDS using study sites with tree species abundance only, the site's management intensity is correlated with Axis 1, which is also correlated to *Acer saccharum* abundance. This can be explained by two reasons: management practices favour the growth of *Acer saccharum* for maple syrup production (for 11 study sites) and this species is relatively resistant to disturbance. Maple syrup producers have typically managed their forests for decades since this production is mostly transferred from generation to generation (Houston et al. 1990). *Acer saccharum* grows well on humid, deep, well-drained and relatively coarse-textured soils (Houston et al. 1990). However, since the traditional management practice is to cut other tree species in order to allow only *Acer saccharum* to grow, creating sugar maple monocultures (Lenière and Houle 2006; Whitney and Upmeyer 2004), the species can be found on sites less suitable like cold and humid lowlands. On such sites, years of management can be perceived by the presence of a canopy dominated by *Acer saccharum* with a regeneration of species more typical to this habitat like *Acer rubrum*, *Fraxinus spp*., *Tilia americana*, or *Abies balsamea* (Houston et al. 1990). Moreover, maple stands are often thinned since trees producing the greatest amount of sugar have the highest and largest crowns (Houston et al. 1990; Messier and Beaudet 1997; Service d'extension en foresterie de l'Est du Québec 1998). Even with such important structural modification, the understorey diversity is sometimes not affected (Aubin et al. 2007). However, composition can also be driving the type of forest management: a natural *Acer saccharum* stand will be favored for maple syrup production. Second, *Acer saccharum*, along with *Acer rubrum*, *Betula populifolia* and *Populus tremuloides*, is relatively resistant to human disturbance. It can indeed persist in woodlot edges adjacent to fields with high-intensity agriculture (cash crops like corn, soy or wheat, pesticides, chemical fertilizers, and annual tillage) when other tree species, like *Carpinus caroliniana*, *Betula alleghaniensis*, *Betula papyrifera*, *Carya cordiformis*, *Fraxinus spp.*, and *Ostrya virginiana* and shrub species like *Amelanchier laevis*, *Aronia melanocarpa*, *Crataegus spp*., *Lonicera spp*., *Prunus spp*., *Ribes spp*., several *Rubus spp*., *Sambucus spp.*, *Vaccinium spp*., and *Viburnum spp*. are either greatly reduced or absent from these ecotones compared to woodlot edges adjacent to a low-intensity cultivated field or pasture (Boutin and Jobin 1998).

The richness in generalist species is also negatively correlated with the management regime as measured by Spearman's rank correlations (with total generalist species richness: rhô=-0.38, p=0.005), which means that the more intensively managed a site is, the fewer generalist species were found. This result is unexpected given that normally, management (especially thinning) locally modifies the environment by, for instance, creating canopy gaps allowing more light to reach the forest floor. Hence early colonizers or generalists, which are light-demanding species and strong competitors, tend to invade these disturbed areas (Decocq et al. 2004; Jamoneau et al. 2011).The unsuspected result obtained in my study can be explained by a coarse estimation of management intensity. This variable was created by grouping different types of management to form one value of intensity. However, each type (cleaning/removal of dead wood; stumps; trails; ditches; traces of furrows from past plowing; and taps and tubes for maple syrup production) can modify local resources' availability at different levels (light, water, soil nutrients). As a result, the effects of management on understorey species can be variable. Aubin et al. (2007) also found that forests managed for maple syrup production had low occurrence of shrub species, yet shrub species in our study area are almost all classified as generalists.

Other hypotheses explaining why management intensity does not affect all species composition in the NMDS can be claimed: study sites have similar management intensity or they all have a generally low level of human disturbance (Brown and Boutin 2009).

4.6. Recent surficial deposits and soils do not influence species patterns

In the Huntington County of the Haut-Saint-Laurent RCM, southwestern Québec, morainic deposits were the first to be cultivated in the first half of the 19th century (Roy et al. 2002). During the last quarter of the 19th century and the beginning of the 20th century, which was the period of agriculture extensification, all deposits were under cultivation. As agriculture specialized on clay soils in the middle of the 20th century, lands on morainic deposits were progressively abandoned thus allowing forest to grow back (Domon and Bouchard 2007).

Hence, if I assume that my study area had the same evolution in terms of deposits allocated to farming at a certain period in time, woodlands left in the landscape are likely on deposits that are less suitable for agriculture. It can equally be that, for each particular owned plot, woodlots were left further away from the farmer's house, at the back end of the rectangular lot (Motzkin et al. 1996).

Since soil data reflect modern conditions, and could have been greatly modified by plowing and sub-soil drainage, results showing that soil order and drainage have no influence on species composition and richness are hardly interpretable.

Another explanation for the non-significant influence of abiotic conditions on plant species composition and richness could also be the lack of accurate site-scale field data or the too large number of categories for each environmental variable.

4.7. Past landscape context affects species dispersal vectors

As in our study, endozoochorous and anemochorous species richness is positively related to forest connectivity (measured as the distance to the surrounding forest patches) in a western Carpathian foothill landscape (Dzwonko and Loster 1988), and for endozoochores only, in southeastern Michigan (McEuen and Curran 2006) and Georgia (Kadmon and Pulliam 1995). Similar results were obtained in the northeastern Netherlands but using past amount of forest habitat around study woodlots within a 100m buffer and animal-dispersed species richness in general (endozoochores, epizoochores, and myrmerochores) (Grashof-Bokdam 1997). However, Kadmon and Pulliam (1995) found an opposite trend for woody anemochores, where wind-dispersed species tend to increase in number when the distance between forest patches increases. This trend was also found for flying tree anemochores by Dzwonko and Loster (1988). A reverse trend was also observed in Spain for animal-dispersed (most of them ingested) tree species: they showed a positive response to deforestation. In fact, animal-dispersed species would be less vulnerable to forest fragmentation than wind-dispersed species since animals actively transport the seeds between suitable habitat, unlike wind, and can then increase their dispersal distance (Montoya et al. 2008). Indeed, endozoochorous species have the longest or the second longest dispersal distance (D’Orangeville et al. 2011; Jacquemyn and Brys 2008; Williams 1982). Another study found no effect of past and present forest connectivity (both proportion of forest and distance within 500m and 100m radii) on endozoochores (van Ruremonde and Kalkhoven 1991). As regards to epizoochorous species, our results suggest that they are more abundant in study sites that were isolated in the past. As for endozoochores, their dispersal distance is long and they are dependent on animal movement, which is less affected by habitat isolation. However, this result is less robust than for endozoochores and anemochores since the number of epizoochorous species is much smaller (endozoochores: 67, anemochores: 107, epizoochores: 11).

The divergent responses obtained in studies that relate dispersal modes (inferred by seed morphology) to colonization ability may be explained by using a misleading proxy to infer real dispersal distances (Butaye et al. 2001; Flinn and Vellend 2005; Vellend et al. 2003). Indeed, anemochorous species should not all be part of the same category but should be divided into light-weighted and heavyweighted wind-dispersed seeds since the latter have lower dispersal distance than the former (Dzwonko and Loster 1992; Grashof-Bokdam 1997). Likewise, animal dispersal is a variable phenomenon and depends greatly on the nature of the matrix in which natural habitats are studied, and on the type of animal (Grivet et al. 2005; Wehncke et al. 2003) and its behavior (Nathan and Muller-Landau 2000). For instance, for a landscape mostly formed by secondary and primary forest patches with some grasslands, bird-dispersed species are not affected by isolation since birds can disperse their seeds on long distances (Dzwonko and Loster 1992). However, when natural habitats are surrounded by agricultural lands, birds that are forest-species dispersers tend to be blocked by this hostile habitat and the dispersal distance can then drop to 100 meters and less (Grashof-Bokdam 1997). It is thus likely that endozoochorous species in my study area, which is dominated by agricultural lands, are affected by isolation.

Chapter 5. Conclusion

My research shows that the evolution of forest cover in the Montérégie in southern Québec is unusual in northeastern North America as it does not follow the forest transition occurring in most developed countries. It is instead characterized by a gradual loss of forest cover and an increase in fragmentation from the 1860s to the 1990s, due to a combination of physical, cultural, political and economic factors characteristic of Québec history.

A novel technique using the Affinity Propagation algorithm allowed me to find six different local trajectories of change based on the size and isolation of forest patches since the 1860s. Trajectories group individual forest patches into clusters with similar characteristics, which helps to explain in more detail the evolution of forest cover in the study area. Trajectories show mostly the general trend observed at the landscape scale, that is progressive deforestation and fragmentation (*Early Clearing*, *Recent Clearing*) though other patches show trajectories of relative stability and local reforestation (*Stability or gradual shrinking, Early Reforestation, Recent Reforestation, Temporary Reforestation*) likely linked to their location on coarse surficial deposits or wetlands that would make them residual agricultural lands. Concentrations of some trajectories were found at the outskirts of Longueuil, around Mt Saint-Hilaire and in the boisé du Fer-à-cheval. They could be explained by the type of deposits, the presence of wetlands, and the creation and spreading of towns. The Forest Patch Change Trajectory analysis is a synthetic way to describe the past land use at a site and is thus used as a categorical variable in statistical analyses.

