

Université de Montréal

Évaluation de l'intégrité écologique des écosystèmes forestiers du Québec méridional

Développement d'une approche basée sur le fonctionnement et la structure du sous-bois

par

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Université de Montréal
Faculté des études supérieures

Cette thèse intitulée :

**Évaluation de l'intégrité écologique des écosystèmes
forestiers du Québec méridional
Développement d'une approche basée sur le fonctionnement et
la structure du sous-bois**

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Résumé

Prédire l'impact de l'anthropisation du domaine forestier est un défi pour les écologistes. Cette thèse propose une approche nouvelle d'évaluation de l'intégrité écologique fondée sur le sous-bois vu comme une force structurante de l'écosystème forestier. Plus spécifiquement, cette thèse synthétise la réponse de la végétation de sous-bois aux principales perturbations humaines de la forêt feuillue du Québec méridional à l'aide d'une classification de la flore basée sur les traits fonctionnels des espèces plutôt que sur la taxonomie. Une telle approche permet de dépasser les disparités régionales dans la distribution des espèces et ainsi obtenir un indicateur global de l'intégrité écologique de l'ensemble de l'écosystème. Cette thèse est divisée en trois volets portant sur autant d'aspects de l'impact de l'homme sur le domaine forestier :

L'intégrité écologique des érablières est évaluée par une comparaison de l'assemblage du sous-bois de forêts ayant un historique d'utilisation varié à celui de forêts anciennes non aménagées servant de référence pour le caractère naturel des forêts de ce domaine. Un résultat marquant de ce volet est la remarquable stabilité de la végétation de sous-bois des érablières. Après 200 ans de perturbations humaines, la structure du sous-bois et la répartition des groupes fonctionnels de sa flore demeurent semblables à celles de forêts non aménagées. Cependant, les résultats de ce volet laissent entrevoir certains risques de modifications de l'assemblage du sous-bois dans le futur qui pourraient affecter l'intégrité écologique des érablières, particulièrement avec une intensification des interventions humaines.

Le potentiel de restauration écologique de friches est analysé via l'étude de leur flore de sous-bois. Plus spécifiquement, ce volet défini la réponse de la végétation, identifie les espèces forestières sensibles et analyse leur rétablissement via l'étude de leurs traits fonctionnels le long d'une chronoséquence de friches issues de pâturage. Ce volet a démontré que la revégétalisation naturelle suite à une déprise agricole est globalement

efficace du point de vue du fonctionnement de l'écosystème. Elle peut cependant prendre des siècles avant d'être complétée. Le succès de rétablissement des espèces à colonisation limitée variait grandement, soulignant le rôle crucial mais méconnu de legs biologiques tels les individus survivant dans un environnement non forestier pour le potentiel de restauration naturelle des anciennes terres agricoles.

À l'aide des traits biologiques, de la structure de la flore de sous-bois ainsi que des conditions environnementales en sous-bois comme indicateurs, ce volet détermine si les plantations peuvent développer les caractéristiques de forêts naturelles. Ce volet a démontré que les plantations de feuillues peuvent se naturaliser et devenir un habitat viable pour la flore de sous-bois. Pour sa part, le sous-bois des plantations de conifères suit un patron de développement différent que celui des forêts naturelles du Québec méridional. Les plantations de feuillues demeurent cependant plus pauvres en espèces forestières à haute valeur écologique que des sites d'âge similaire n'ayant pas été plantés. Ces résultats suggèrent que la capacité de naturalisation d'une plantation pourrait être améliorée par des modifications de nos pratiques sylvicoles.

Mots-clés : érablière, flore, forêt ancienne, forêt secondaire, groupe fonctionnel, perturbations humaines, plantation, restauration écologique, structure verticale.