Stands in the study area today have different species composition and richness, which is correlated with past landscape context—the amount of forest that surrounded study sites in the past—especially in the 1910s, within a 200m radius. Study sites that had a greater amount of forest around them in the past are richer in total, endozoochorous, and anemochorous species, and poorer in epizoochorous species than study sites that were more isolated in the past. Since 35 study sites out of 52 are ancient forest stands (originated before the 1860s), the results cannot only be explained by a dispersal or recruitment limitation during the colonization of old fields. I rather invoke the theory of island biogeography and especially the metapopulation theory to explain the imbalance between local extinction and immigration of species likely occurring in those sites. When a stand was isolated for a long time, the loss of species was not counterbalanced by colonization since neighbouring forest was too far or too small. On the other hand, a forest stand that has always been connected still loses species but they are replaced by colonizers from neighbouring forest so that the number of individuals is sufficient to maintain the population.

Past landscape context around study sites is correlated with past land-use history and thus forest patch change trajectory. Hence, sites that had less forest around them in the past were sometimes also partially or entirely cleared at some point. Sites of the *Early reforestation* trajectory (which have an agricultural land-use history) are thus poorer in species than those of the *Stability or gradual shrinking* trajectory (which have been forested since the 1860s) and their species composition differs. Despite the difference—which is rather due to past landscape context variables, because of this autocorrelation—the signal of past land use on both species composition and richness appears to be weak, perhaps due to the resilience of ecosystems after a clearing with low level of soil disturbance that mostly happened in the 1860s.

Management intensity (defined as the intensity of past and present management practices measured as a sum of features present on site like cleaning/removal of dead wood, stumps, trails, ditches, traces of furrows from past plowing, and taps and tubes for maple syrup production) does not affect understorey species composition in the study sites, but does strongly affect tree species composition, especially the abundance of *Acer saccharum*. The influence of management activities on ecosystems is hard to isolate and measure. In this study, the use of only one variable accounting for the presence of features associated with management practices in the field was likely not the best way to estimate the actual intensity of human disturbance in the forest. Nevertheless, other studies have shown that understorey species are not greatly affected by management, and the forest stands I sampled have almost all the same, relatively low level of management. However, stands managed for maple syrup production are structurally different from other forest stands, which is highlighted in the NMDS analysis. The more managed a forest is (including maple syrup taps on trees), the more individual *Acer saccharum* trees are found on site.

Species composition and richness are not correlated with surficial deposits (clay vs coarse deposits) in my study sites nor with soils' order or drainage. However, further research including accurate field measurements of abiotic variables are needed to verify this statement.

This study brings a new perspective to our understanding of biodiversity changes. Instead of only looking at the environmental conditions and the past land use of a site, I show that historical landscape context is a key determinant in explaining the species composition and richness of a forest stand, even for ancient woodlands. The Forest Patch Change Trajectory analysis is a new tool that I used to combine the past land-use and the evolution of a forest patch into one synthetic variable. It can be used both on its own, to assess landscape change, or as an explanatory variable integrated in another analysis. This research underlines the need to include historical forest cover in determining which forest patches to prioritize for conservation. This study also supports the ongoing establishment of ecological corridors so that patches having corridors connecting them to other forests today are likely to be richer in species in the future.

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Appendix I

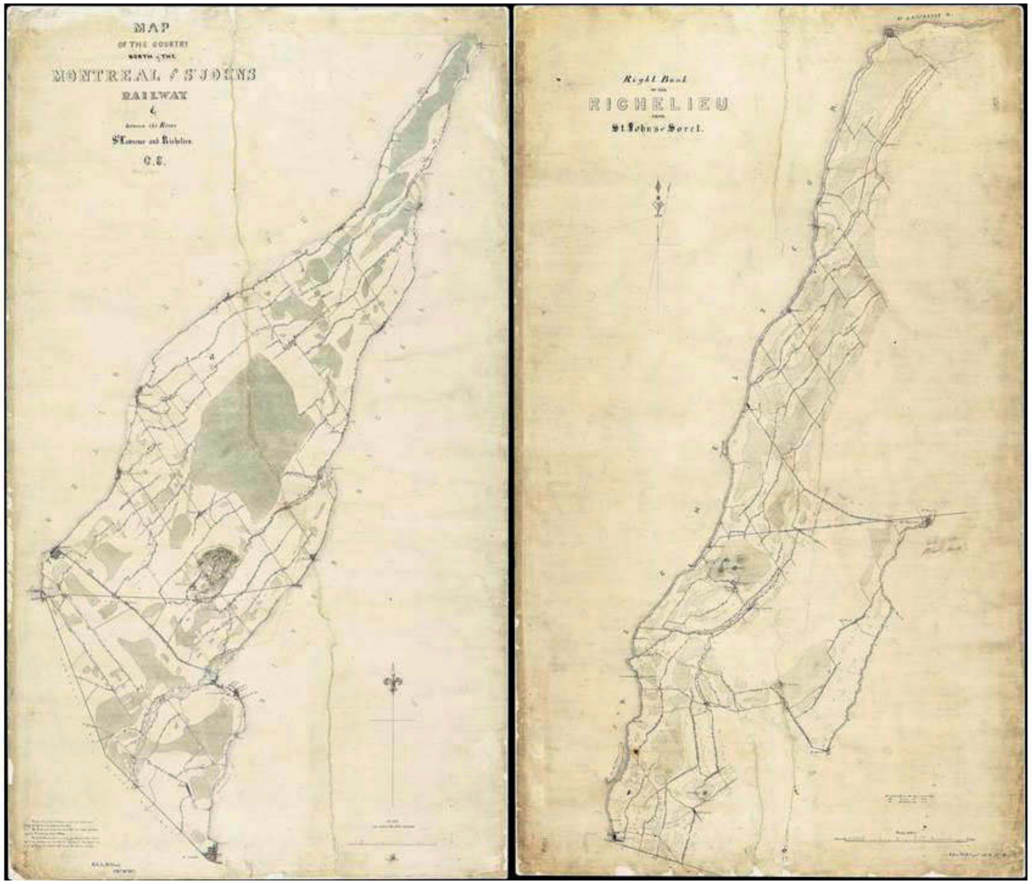

Figure 15: Two topographic maps, from 1864 and 1867, covering respectively the left and the right bank of the Richelieu River. Source: National Archives Canada.

Appendix II

Table 9: List of all species found in the 52 study sites, with their mode of dispersal and habitat preference. Dispersal: ane: anemochore, bal: ballistichore, bar: barochore end: endozoochore, epi: epizoochore, hyd: hydrochore, myr: myrmerochores, unk: unknown. Habitat: for: forest, op: open habitat, unk: unknown.

Name	Dispersal	Source	Habitat	Source
Herb				
Actaea spp. L.	End	Bell et al. 2011; Bellemare et al. 2002	for	Bellemare et al. 2002; Gleason and Cronquist 1991; Singleton et al. 2001
Adiantum pedatum L.	Ane	Brown 2008	for	Bellemare et al. 2002
Alliaria petiolata Bieb. Cavara & Grande	Bal	Dupré and Ehrlén 2002	op	Gleason and Cronquist 1991
Amphicarpaea bracteata L. Fern.	Bal	Brown 2008	op	Gleason and Cronquist 1991
Aralia nudicaulis L.	End	Brown 2008	for	Gleason and Cronquist 1991; Singleton et al. 2001
Aralia racemosa L.	End	Brown 2008	for	Gleason and Cronquist 1991
Arisaema triphyllum L. Schott	End	Brown 2008	for	Gleason and Cronquist 1991; Matlack 1994; Singleton et al. 2001
Asarum canadense L.	Myr	Brown 2008	for	Bellemare et al. 2002; Cain et al. 1998;Matlack 1994; Singleton et al. 2001
Aster acuminatus Michx.	Ane	Cain et al. 1998; Singleton et al. 2001	for	Cain et al. 1998; Gleason and Cronquist 1991; Singleton et al. 2001
Aster cordifolius L.	Ane	Gachet et al. 2007	op	Gleason and Cronquist 1991
Aster macrophyllus L.	Ane	Brown 2008; Singleton et al. 2001	for	Gleason and Cronquist 1991; Singleton et al. 2001
Aster umbellatus Miller	Ane	Gachet et al. 2007	op	Gleason and Cronquist 1991
Athyrium filix-femina L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Athyrium thelypterioides Michx. Desv.	Ane	Bell et al. 2011; Bellemare et al. 2002	for	Gleason and Cronquist 1991