Abstract

With an increasing proportion of natural forests being replaced by plantations or managed forests, evaluating the impact human-induced transformation of forests is a major challenge for ecologists. This thesis presents a new approach to evaluate forest integrity based on understory seen as an ecosystem driver. More specifically, this thesis synthesizes understory response to the principal human disturbances found in sugar maple-dominated stands of southern Québec, using a classification of the vegetation based on universal vegetation traits rather than on site-specific vegetation composition. This approach offers the possibility of inter-regional comparisons that could reveal patterns of organization that would be difficult to detect with a taxonomic approach. A global indicator of the ecological integrity of the entire ecosystem is then obtained. This thesis is divided in three parts which each focus on a different aspect of human impact on forest ecosystems:

Ecological integrity of sugar maple-dominated stands with a varying history of human disturbance is evaluated by the divergence of their understory species assemblages from those observed in comparable unmanaged forest. Overall, the understory vegetation assemblage was found to be relatively stable among all human disturbances investigated. However, our results suggest some issues of possible long-term conservation concern given a continuation of human disturbances.

With the goal of evaluating the potential of pasture to recover an understory flora similar to mature maple forests, changes in trait dominance and forest herb recovery were studied along a chronosequence which extended from active pasture to mature northern hardwood forest of pasture origin. This study indicates that abandoned pastures of the northern hardwood biome have a good potential for natural restoration. However, their complete restoration may take centuries. Sensitive forest herb species with limited dispersal mean were found to comprise a varying recovery capacity. These differences seem in part related to their potential to survive in a non-forested environment.

Using plant traits as well as understory structure and environmental conditions as indicators, this study evaluated the extent to plantations develop understory attributes comparable to natural forests. While the understory functional groups and environmental conditions of deciduous plantations converged toward those of natural forests, conifer plantations show a completely different pathway of understory development. However, richness of high ecological value forest species remains lower in deciduous plantations than in similar unplanted stands. These results suggest that the capacity of natural restoration of plantations may be enhanced with modification of our plantation management practices.

Keywords : ecological restoration, forest flora, human disturbance, old growth, functional group, plantation, second growth, sugar maple-dominated stand, vertical structure.

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Chapitre 1

Introduction

Introduction

Le deuxième millénaire voit la disparition des derniers pans de forêts naturelles à l'échelle de la planète dans un phénomène marqué d'anthropisation du domaine forestier (FAO, 2006). L'humain influence maintenant les moindres recoins de la planète, même les forêts, autrefois synonyme de la limite du non civilisé (Lund, 2007). L'impact de l'homme sur les écosystèmes forestiers non seulement s'accentue, mais se conjugue également à diverses échelles spatiales et temporelles, modelant l'assemblage des communautés végétales et créant de nouveaux agencements d'espèces. Pour répondre à nos besoins en fibre ligneuse, de vastes monocultures, qualifiées de « déserts verts » par les environmentalistes, voit le jour. Même les forêts naturelles non touchées directement par les interventions humaines le sont indirectement par la pollution de l'air, les changements climatiques, par des modifications des populations fauniques (ex : chevreuils; Boucher et al., 2004) ou par l'introduction d'organismes exotiques (ex : vers de terre; Bohlen et al., 2004).

Prédire l'impact de l'anthropisation du domaine forestier est un défi pour les écologistes. Notre connaissance du domaine forestier est solide en terme de ce qui est quantifiable. Par exemple au Québec, nous connaissons la superficie exacte de forêts qui a été coupée, déboisée ou replantée et nous utilisons des modèles sophistiqués permettant de prédire la croissance des arbres. Nous ne possédons cependant qu'une connaissance fragmentaire de la qualité de nos écosystèmes forestiers et de l'impact de nos interventions. Nous avons en fait bien de la difficulté à jongler avec la complexité des écosystèmes forestiers naturels de même que de définir ce qu'est un écosystème de qualité ! De plus, en entraînant une raréfaction des forêts naturelles, l'anthropisation du domaine forestier nous prive de témoin ou référence de ce qui est un milieu intègre. L'impact de l'homme sur les écosystèmes forestiers est donc non seulement une préoccupation majeure mais également difficile à évaluer.