Name	**Dispersal**	**Source**	**Habitat**	**Source**
Bidens frondosa L.	Epi	Brown 2008	op	Gleason and Cronquist 1991
Botrychium dissectum Spreng.	Ane	Matlack 1994	for	Matlack 1994
Botrychium lanceolatum S.G. Gmelin Angström	Ane	Matlack 1994	for	Gleason and Cronquist 1991; Matlack 1994
Cardamine diphylla Michx. A. Wood	Bar	Brown 2008	for	Bellemare et al. 2002; Gleason and Cronquist 1991
Cardamine pensylvanica Muhl.	Bal	Molofsky and Ferdy 2005	for	Gleason and Cronquist 1991
Carex spp. L.	unk		op	Gleason and Cronquist 1991
Caulophyllum thalictroides L. Michx.	End	Brown 2008	for	Bellemare et al. 2002; Gleason and Cronquist 1991; Matlack 1994; Singleton et al. 2001
Circaea lutetiana L.	Epi	Brown 2008	for	Gleason and Cronquist 1991; Singleton et al. 2001
Claytonia caroliniana Michx.	Myr	Bell et al. 2011; Bellemare et al. 2002	for	Gleason and Cronquist 1991
Clematis virginiana L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Clintonia borealis Aiton Raf.	End	Brown 2008	for	Gleason and Cronquist 1991
Coptis trifolia L. Salisb.	Bar	Brown 2008	for	Gleason and Cronquist 1991
Cornus canadensis L.	End	Burger 1987	for	Gleason and Cronquist 1991
Cypripedium acaule Aiton	Ane	Gachet et al. 2007	op	Gleason and Cronquist 1991
Dennstaedtia punctilobula Michx. Moore	Ane	Penrod and McCormick 1996	op	Gleason and Cronquist 1991
Desmodium glutinosum Muhl. A. Wood.	Epi	Matlack 1994	for	Gleason and Cronquist 1991
Dryopteris cristata L. A. Gray	Ane	Brown 2008	for	Gleason and Cronquist 1991
Dryopteris intermedia Muhl. A. Gray	Ane	Brown 2008; Gachet et al. 2007; Singleton et al. 2001	for	Gleason and Cronquist 1991; Singleton et al. 2001
Dryopteris marginalis L. A. Gray	Ane	Brown 2008	for	Singleton et al. 2001
Echinocystis lobata Michx. T. and G.	Bar	Brown 2008	op	Gleason and Cronquist 1991
Epifagus virginiana L. Barton	Hyd	Thieret 1969	for	Gleason and Cronquist 1991

Name	**Dispersal**	**Source**	**Habitat**	**Source**
Epipactis helleborine L. Crantz	Ane	Brown 2008	op	Gleason and Cronquist 1991
Equisetum arvense L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Equisetum hyemale L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Equisetum sylvaticum L.	Ane	Brown 2008	for	Gleason and Cronquist 1991
Eupatorium maculatum L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Eupatorium rugosum Houttuyn	Ane	Brown 2008	for	Cain et al. 1998; Gleason and Cronquist 1991
Fragaria vesca L.	End	Brown 2008	op	Blatt et al. 2005
Galium palustre L.	Epi	Brown 2008	op	Gleason and Cronquist 1991
Galium sp. L.	Epi	Brown 2008	op	Gleason and Cronquist 1991
Galium triflorum Michx.	Epi	Brown 2008	for	Gleason and Cronquist 1991; Matlack 1994
Geum aleppicum Jacq.	Epi	Brown 2008	op	Gleason and Cronquist 1991
Geum canadense Jacq.	Epi	Brown 2008	for	Gleason and Cronquist 1991
Grass	unk		op	
Gymnocarpium dryopteris L. Newman	Ane	Brown 2008	op	Gleason and Cronquist 1991
Hepatica acutiloba DC.	Myr	Brown 2008	for	Bellemare et al. 2002; Gleason and Cronquist 1991; Singleton et al. 2001
Hydrophyllum virginianum L.	Bal	Brown 2008	for	Bellemare et al. 2002; Singleton et al. 2001
Impatiens capensis Meerb.	Bal	Brown 2008	for	Cain et al. 1998; Singleton et al. 2001
Iris versicolor L.	Bar	Brown 2008	op	Gleason and Cronquist 1991
Lactuca canadensis L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Laportea canadensis L. Wedd.	Bar	Brown 2008	for	Gleason and Cronquist 1991
Lycopodium annotinum L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Lycopodium complanatum L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Lycopodium lucidulum Michx.	Ane	Gachet et al. 2007; Singleton et al. 2001	for	Singleton et al. 2001

Name	**Dispersal**	**Source**	**Habitat**	**Source**
Lycopodium obscurum L.	Ane	Brown 2008	for	Gleason and Cronquist 1991; Singleton et al. 2001
Lycopus americanus Muhl.	Hyd	Brown 2008	op	Gleason and Cronquist 1991
Lysimachia ciliata L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Maianthemum canadense Desf.	End	Brown 2008	for	Gleason and Cronquist 1991; Singleton et al. 2001
Matteuccia struthiopteris L. Todaro	Ane	Brown 2008	op	Gleason and Cronquist 1991
Medeola virginiana L.	End	Brown 2008	for	Gleason and Cronquist 1991; Singleton et al. 2001
Mitchella repens L.	End	Brown 2008	for	Gleason and Cronquist 1991; Singleton et al. 2001
Monotropa uniflora L.	Ane	Brown 2008	for	Gleason and Cronquist 1991
Moss	unk		unk	
Onoclea sensibilis L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Osmorhiza claytonii Michx C.B. Clarke	Epi	Brown 2008	for	Bellemare et al. 2002; Gleason and Cronquist 1991; Matlack 1994; Singleton et al. 2001
Osmunda cinnamomea L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Osmunda claytoniana L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Osmunda regalis L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Oxalis acetosella L.	Bal	Gachet et al. 2007	for	Gleason and Cronquist 1991
Oxalis stricta L.	Bal	Brown 2008	op	Gleason and Cronquist 1991
Panax quinquefolium L.	Bar	Whigham 2004	for	Gleason and Cronquist 1991
Panax trifolium L.	End	Matlack 1994	for	Gleason and Cronquist 1991; Matlack 1994
Phryma leptostachya L.	Epi	Brown 2008	for	Gleason and Cronquist 1991
Polygonatum pubescens Willd. Pursh	End	Brown 2008	for	Singleton et al. 2001

Name	**Dispersal**	**Source**	**Habitat**	**Source**
Polygonum hydropiper L.	unk		unk	
Polystichum acrostichoides Michx. Schott	Ane	Brown 2008	for	Singleton et al. 2001
Prenanthes spp. L.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Pteridium aquilinum L. Kuhn	Ane	Brown 2008	op	Gleason and Cronquist 1991
Pyrola elliptica Nutt.	Ane	Brown 2008	for	Gleason and Cronquist 1991
Ranunculus abortivus L.	Ane	Brown 2008	for	Matlack 1994
Rosa nitida Willd.	unk		op	Gleason and Cronquist 1991
Rubus allegheniensis T.C. Porter	End	Matlack 1994	op	Gleason and Cronquist 1991
Rubus hispidus L.	End	Matlack 1994	for	Matlack 1994
Rubus idaeus L.	End	Aubin et al. 2009; Bell et al. 2011; Bellemare et al. 2002	op	Gleason and Cronquist 1991
Rubus odoratus L.	End	Bell et al. 2011; Bellemare et al. 2002	op	Gleason and Cronquist 1991
Rubus pubescens Raf.	End	Brown 2008	for	Gleason and Cronquist 1991
Sanguinaria canadensis L.	Myr	Brown 2008	for	Bellemare et al. 2002; Cain et al. 1998; Gleason and Cronquist 1991; Matlack 1994
Sanicula gregaria E. Bickn.	Epi	Brown 2008	for	Gleason and Cronquist 1991; Matlack 1994
Sanicula trifoliata E. Bickn.	Epi	Matlack 1994	for	Gleason and Cronquist 1991
Scutellaria lateriflora L.	Bar	Brown 2008	op	Gleason and Cronquist 1991
Smilacina racemosa L. Desf.	End	Brown 2008; Matlack 1994	for	Gleason and Cronquist 1991; Matlack 1994; Singleton et al. 2001
Smilax herbacea L.	End	Brown 2008	op	Gleason and Cronquist 1991
Solidago caesia L.	Ane	Bell et al. 2011; Bellemare et al. 2002; Singleton et al. 2001	for	Gleason and Cronquist 1991; Singleton et al. 2001
Solidago flexicaulis L.	Ane	Bell et al. 2011; Bellemare et al. 2002; Singleton et al. 2001	for	Gleason and Cronquist 1991; Singleton et al. 2001
Solidago spp. L.	unk		op	Gleason and Cronquist 1991

Name	Dispersal	Source	Habitat	Source
Sphagnum spp.	unk		unk	
Streptopus roseus Michx.	End	Gachet et al. 2007	for	Gleason and Cronquist 1991
Symplocarpus foetidus L. Nutt.	End	Small 1959	op	Gleason and Cronquist 1991
Taraxacum officinale Weber.	Ane	Brown 2008	op	Gleason and Cronquist 1991
Thalictrum pubescens Pursh	Bar	Brown 2008	op	Gleason and Cronquist 1991
Thelypteris noveboracensis L. Nieuwl.	Ane	Brown 2008	for	Gleason and Cronquist 1991; Matlack 1994; Singleton et al. 2001
Thelypteris palustris Schott	Ane	Brown 2008	op	Gleason and Cronquist 1991
Thelypteris phegopteris L. Slosson	Ane	Svenning and Skov 2008	for	Gleason and Cronquist 1991
Tiarella cordifolia L.	Bar	Brown 2008	for	Gleason and Cronquist 1991; Singleton et al. 2001
Trientalis borealis Raf.	Ane	Brown 2008	for	Gleason and Cronquist 1991; Singleton et al. 2001
Trillium spp. L.	Myr	Brown 2008	for	Gleason and Cronquist 1991
Uvularia grandiflora J. E. Smith	Myr	Brown 2008	for	Gleason and Cronquist 1991
Uvularia sessilifolia L.	End	Singleton et al. 2001	for	Gleason and Cronquist 1991; Singleton et al. 2001
Valeriana officinalis L.	Ane	Geertsema 2005	op	Gleason and Cronquist 1991
Viola spp. L.	Myr	Brown 2008	for	Cain et al. 1998; Matlack 1994; Singleton et al. 2001
Unknown 1	unk		unk	
Unknown 2	unk		unk	
Unknown 3	unk		unk	

Name	Dispersal	Source	Habitat	Source
Seedling				
Abies balsamea L. Miller	Ane	Bell et al. 2011; Gachet et al. 2007	for	Gleason and Cronquist 1991
Acer negundo L.	Ane	Cain et al. 1998	op	Gleason and Cronquist 1991
Acer pensylvanicum L.	Ane	Bell et al. 2011; Bellemare et al. 2002	for	Gleason and Cronquist 1991
Acer rubrum L.	Ane	Cain et al. 1998	for	Cain et al. 1998
Acer saccharum Marshall	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Acer spicatum Lam.	Ane	Gachet et al. 2007	for	Gleason and Cronquist 1991
Betula alleghaniensis Britton	Ane	Willson 1993	for	Gleason and Cronquist 1991
Betula papyrifera Marshall	Ane	Cain et al. 1998	op	Cain et al. 1998
Carpinus caroliniana Walter	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Carya spp. Nutt.	End	Bell et al. 2011; Bellemare et al. 2002; Hewitt and Kellman 2002	for	Gleason and Cronquist 1991; Graney 1990
Fagus grandifolia Ehrh.	End	Bell et al. 2011; Bellemare et al. 2002; Cain et al. 1998	for	Cain et al. 1998
Fraxinus spp. L.	Ane	Cain et al. 1998; Tardif and Bergeron 1999	for	Cain et al. 1998; Gleason and Cronquist 1991
Ostrya virginiana Miller K. Koch	Ane	Aubin et al. 2009	for	Gleason and Cronquist 1991
Picea rubens Sarg.	Ane	Gachet et al. 2007	for	Gleason and Cronquist 1991
Pinus strobus L.	Ane	Cain et al. 1998	for	Cain et al. 1998
Populus grandidentada Michx.	Ane	Cain et al. 1998	op	Laidly 1990
Populus spp. L.	Ane	Cain et al. 1998; Gachet et al. 2007	op	Gleason and Cronquist 1991
Populus tremuloides Michx.	Ane	Gachet et al. 2007	op	Gleason and Cronquist 1991
Quercus macrocarpa Michx.	End	Cain et al. 1998	for	Cain et al. 1998
Quercus rubra L.	End	Sork 1984	for	Sander 1990
Thuja occidentalis L.	unk		for	Johnston 1990

Name	**Dispersal**	**Source**	**Habitat**	**Source**
Tilia americana L.	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Tsuga canadensis L. Carrière	Ane	Cain et al. 1998	for	Cain et al. 1998
Ulmus americana L.	Ane	Aubin et al. 2009	for	Bey 1990
Sapling				
Abies balsamea L. Miller	Ane	Bell et al. 2011; Gachet et al. 2007	for	Gleason and Cronquist 1991
Acer pensylvanicum L.	Ane	Bell et al. 2011; Bellemare et al. 2002	for	Gleason and Cronquist 1991
Acer rubrum L.	Ane	Cain et al. 1998	for	Cain et al. 1998
Acer saccharum Marshall	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Acer spicatum Lam.	Ane	Gachet et al. 2007	for	Gleason and Cronquist 1991
Betula alleghaniensis Britton	Ane	Willson 1993	for	Gleason and Cronquist 1991
Betula papyrifera Marshall	Ane	Cain et al. 1998	op	Cain et al. 1998
Carpinus caroliniana Walter	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Carya cordiformis Wangenh. K. Koch	End	Bell et al. 2011; Bellemare et al. 2002	for	Gleason and Cronquist 1991
Carya ovata Miller K. Koch	End	Hewitt and Kellman 2002	for	Graney 1990
Fagus grandifolia Ehrh.	End	Bell et al. 2011; Bellemare et al. 2002; Cain et al. 1998	for	Cain et al. 1998
Fraxinus americana L.	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Fraxinus nigra Marshall	Ane	Tardif and Bergeron 1999	for	Gleason and Cronquist 1991
Fraxinus pennsylvanica Marshall	Ane	Hanson et al. 1990	for	Gleason and Cronquist 1991
Ostrya virginiana Miller K. Koch	Ane	Aubin et al. 2009	for	Gleason and Cronquist 1991
Populus tremuloides Michx.	Ane	Gachet et al. 2007	op	Gleason and Cronquist 1991
Quercus macrocarpa Michx.	End	Cain et al. 1998	for	Cain et al. 1998

Name	Dispersal	Source	Habitat	Source
Tilia americana L.	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Tsuga canadensis L. Carrière	Ane	Cain et al. 1998	for	Cain et al. 1998
Ulmus americana L.	Ane	Aubin et al. 2009	for	Bey 1990
Shrub				
Amelanchier Medikus.	End	Bell et al. 2011	op	Gleason and Cronquist 1991
Cornus alternifolia L.f.	End	Bell et al. 2011; Bellemare et al. 2002	op	Gleason and Cronquist 1991
Cornus sericea L.	End	Gachet et al. 2007	for	Gleason and Cronquist 1991
Corylus cornuta Marshall	End	Gachet et al. 2007	op	Gleason and Cronquist 1991
Crataegus spp. L.	End	Phipps 1983	op	Gleason and Cronquist 1991
Diervilla lonicera Miller	End	Bell et al. 2011; Gachet et al. 2007	op	Gleason and Cronquist 1991
Ilex verticillata L. A. Gray	End	Stiles 1980	for	Gleason and Cronquist 1991
Ledum groenlandicum Oeder	Ane	CampBell et al. 2011; Karlin and Bliss 1983	op	Gleason and Cronquist 1991
Lonicera canadensis Marshall	End	Gachet et al. 2007	for	Gleason and Cronquist 1991
Parthenocissus quinquefolia L. Planchon	End	Cain et al. 1998; Matlack 1994	op	Gleason and Cronquist 1991
Prunus serotina Ehrh.	End	Cain et al. 1998	op	Gleason and Cronquist 1991
Prunus virginiana L.	End	Bell et al. 2011	op	Gleason and Cronquist 1991
Rhamnus cathartica L.	End	Godwin	op	Gleason and Cronquist 1991
Rhamnus frangula L.	End	Frappier	op	Gleason and Cronquist 1991
Ribes lacustre Pers. Poiret	End	Bell et al. 2011; Gachet et al. 2007	op	Gleason and Cronquist 1991
Ribes sativum Syme	End	Bell et al. 2011; Gachet et al. 2007	op	Gleason and Cronquist 1991
Ribes spp. L.	End	Bell et al. 2011; Gachet et al. 2007	unk	
Ribes triste Pallas	End	Gachet et al. 2007	for	Gleason and Cronquist 1991
Sambucus canadensis L.	End	Gachet et al. 2007	op	Gleason and Cronquist 1991
Spiraea alba DuRoi	unk		op	Gleason and Cronquist 1991