Cette thèse relève ce défi et propose une approche nouvelle d'évaluation de l'intégrité écologique, basée sur le sous-bois vu comme une force structurante de l'écosystème forestier. La flore de sous-bois, de par sa sensibilité et sa rapidité de réponse aux perturbations nous apparaît comme un excellent indicateur de l'intégrité écologique de l'écosystème. Sa grande diversité fonctionnelle, structurelle et en composition, ainsi que ses nombreuses interactions avec différents niveaux trophiques en font une composante majeure de l'écosystème forestier. Des études récentes ont démontré son rôle déterminant dans le fonctionnement de nombreux écosystèmes forestiers (George & Bazzaz, 2003; Gilliam & Roberts, 2003; Nilsson & Wardle, 2005). Elle agit notamment comme filtre déterminant quelles espèces arborescentes pourront s'établir et composer la canopée de demain (George & Bazzaz, 2003; Nilsson & Wardle, 2005). Elle joue également un rôle déterminant sur la fertilité des sols, la disponibilité en élément nutritif et en lumière (Aubin, Beaudet & Messier, 2000; Nilsson & Wardle, 2005)

Dans le cadre de cette introduction, nous débuterons en discutant de la place occupée par la végétation de sous-bois dans les études en écologie forestière à la lumière des différents courants scientifiques et sociaux qui ont influencé cette discipline. Nous poursuivrons en présentant les connaissances actuelles sur le rôle de la végétation de sous-bois dans le fonctionnement des écosystèmes forestiers. Nous présenterons ensuite les principaux groupes d'espèces de sous-bois en fonction de leurs caractéristiques biologiques et de leur rôle spécifique dans l'écosystème. Nous terminerons en présentant l'approche que nous avons développée dans le cadre de cette thèse ainsi que les trois chapitres qui en découlent.

1.1 Place accordée à la végétation de sous-bois en écologie forestière

De tout temps, l'homme a inventorié la flore forestière dans le but d'exploiter ses richesses ou à titre d'attraits de curiosité et d'exotisme. L'écologie forestière est cependant une discipline récente apparaissant au début du 20^e siècle (Kimmins, 1987). Se détachant des études floristiques et taxonomiques du 19^e siècle, cette discipline s'intéresse à caractériser, comprendre et classifier les variations naturelles des écosystèmes forestiers. Se basant sur les nouvelles notions d'écologie (Warming, 1895) et d'écosystème (Tansley, 1935), son domaine d'étude s'étend à tous les niveaux d'organisations biologiques des écosystèmes forestiers. Cette discipline doit donc composer avec la complexité (Kimmins, 1987). Comme le souligne Dansereau (1951) : « All such endavours evoke the general problem of description of vegetation. What should be considered first, second and last ? How far can one simplify in order to present a synthesis? »

Dans cette recherche d'une approche permettant d'aborder cette complexité, il est possible de distinguer deux courants : une vision réductionniste et une vision holistique. Ces deux courants ont leur racine dans les débuts de la philosophie grecque entre la conception parcellaire de Héraclite et la vision unifiante de Parménide (Valcke, 1972). La vision réductionniste cherche à comprendre le fonctionnement de la nature par l'étude isolée de ses composantes. Trouvant ses fondements dans l'éthique victorienne, cette vision prône la domination de l'homme sur la nature par le raisonnement et le travail (Worster, 1992). À l'opposé, la vision holistique découle d'une philosophie organiciste. Elle est basée sur des notions d'interdépendance et de globalité et recherche une coexistence pacifique entre l'homme et la nature (Worster, 1992). Au 18^e siècle, ces visions se retrouvent déjà dans la vision romantique de la nature de White et Thoreau versus l'œuvre de Linné et ses successeurs (Worster, 1992). Elles sont bien représentées au 19^e siècle dans la vision individualistique de Darwin versus celle plus holistique de Humboldt (White, 1985). Dans

les prochaines pages, je présenterai l'évolution de l'écologie forestière à la lumière de ces deux visions ainsi que des différents courants sociaux et scientifiques du 20^e siècle qui l'ont influencée. Cette revue servira de base à une réflexion sur la place accordée à la végétation de sous-bois dans notre vision des écosystèmes forestiers.