Name	**Dispersal**	**Source**	**Habitat**	**Source**
Symphoricarpos albus L. S. F. Blake	End	Stiles 1980	op	Gleason and Cronquist 1991
Taxus canadensis Marshall	Ane	Gachet et al. 2007	for	Gleason and Cronquist 1991
Toxicodendron radicans L. Kuntze	End	Cain et al. 1998; Matlack 1994	op	Gleason and Cronquist 1991
Vaccinium corymbosum L.	End	Stiles 1980	op	Gleason and Cronquist 1991
Vaccinium myrtilloides Michx.	End	Gachet et al. 2007	op	Gleason and Cronquist 1991
Viburnum alnifolium Marshall	End	Whitney and Foster 1988	for	Gleason and Cronquist 1991
Viburnum lentago L.	End	Stiles 1980	op	Gleason and Cronquist 1991
Viburnum nudum L.	End	Gachet et al. 2007	for	Gleason and Cronquist 1991
Viburnum opulus L.	End	Gachet et al. 2007	for	Gleason and Cronquist 1991
Vitis riparia Michx.	End	Aubin et al. 2009	op	Gleason and Cronquist 1991
Tree				
Abies balsamea L. Miller	Ane	Bell et al. 2011; Gachet et al. 2007	for	Gleason and Cronquist 1991
Acer negundo L.	Ane	Cain et al. 1998	op	Gleason and Cronquist 1991
Acer pensylvanicum L.	Ane	Bell et al. 2011; Bellemare et al. 2002	for	Gleason and Cronquist 1991
Acer rubrum L.	Ane	Cain et al. 1998	for	Cain et al. 1998
Acer saccharinum L.	Ane	Hanson et al. 1990	for	Gabriel 1990
Acer saccharum Marshall	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Alnus incana L. Moench	Ane	Bell et al. 2011; Gachet et al. 2007	op	Gleason and Cronquist 1991
Betula alleghaniensis Britton	Ane	Willson 1993	for	Gleason and Cronquist 1991
Betula papyrifera Marshall	Ane	Cain et al. 1998	op	Gleason and Cronquist 1991
Betula populifolia Marshall	Ane	Cain et al. 1998	op	Gleason and Cronquist 1991
Carpinus caroliniana Walter	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Carya cordiformis Wangenh. K. Koch	End	Bell et al. 2011; Bellemare et al. 2002	for	Gleason and Cronquist 1991
Carya ovata Miller K. Koch	End	Hewitt and Kellman 2002	for	Graney 1990

Name	**Dispersal**	**Source**	**Habitat**	**Source**
Fagus grandifolia Ehrh.	End	Bell et al. 2011; Bellemare et al. 2002; Cain et al. 1998	for	Cain et al. 1998
Fraxinus americana L.	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Fraxinus nigra Marshall	Ane	Tardif and Bergeron 1999	for	Gleason and Cronquist 1991
Fraxinus pennsylvanica Marshall	Ane	Hanson et al. 1990	for	Gleason and Cronquist 1991
Juglans cinerea L.	End	Cain et al. 1998	for	Rink 1990
Ostrya virginiana Miller K. Koch	Ane	Aubin et al. 2009	for	Gleason and Cronquist 1991
Picea rubens Sarg.	Ane	Gachet et al. 2007	for	Gleason and Cronquist 1991
Pinus strobus L.	Ane	Cain et al. 1998	for	Cain et al. 1998
Populus grandidentada Michx.	Ane	Cain et al. 1998	op	Laidly 1990
Populus tremuloides Michx.	Ane	Gachet et al. 2007	op	Gleason and Cronquist 1991
Prunus serotina Ehrh.	End	Cain et al. 1998	op	Gleason and Cronquist 1991
Prunus virginiana L.	End	Gachet et al. 2007	op	Gleason and Cronquist 1991
Quercus macrocarpa Michx.	End	Cain et al. 1998	for	Cain et al. 1998
Quercus rubra L.	End	Sork 1984	for	Sander 1990
Tilia americana L.	Ane	Cain et al. 1998	for	Cain et al. 1998; Gleason and Cronquist 1991
Tsuga canadensis L. Carrière	Ane	Cain et al. 1998	for	Cain et al. 1998
Ulmus americana L.	Ane	Aubin et al. 2009	for	Bey 1990

Appendix III

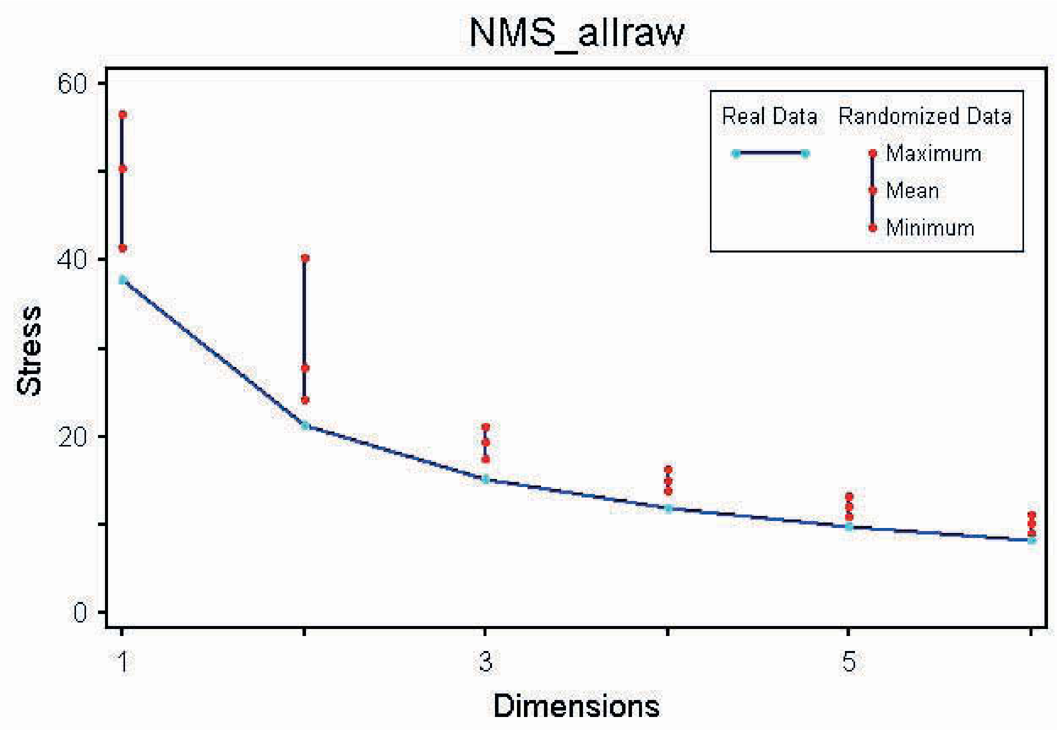

Figure 16: Scree plot of the NMDS of study sites using all species showing that the reduction in stress from three to four dimensions is little compared to that between two and three dimensions

Table 10: Stress in relation to dimensionality (Number of Axes) or Monte Carlo test for the NMDS of study sites using all species. It shows that the reduction in stress from three to four dimensions is little compared to that between two and three dimensions

	Stress in real data 250 run(s)			Stress in randomized data Monte Carlo test, 249 runs			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
1	37.733	49.367	56.614	41.441	50.444	56.614	0.004
2	21.282	22.469	40.129	24.207	27.714	40.202	0.004
3	15.091	15.326	16.846	17.371	19.373	21.015	0.004
4	11.851	11.892	12.338	13.744	15.008	16.236	0.004
5	9.709	9.782	10.082	10.94	12.153	13.144	0.004
6	8.206	8.245	8.647	8.952	10.114	11.044	0.004

p = proportion of randomized runs with stress < or = observed stress
i.e., p = (1 + no. permutations <= observed)/(1 + no. permutations)

Appendix IV

Table 11: Correlations between axes of the NMDS of study sites using all species with explanatory variables, species richness variables, and each species' abundance.

Variables	Correlations with NMDS AXES (r^2)					
Explanatory-quantitative	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Canopy cover	(-)	0.061	(+)	0.006	(+)	0.106
Management intensity	(-)	0.035	(+)	0.003	(+)	0.116
Past land-use intensity	(-)	0.117	(-)	0.000	(+)	0.001
Landscape context in the 1860s-200m buffer	(+)	0.122	(-)	0.004	(-)	0.030
Landscape context in the 1860s-500m buffer	(+)	0.170	(+)	0.001	(-)	0.035
Landscape context in the 1860s-1000m buffer	(+)	0.183	(+)	0.015	(-)	0.011
Landscape context in the 1910s-200m buffer	(+)	0.318	(+)	0.016	(-)	0.000
Landscape context in the 1910s-500m buffer	(+)	0.297	(+)	0.006	(+)	0.000
Landscape context in the 1910s-1000m buffer	(+)	0.286	(+)	0.016	(+)	0.010
Landscape context in the 1990s-200m buffer	(+)	0.268	(+)	0.008	(-)	0.002
Landscape context in the 1990s-500m buffer	(+)	0.211	(+)	0.022	(+)	0.002
Landscape context in the 1990s-1000m buffer	(+)	0.229	(+)	0.025	(+)	0.022
Species richness	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Herbaceous	(+)	0.061	(-)	0.032	(-)	0.399
Sapling	(+)	0.045	(+)	0.003	(+)	0.000
Seedling	(+)	0.024	(-)	0.005	(+)	0.000
Shrub	(+)	0.001	(-)	0.002	(-)	0.493
Tree	(+)	0.020	(+)	0.004	(-)	0.077
Woody	(+)	0.035	(-)	0.000	(-)	0.184
Total	(+)	0.062	(-)	0.014	(-)	0.374
Anemochorous	(+)	0.153	(-)	0.043	(-)	0.134
Ballistichorous	(-)	0.005	(+)	0.002	(-)	0.356
Barochorous	(-)	0.001	(-)	0.106	(-)	0.298
Endozoochorous	(+)	0.043	(+)	0.000	(-)	0.347
Epizoochorous	(-)	0.128	(+)	0.004	(-)	0.254
Hydrochorous	(+)	0.029	(-)	0.042	(+)	0.001
Myrmerochorous	(-)	0.009	(+)	0.004	(-)	0.015
Unknown dispersal	(+)	0.146	(+)	0.000	(-)	0.223
Anemochorous -herb.	(+)	0.164	(-)	0.074	(-)	0.224
Ballistichorous -herb.	(-)	0.005	(+)	0.002	(-)	0.356
Barochorous -herb.	(-)	0.001	(-)	0.106	(-)	0.298
Endozoochorous -herb.	(+)	0.118	(-)	0.012	(-)	0.147
Epizoochorous -herb.	(-)	0.128	(+)	0.004	(-)	0.254
Hydrochorous -herb.	(+)	0.029	(-)	0.042	(+)	0.001
Myrmerochorous -herb.	(-)	0.009	(+)	0.004	(-)	0.015
Unknown dispersal -herb.	(+)	0.160	(+)	0.002	(-)	0.145