1.1.1 1900-1950 : la classification des communautés végétales

La classification des communautés végétales a été une question longuement abordée en écologie, principalement dans la première portion du 20^e siècle. Les écologistes américains et européens ont développé des approches de classification très différentes reflétant leur préoccupation, leur histoire et leur territoire. Ces deux écoles accorderont une importance différente à la végétation de sous-bois dans leurs études. Ainsi, les écologistes européens poursuivent une longue tradition d'études floristiques. Les forêts sont plus petites et l'influence de l'homme prédomine souvent sur celle des variables environnementales (Whittaker, 1962). L'approche phytosociologique de Braun-Blanquet met l'emphase sur la composition floristique. La classification des communautés végétales est la base et le but de cette approche (Whittaker, 1962). Elle se fait selon des règles strictes en comparant des listes exhaustives (relevés) des espèces retrouvées dans des parcelles de petite taille qui sont choisies par l'investigateur. La végétation de sous-bois est étudiée de façon détaillée et sert d'indicateur d'un type de communauté (Whittaker, 1962).

Pour sa part, la jeune école de pensée américaine s'attaque de façon novatrice à un grand territoire forestier peu connu. Elle met l'accent sur les grands gradients environnementaux pour expliquer la distribution de la végétation. Les Américains s'intéressent peu à l'approche phytosociologique qu'ils trouvent fastidieuses, biaisées et essentiellement descriptives (Whittaker, 1962). Ils basent leur approche de classification des communautés végétales sur les espèces dominantes. La végétation de sous-bois n'est pas prise en compte, à l'exception d'espèces dominantes présentes sur un large éventail d'habitats, et seulement lorsqu'une classification fine est nécessaire (Whittaker, 1962).

Cette méthode rapide, à grande échelle, facile et flexible répond bien aux besoins des écologistes américains de l'époque qui ont un grand territoire à découvrir et peu de main-d'œuvre qualifiée pour le couvrir.

Les études américaines influencent rapidement l'ensemble de la communauté scientifique. L'américain F. Clements (1916) étudiant les prairies et les forêts de conifère de l'ouest américain révolutionne l'écologie avec sa théorie de la succession végétale. Il propose une vision holistique des communautés végétales (Worster, 1992). La communauté est perçue comme un organisme évoluant vers un état de climax stable. Les processus autogéniques y jouent un rôle déterminant (White, 1985; Glenn-Lewin & Van Der Maarel, 1992). Les espèces de sous-bois sont considérées comme un élément de cet organisme. Elles sont associées et subordonnées à un type de communauté précis. Elles ont leur rôle à jouer dans l'évolution de la communauté par le processus de réaction (modification des conditions environnementales par les espèces présentes).

Une confrontation des visions réductionniste et holistique s'est exprimée dans les vives critiques qu'a soulevées la théorie de Clements. Tandis que Clements affirmait que « le tout est d'avantage que la somme de ses parties » (Worster, 1992), ses détracteurs rejettait cette vision organiciste des communautés végétales. Ainsi, Tansley (1935) souhaite bannir du vocabulaire scientifique tous les termes à connotations anthropomorphiques tel que communauté (Worster, 1992). Il veut faire de l'écologie une discipline rigoureusement basée sur la quantification et l'analyse (Worster, 1992). Dans cette optique, il suggère le concept d'écosystème, basé sur la physique moderne. Il affirme qu'une « science adulte doit isoler les unités fondamentales de la nature et réduire son objet d'études à ses composantes individuelles » (Worster, 1992).

Pour Gleason (1926), qui penchait vers une vision réductionniste des associations végétales, les communautés ne sont que le résultat de coïncidence dans la distribution d'espèces possédant une tolérance environnementale similaire. Gleason met l'accent sur l'importance des processus stochastiques dans l'évolution des communautés végétales

(Whittaker, 1962; Kingsland, 1991; Glenn-Lewin et al., 1992). À partir de 1930, mais surtout après la mort de Clements en 1945, l'écologie forestière est de plus en plus influencée par Gleason et le courant réductionniste. Il faudra cependant attendre la fin des années 1950 et les travaux de Curtis (1959) et de Whittaker (1962) pour que la vision de Gleason soit testée et celle de Clements rejetée. Ces travaux transformèrent ainsi l'écologie des communautés vers un champ d'étude résolument orienté vers l'étude des populations les composant (Peet, 1991).