Species richness	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Forest specialist	(+)	0.054	(-)	0.017	(-)	0.061
Generalist	(+)	0.022	(-)	0.004	(-)	0.614
Unknown habitat	(+)	0.053	(+)	0.015	(-)	0.093
Forest specialist -herb.	(+)	0.052	(-)	0.033	(-)	0.083
Generalist -herb.	(+)	0.026	(-)	0.017	(-)	0.640
Unknown habitat -herb.	(+)	0.064	(+)	0.018	(-)	0.035

Herb	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Actaea spp. L.	(-)	0.028	(+)	0.013	(-)	0.050
Adiantum pedatum L.	(-)	0.000	(-)	0.000	(+)	0.003
Alliaria petiolata Bieb. Cavara & Grande	(-)	0.003	(+)	0.024	(-)	0.086
Amphicarpaea bracteata L. Fern.	(+)	0.051	(+)	0.007	(-)	0.066
Aralia nudicaulis L.	(+)	0.023	(-)	0.011	(-)	0.148
Aralia racemosa L.	(-)	0.022	(-)	0.004	(+)	0.032
Arisaema triphyllum L. Schott	(-)	0.112	(-)	0.008	(-)	0.000
Asarum canadense L.	(-)	0.001	(+)	0.029	(-)	0.000
Aster acuminatus Michx.	(-)	0.002	(+)	0.021	(-)	0.086
Aster cordifolius L.	(-)	0.003	(+)	0.012	(+)	0.024
Aster macrophyllus L.	(+)	0.011	(-)	0.029	(-)	0.053
Aster umbellatus Miller	(-)	0.014	(-)	0.006	(-)	0.254
Athyrium filix-femina L.	(-)	0.125	(-)	0.044	(-)	0.011
Athyrium thelypterioides Michx. Desv.	(+)	0.000	(+)	0.000	(+)	0.002
Bidens frondosa L.	(-)	0.007	(-)	0.021	(-)	0.097
Botrychium dissectum Spreng.	(-)	0.001	(-)	0.001	(+)	0.009
Botrychium lanceolatum S.G. Gmelin Angström	(+)	0.042	(+)	0.014	(-)	0.011
Cardamine diphylla Michx. A. Wood	(-)	0.005	(-)	0.160	(+)	0.002
Cardamine pensylvanica Muhl.	(-)	0.002	(+)	0.046	(-)	0.013
Carex spp. L.	(-)	0.009	(-)	0.055	(-)	0.268
Caulophyllum thalictroides L. Michx.	(-)	0.039	(+)	0.035	(+)	0.017
Circaea lutetiana L.	(-)	0.037	(+)	0.011	(+)	0.000
Claytonia caroliniana Michx.	(-)	0.053	(-)	0.019	(-)	0.012
Clematis virginiana L.	(+)	0.008	(+)	0.001	(-)	0.093
Clintonia borealis Aiton Raf.	(+)	0.004	(-)	0.097	(-)	0.149
Coptis trifolia L. Salisb.	(+)	0.209	(-)	0.024	(-)	0.036
Cornus canadensis L.	(+)	0.013	(-)	0.123	(-)	0.036
Cypripedium acaule Aiton	(+)	0.134	(+)	0.000	(-)	0.041
Dennstaedtia punctilobula Michx. Moore	(+)	0.019	(+)	0.013	(+)	0.017
Desmodium glutinosum Muhl. A. Wood.	(-)	0.026	(+)	0.000	(+)	0.008
Dryopteris cristata L. A. Gray	(+)	0.021	(+)	0.004	(-)	0.013
Dryopteris intermedia Muhl. A. Gray	(+)	0.166	(-)	0.292	(-)	0.023
Dryopteris marginalis L. A. Gray	(-)	0.007	(-)	0.022	(+)	0.021
Echinocystis lobata Michx. T. and G.	(-)	0.016	(+)	0.005	(+)	0.004

Herb	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Epifagus virginiana L. Barton	(+)	0.027	(+)	0.003	(+)	0.008
Epipactis helleborine L. Crantz	(-)	0.030	(-)	0.011	(-)	0.000
Equisetum arvense L.	(+)	0.001	(-)	0.017	(-)	0.106
Equisetum hyemale L.	(-)	0.050	(-)	0.001	(+)	0.015
Equisetum sylvaticum L.	(+)	0.031	(+)	0.003	(-)	0.013
Eupatorium maculatum L.	(+)	0.008	(+)	0.001	(-)	0.093
Eupatorium rugosum Houttuyn	(-)	0.018	(-)	0.006	(-)	0.088
Fragaria vesca L.	(-)	0.012	(+)	0.030	(-)	0.249
Galium palustre L.	(-)	0.008	(+)	0.000	(-)	0.132
Galium sp. L.	(-)	0.004	(+)	0.069	(-)	0.067
Galium triflorum Michx.	(-)	0.003	(+)	0.015	(-)	0.123
Geum aleppicum Jacq.	(-)	0.044	(+)	0.006	(-)	0.253
Geum canadense Jacq.	(-)	0.011	(+)	0.037	(-)	0.052
Grass	(-)	0.038	(+)	0.016	(-)	0.183
Gymnocarpium dryopteris L. Newman	(-)	0.008	(-)	0.000	(+)	0.009
Hepatica acutiloba DC.	(-)	0.005	(+)	0.003	(+)	0.009
Hydrophyllum virginianum L.	(-)	0.018	(+)	0.006	(-)	0.025
Impatiens capensis Meerb.	(-)	0.015	(+)	0.012	(-)	0.145
Iris versicolor L.	(+)	0.065	(+)	0.000	(-)	0.138
Lactuca canadensis L.	(+)	0.008	(+)	0.001	(-)	0.093
Laportea canadensis L. Wedd.	(-)	0.084	(-)	0.018	(-)	0.004
Lycopodium annotinum L.	(+)	0.050	(-)	0.026	(+)	0.000
Lycopodium complanatum L.	(+)	0.104	(+)	0.010	(+)	0.009
Lycopodium lucidulum Michx.	(+)	0.066	(-)	0.073	(-)	0.000
Lycopodium obscurum L.	(+)	0.075	(-)	0.028	(+)	0.000
Lycopus americanus Muhl.	(+)	0.004	(-)	0.103	(-)	0.083
Lysimachia ciliata L.	(-)	0.030	(+)	0.042	(-)	0.127
Maianthemum canadense Desf.	(+)	0.347	(-)	0.042	(-)	0.091
Matteuccia struthiopteris L. Todaro	(-)	0.148	(+)	0.012	(+)	0.036
Medeola virginiana L.	(+)	0.089	(-)	0.006	(+)	0.007
Mitchella repens L.	(+)	0.009	(-)	0.036	(+)	0.001
Monotropa uniflora L.	(+)	0.043	(+)	0.006	(+)	0.034
Moss	(+)	0.005	(+)	0.033	(-)	0.133
Onoclea sensibilis L.	(-)	0.056	(-)	0.050	(-)	0.141
Osmorhiza claytonii Michx C.B. Clarke	(-)	0.045	(-)	0.009	(-)	0.001
Osmunda cinnamomea L.	(-)	0.003	(-)	0.198	(-)	0.026
Osmunda claytoniana L.	(+)	0.018	(-)	0.039	(-)	0.047
Osmunda regalis L.	(+)	0.116	(+)	0.002	(-)	0.049
Oxalis acetosella L.	(+)	0.004	(-)	0.065	(-)	0.022
Oxalis stricta L.	(-)	0.021	(+)	0.035	(-)	0.099
Panax quinquefolium L.	(-)	0.020	(+)	0.000	(+)	0.009
Panax trifolium L.	(+)	0.046	(-)	0.027	(+)	0.000