1.1.2 Les années 1950 - 1960 : la domination de l'homme sur la nature

L'Amérique d'après-guerre consacre la mainmise de l'homme sur la nature grâce à la technologie et la science (Valcke, 1972). Vernadsky (1945) annonce le début de la « noosphère », soit la domination de l'intelligence humaine qui remplace la biosphère. Fort de ce sentiment de supériorité, plusieurs domaines d'études basés sur la vision réductionniste voient le jour en écologie forestière. Laissant de côté les études comparatives basées sur l'observation des phénomènes naturels, les écologistes se lancent dans des études expérimentales. Sous l'influence de l'agronomie, les études en serre sont à la mode. L'étude des communautés se fait en terme de la dynamique des espèces qui la constituent, isolées de leur environnement. La classification des communautés perd graduellement de l'importance au profit d'études portant sur les facteurs environnementaux, les processus allogéniques et les études démographiques (White, 1985; Glenn-Lewin et al., 1992). Ces études, mettent l'emphase sur les espèces dominantes et rentables (les arbres) et accorderont peu d'importance à la diversité végétale (la végétation de sous-bois).

1.1.2.1 La classification des communautés végétales selon les grands gradients environnementaux

De nouvelles méthodes d'analyses de classification des communautés végétales utilisant les statistiques sont développées. Les développements récents dans le domaine de

l'informatique sont alors un outil précieux pour les écologistes. Curtis (1959) et Whittaker (1962) utilisent l'ordination afin de relier la distribution des espèces végétales aux grands gradients environnementaux. La présence de communautés est due à la dominance de certaines espèces (les arbres) qui ont la capacité d'exercer un contrôle sur le reste des espèces végétales. Les espèces de sous-bois s'associent à certains types d'arbres qui créent un environnement favorable à leur croissance. Cependant, cette association n'est pas fixe mais plutôt sous la forme d'un gradient d'occurrences (Curtis, 1959). Cette méthode de classification discrimine les communautés selon leur degré de similarité qui est basé sur le nombre d'espèces qu'ils ont en commun. La végétation de sous-bois est mesurée en terme de pourcentage d'occurrence et pris en compte à titre d'espèces prévalentes (espèces revenant le plus souvent pour un type de communauté donné) ainsi qu'à titre d'espèces modales (similaire au concept d'espèces indicatrices mais non testé statistiquement; Curtis, 1959). La végétation de sous-bois sert donc d'espèces discriminantes dans la comparaison de deux communautés.

À la même époque, Dansereau (1951) se détache de l'approche américaine en utilisant une méthode de classification proche de celle de l'école de Braun-Blanquet. Comme les Européens, il prend en compte la présence de l'homme comme facteur modifiant les communautés végétales et accorde une importance plus grande aux espèces de sous-bois. Par une méthode fortement hiérarchique et intégrée, il essaie de dépasser l'énumération d'espèces des études de floristique qui était courante à cette époque au Québec (e.g. Grandtner, 1966), pour plutôt s'attarder aux processus. Il prend en compte la végétation de sous-bois lorsqu'elle est abondante, exclusive ou indicatrice, et ce à un niveau hiérarchique bas (sociès).