Herb	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Phryma leptostachya L.	(-)	0.038	(-)	0.000	(+)	0.007
Polygonatum pubescens Willd. Pursh	(-)	0.033	(+)	0.001	(+)	0.006
Polygonum hydropiper L.	(-)	0.038	(-)	0.000	(+)	0.007
Polystichum acrostichoides Michx. Schott	(-)	0.024	(+)	0.082	(+)	0.040
Prenanthes spp. L.	(-)	0.001	(+)	0.002	(-)	0.042
Pteridium aquilinum L. Kuhn	(+)	0.053	(-)	0.022	(-)	0.072
Pyrola elliptica Nutt.	(-)	0.001	(-)	0.011	(+)	0.011
Ranunculus abortivus L.	(-)	0.002	(+)	0.021	(-)	0.151
Rosa nitida Willd.	(+)	0.016	(-)	0.002	(-)	0.141
Rubus allegheniensis T.C. Porter	(+)	0.000	(+)	0.002	(-)	0.093
Rubus hispidus L.	(+)	0.024	(+)	0.002	(-)	0.016
Rubus idaeus L.	(+)	0.009	(-)	0.000	(-)	0.139
Rubus odoratus L.	(-)	0.019	(+)	0.008	(-)	0.033
Rubus pubescens Raf.	(-)	0.016	(-)	0.001	(-)	0.396
Sanguinaria canadensis L.	(-)	0.034	(+)	0.001	(+)	0.012
Sanicula gregaria E. Bickn.	(-)	0.024	(+)	0.000	(-)	0.136
Sanicula trifoliata E. Bickn.	(+)	0.044	(+)	0.032	(+)	0.000
Scutellaria lateriflora L.	(+)	0.005	(-)	0.001	(-)	0.290
Smilacina racemosa L. Desf.	(-)	0.003	(+)	0.002	(-)	0.126
Smilax herbacea L.	(-)	0.011	(+)	0.004	(-)	0.084
Solidago caesia L.	(+)	0.000	(+)	0.001	(+)	0.003
Solidago flexicaulis L.	(-)	0.038	(-)	0.000	(+)	0.008
Solidago spp. L.	(+)	0.009	(+)	0.000	(-)	0.099
Sphagnum spp.	(+)	0.135	(+)	0.000	(-)	0.041
Streptopus roseus Michx.	(+)	0.003	(-)	0.150	(-)	0.053
Symplocarpus foetidus L. Nutt.	(-)	0.034	(+)	0.001	(+)	0.002
Taraxacum officinale Weber.	(-)	0.000	(+)	0.035	(-)	0.077
Thalictrum pubescens Pursh	(-)	0.009	(+)	0.016	(-)	0.094
Thelypteris noveboracensis L. Nieuwl.	(+)	0.015	(-)	0.033	(+)	0.018
Thelypteris palustris Schott	(-)	0.000	(-)	0.075	(-)	0.036
Thelypteris phegopteris L. Slosson	(+)	0.000	(-)	0.105	(-)	0.023
Tiarella cordifolia L.	(-)	0.035	(-)	0.021	(-)	0.077
Trientalis borealis Raf.	(+)	0.164	(-)	0.078	(-)	0.139
Trillium spp. L.	(-)	0.005	(+)	0.022	(-)	0.083
Uvularia grandiflora J. E. Smith	(-)	0.020	(+)	0.000	(+)	0.009
Uvularia sessilifolia L.	(+)	0.031	(-)	0.014	(+)	0.001
Valeriana officinalis L.	(-)	0.015	(+)	0.001	(-)	0.081
Viola spp. L.	(-)	0.018	(+)	0.003	(-)	0.042
Unknown 1	(+)	0.001	(+)	0.020	(+)	0.014
Unknown 2	(+)	0.021	(+)	0.004	(-)	0.013
Unknown 3	(-)	0.018	(+)	0.006	(-)	0.025
Abies balsamea L. Miller	(+)	0.217	(+)	0.001	(-)	0.072

Seedling	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Acer negundo L.	(-)	0.015	(+)	0.001	(-)	0.081
Acer pensylvanicum L.	(+)	0.073	(+)	0.005	(+)	0.038
Acer rubrum L.	(+)	0.133	(-)	0.003	(-)	0.057
Acer saccharum Marshall	(-)	0.091	(+)	0.014	(+)	0.095
Acer spicatum Lam.	(-)	0.002	(-)	0.092	(+)	0.006
Betula alleghaniensis Britton	(+)	0.006	(-)	0.073	(-)	0.002
Betula papyrifera Marshall	(+)	0.034	(-)	0.001	(+)	0.018
Carpinus caroliniana Walter	(-)	0.002	(+)	0.079	(-)	0.093
Carya spp. Nutt.	(-)	0.033	(+)	0.067	(+)	0.020
Fagus grandifolia Ehrh.	(+)	0.164	(+)	0.007	(+)	0.091
Fraxinus spp. L.	(+)	0.005	(+)	0.015	(+)	0.002
Ostrya virginiana Miller K. Koch	(+)	0.011	(+)	0.096	(-)	0.004
Picea rubens Sarg.	(+)	0.101	(+)	0.010	(+)	0.010
Pinus strobus L.	(+)	0.166	(-)	0.002	(-)	0.053
Populus grandidentada Michx.	(+)	0.055	(+)	0.019	(+)	0.019
Populus spp. L.	(-)	0.010	(+)	0.008	(+)	0.029
Populus tremuloides Michx.	(+)	0.040	(-)	0.005	(-)	0.003
Quercus macrocarpa Michx.	(+)	0.022	(-)	0.012	(-)	0.196
Quercus rubra L.	(+)	0.042	(-)	0.006	(+)	0.002
Thuja occidentalis L.	(-)	0.009	(-)	0.033	(-)	0.029
Tilia americana L.	(+)	0.003	(+)	0.011	(+)	0.004
Tsuga canadensis L. Carrière	(+)	0.097	(-)	0.053	(+)	0.000
Ulmus americana L.	(-)	0.009	(-)	0.050	(-)	0.186

Sapling	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Abies balsamea L. Miller	(+)	0.284	(-)	0.001	(-)	0.032
Acer pensylvanicum L.	(+)	0.001	(+)	0.008	(+)	0.091
Acer rubrum L.	(+)	0.032	(-)	0.062	(-)	0.030
Acer saccharum Marshall	(-)	0.320	(+)	0.042	(+)	0.363
Acer spicatum Lam.	(-)	0.005	(-)	0.160	(+)	0.002
Betula alleghaniensis Britton	(+)	0.007	(-)	0.030	(+)	0.013
Betula papyrifera Marshall	(+)	0.021	(+)	0.004	(-)	0.013
Carpinus caroliniana Walter	(-)	0.018	(+)	0.063	(-)	0.012
Carya cordiformis Wangenh. K. Koch	(-)	0.017	(-)	0.010	(-)	0.014
Carya ovata Miller K. Koch	(-)	0.020	(+)	0.018	(-)	0.042
Fagus grandifolia Ehrh.	(+)	0.096	(+)	0.089	(+)	0.147
Fraxinus americana L.	(-)	0.001	(-)	0.000	(+)	0.002
Fraxinus nigra Marshall	(+)	0.000	(+)	0.000	(-)	0.001
Fraxinus pennsylvanica Marshall	(+)	0.019	(-)	0.001	(-)	0.115
Ostrya virginiana Miller K. Koch	(+)	0.021	(+)	0.178	(-)	0.000
Populus tremuloides Michx.	(+)	0.008	(+)	0.001	(-)	0.093
Quercus macrocarpa Michx.	(+)	0.020	(-)	0.010	(-)	0.144
Tilia americana L.	(-)	0.074	(+)	0.031	(-)	0.013

Sapling	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Tsuga canadensis L. Carrière	(-)	0.010	(-)	0.054	(+)	0.021
Ulmus americana L.	(-)	0.001	(-)	0.071	(-)	0.202
Shrub	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Amelanchier Medikus.	(+)	0.032	(-)	0.000	(-)	0.071
Cornus alternifolia L.f.	(+)	0.023	(+)	0.006	(-)	0.093
Cornus sericea L.	(-)	0.018	(+)	0.020	(-)	0.145
Corylus cornuta Marshall	(+)	0.024	(-)	0.109	(-)	0.142
Crataegus spp. L.	(-)	0.000	(-)	0.012	(-)	0.061
Diervilla lonicera Miller	(+)	0.004	(-)	0.002	(-)	0.010
Ilex verticillata L. A. Gray	(+)	0.067	(+)	0.000	(-)	0.132
Ledum groenlandicum Oeder	(+)	0.134	(+)	0.000	(-)	0.041
Lonicera canadensis Marshall	(+)	0.017	(+)	0.005	(-)	0.026
Parthenocissus quinquefolia L. Planchon	(-)	0.003	(+)	0.049	(-)	0.232
Prunus serotina Ehrh.	(+)	0.020	(+)	0.001	(-)	0.144
Prunus virginiana L.	(-)	0.056	(-)	0.000	(-)	0.366
Rhamnus cathartica L.	(-)	0.018	(+)	0.001	(-)	0.097
Rhamnus frangula L.	(-)	0.033	(+)	0.024	(+)	0.000
Ribes lacustre Pers. Poiret	(-)	0.020	(-)	0.006	(-)	0.109
Ribes sativum Syme	(-)	0.000	(-)	0.015	(-)	0.051
Ribes spp. L.	(-)	0.000	(+)	0.002	(-)	0.039
Ribes triste Pallas	(-)	0.036	(+)	0.002	(+)	0.000
Sambucus canadensis L.	(+)	0.001	(-)	0.131	(-)	0.003
Spiraea alba DuRoi	(+)	0.021	(+)	0.003	(-)	0.110
Symphoricarpos albus L. S. F. Blake	(-)	0.002	(+)	0.046	(-)	0.013
Taxus canadensis Marshall	(-)	0.039	(-)	0.147	(+)	0.113
Toxicodendron radicans L. Kuntze	(+)	0.018	(-)	0.013	(-)	0.175
Vaccinium corymbosum L.	(+)	0.134	(+)	0.000	(-)	0.041
Vaccinium myrtilloides Michx.	(+)	0.188	(-)	0.044	(-)	0.086
Viburnum alnifolium Marshall	(-)	0.002	(-)	0.017	(+)	0.039
Viburnum lentago L.	(-)	0.042	(+)	0.000	(-)	0.193
Viburnum nudum L.	(-)	0.000	(+)	0.060	(-)	0.065
Viburnum opulus L.	(+)	0.003	(+)	0.045	(+)	0.009
Vitis riparia Michx.	(-)	0.055	(+)	0.006	(-)	0.001
Tree	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Abies balsamea L. Miller	(+)	0.223	(-)	0.028	(-)	0.059
Acer negundo L.	(-)	0.003	(+)	0.022	(-)	0.087
Acer pensylvanicum L.	(+)	0.003	(-)	0.050	(-)	0.019
Acer rubrum L.	(+)	0.017	(-)	0.073	(-)	0.214
Acer saccharinum L.	(-)	0.009	(+)	0.006	(-)	0.076
Acer saccharum Marshall	(-)	0.089	(+)	0.073	(+)	0.302
Alnus incana L. Moench	(-)	0.003	(+)	0.022	(-)	0.087
Betula alleghaniensis Britton	(-)	0.000	(-)	0.036	(+)	0.031

Tree	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Betula papyrifera Marshall	(-)	0.010	(+)	0.008	(+)	0.029
Betula populifolia Marshall	(+)	0.015	(-)	0.030	(-)	0.007
Carpinus caroliniana Walter	(+)	0.042	(+)	0.051	(-)	0.011
Carya cordiformis Wangenh. K. Koch	(-)	0.023	(+)	0.034	(+)	0.005
Carya ovata Miller K. Koch	(-)	0.005	(+)	0.001	(-)	0.003
Fagus grandifolia Ehrh.	(+)	0.012	(+)	0.001	(+)	0.172
Fraxinus americana L.	(-)	0.015	(+)	0.004	(-)	0.004
Fraxinus nigra Marshall	(-)	0.001	(-)	0.000	(-)	0.069
Fraxinus pennsylvanica Marshall	(-)	0.026	(-)	0.001	(-)	0.216
Juglans cinerea L.	(-)	0.003	(+)	0.022	(-)	0.087
Ostrya virginiana Miller K. Koch	(-)	0.060	(+)	0.034	(+)	0.015
Picea rubens Sarg.	(+)	0.140	(+)	0.025	(+)	0.009
Pinus strobus L.	(+)	0.160	(-)	0.018	(-)	0.048
Populus grandidentada Michx.	(+)	0.000	(+)	0.001	(+)	0.036
Populus tremuloides Michx.	(+)	0.110	(+)	0.011	(+)	0.000
Prunus serotina Ehrh.	(-)	0.000	(-)	0.004	(-)	0.109
Prunus virginiana L.	(-)	0.019	(+)	0.014	(-)	0.003
Quercus macrocarpa Michx.	(+)	0.007	(-)	0.039	(-)	0.028
Quercus rubra L.	(-)	0.001	(+)	0.039	(-)	0.027
Tilia americana L.	(-)	0.062	(+)	0.052	(-)	0.008
Tsuga canadensis L. Carrière	(+)	0.082	(-)	0.072	(+)	0.038
Ulmus americana L.	(-)	0.024	(-)	0.009	(-)	0.178

Appendix V

Table 12: Correlations between axes of the NMDS of study sites using tree species with explanatory variables, and each tree species' abundance.

Variables	**Correlations with NMDS AXES (r^2)**					
Explanatory-quantitative	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Canopy cover	(+)	0.020	(+)	0.010	(+)	0.047
Management intensity	(+)	0.373	(-)	0.002	(-)	0.108
Past land-use intensity	(+)	0.004	(-)	0.032	(-)	0.007
Landscape context in the 1860s-200m buffer	(-)	0.042	(+)	0.034	(+)	0.018
Landscape context in the 1860s-500m buffer	(-)	0.047	(+)	0.024	(+)	0.005
Landscape context in the 1860s-1000m buffer	(-)	0.020	(+)	0.024	(+)	0.002
Landscape context in the 1910s-200m buffer	(-)	0.005	(+)	0.009	(+)	0.003
Landscape context in the 1910s-500m buffer	(-)	0.001	(+)	0.001	(+)	0.016
Landscape context in the 1910s-1000m buffer	(+)	0.002	(+)	0.000	(+)	0.021
Landscape context in the 1990s-200m buffer	(-)	0.011	(-)	0.001	(+)	0.040
Landscape context in the 1990s-500m buffer	(-)	0.000	(-)	0.016	(+)	0.019
Landscape context in the 1990s-1000m buffer	(+)	0.005	(-)	0.007	(+)	0.025
Tree	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Abies balsamea L. Miller	(-)	0.095	(+)	0.075	(+)	0.060
Acer negundo L.	(-)	0.036	(+)	0.004	(-)	0.012
Acer pensylvanicum L.	(+)	0.000	(+)	0.005	(+)	0.069
Acer rubrum L.	(-)	0.200	(+)	0.649	(-)	0.000
Acer saccharum Marshall	(+)	0.800	(-)	0.020	(-)	0.029
Acer saccharinum L.	(-)	0.027	(-)	0.055	(-)	0.045
Alnus incana L. Moench	(-)	0.036	(+)	0.004	(-)	0.012
Betula alleghaniensis Britton	(+)	0.005	(-)	0.045	(+)	0.139
Betula papyrifera Marshall	(+)	0.000	(+)	0.036	(-)	0.026
Betula populifolia Marshall	(-)	0.018	(+)	0.051	(+)	0.004
Carpinus caroliniana Walter	(+)	0.007	(+)	0.000	(+)	0.000
Carya cordiformis Wangenh. K. Koch	(+)	0.019	(-)	0.021	(-)	0.076
Carya ovata Miller K. Koch	(-)	0.004	(+)	0.000	(-)	0.060
Fagus grandifolia Ehrh.	(+)	0.083	(-)	0.002	(+)	0.243
Fraxinus americana L.	(-)	0.012	(+)	0.038	(-)	0.140
Fraxinus nigra Marshall	(-)	0.035	(+)	0.036	(-)	0.029
Fraxinus pennsylvanica Marshall	(-)	0.152	(-)	0.197	(-)	0.088
Juglans cinerea L.	(-)	0.036	(+)	0.004	(-)	0.012
Ostrya virginiana Miller K. Koch	(-)	0.009	(-)	0.028	(-)	0.003
Picea rubens Sarg.	(+)	0.032	(-)	0.021	(+)	0.019
Pinus strobus L.	(-)	0.177	(+)	0.110	(+)	0.046
Populus grandidentada Michx.	(+)	0.000	(+)	0.038	(+)	0.020

Tree	**Sign**	**Axis 1**	**Sign**	**Axis 2**	**Sign**	**Axis 3**
Populus tremuloides Michx.	(+)	0.007	(-)	0.006	(+)	0.009
Prunus serotina Ehrh.	(-)	0.036	(+)	0.083	(-)	0.014
Prunus virginiana L.	(-)	0.029	(-)	0.029	(+)	0.041
Quercus macrocarpa Michx.	(+)	0.000	(+)	0.003	(+)	0.071
Quercus rubra L.	(-)	0.053	(-)	0.000	(-)	0.111
Tilia americana L.	(-)	0.031	(-)	0.102	(-)	0.308
Tsuga canadensis L. Carrière	(-)	0.008	(-)	0.218	(+)	0.331
Ulmus americana L.	(-)	0.163	(-)	0.071	(-)	0.026