1.1.2.2 Développement de la foresterie et de la sylviculture

Avec l'industrialisation et particulièrement à partir de la deuxième guerre mondiale, la demande en bois a décuplé. La discipline de la sylviculture, apparue en Europe depuis

déjà 300 ans, prend alors de l'essor à l'échelle mondiale. Elle a pour objectif une production de bois accrue (Oldeman, 1990). La sylviculture est influencée par l'agronomie et la notion de la suprématie de l'homme sur la nature. De vastes monocultures souvent composées d'espèces exotiques reconnues pour leur forte croissance virent le jour. La domestication des écosystèmes passe par leur simplification, ce qui facilite leur gestion. Tel que décrit par Holling et Meffe (1996), l'objectif est de maîtriser les systèmes naturels que l'on trouve imprévisibles et « peu productifs », afin de les transformer en systèmes productifs, prévisibles et rentables. Dans cette optique, la végétation de sous-bois est considérée comme inutile. La dynamique des espèces non commerciales est négligée tandis que les pratiques sylvicoles contribuent à la prolifération de certaines espèces au détriment de la régénération arborescente. La solution de l'époque pour maîtriser cette végétation est l'utilisation d'herbicides (ex: Vincent, 1965). En effet, c'est alors l'âge d'or de l'industrie chimique, une des principales bénéficiaires de la technologie d'après-guerre (Carson, 1962).

1.1.3 Les années 1970

Les études portant sur la dynamique des perturbations naturelles reçoivent un intérêt grandissant au courant des années 1970 (Kingsolver & Paine, 1991). Cet intérêt pour l'aspect dynamique des communautés végétales culminera dans les années 1980 notamment avec le livre de Pickett et White (1985) sur la dynamique des trouées. Les études en serre des décennies précédentes ont donné des résultats limités. On s'aperçoit que le comportement d'une espèce dans son milieu naturel diffère de celui en milieu contrôlé (White, 1985). De nombreuses études expérimentales en milieu naturel sont donc menées. Mais afin de répondre aux postulats méthodologiques, les écologistes privilégient l'étude de systèmes simples, faciles à échantillonner (Wilmanns, 1985). L'emphase est mise sur les facteurs allogéniques plutôt que sur les facteurs autogéniques qui sont des changements graduels produits de nombreuses interactions et donc difficiles à mesurer. Dans la même optique, les écologistes privilégient les études touchant la dynamique de la végétation à

l'échelle des populations plutôt que des communautés. L'approche découle donc d'une vision réductionniste. On décortique les écosystèmes et étudie les processus un à la fois, sans prendre en compte les multiples interactions entre les composantes et les processus d'un écosystème. La place accordée à la végétation demeure plutôt limitée et de nature descriptive.

1.1.3.1 Approche écosystémique

En marge du courant réductionniste qui prédomine à l'époque, la vision holistique regagne de l'importance avec le développement d'une approche écosystémique basée sur le concept d'écosystème de Tansley. Cette nouvelle vision holistique se détache cependant de la métaphore organiciste de Clements et recherche une compréhension globale du fonctionnement des écosystèmes par des études systématiques et quantitatives (Kingsolver & Paine, 1991). Par exemple, dès la fin des années 1960, Borman et Likens (1967) expliquent le cycle des éléments nutritifs par l'étude des flux d'énergie dans l'écosystème. À la même époque, Margalef (1968) et Odum (1969) appliquent la théorie de l'information afin de développer des patrons universels expliquant les processus régissant les écosystèmes (Glenn-Lewin et al., 1992). Les études de ce type demeurent cependant limitées en écologie forestière. Ces chercheurs proposent principalement une vision conceptuelle de la manière dont la nature devrait être plutôt qu'une théorie basée sur des données empiriques et testées. Ces théories demeurent difficilement vérifiables et applicables.

Dans cette nouvelle approche écosystémique, la végétation de sous-bois est perçue comme de l'information, de l'énergie et de la diversité. Elle est donc conceptuellement un élément important du système et la base de sa stabilité (Margalef, 1975). Cette approche met l'accent sur les interactions au sein de la communauté en tant que moteur des processus fondamentaux de l'écosystème.

1.1.3.2 Concept de compétition

Avec l'intérêt pour les perturbations, le développement de la foresterie et l'étude de systèmes simples, les interactions entre les espèces sont principalement perçues sous l'angle de la compétition. La végétation de sous-bois est donc étudiée en fonction de la compétition avec les espèces arborescentes. De nombreuses études sont menées portant sur les populations d'espèces envahissantes suite à des perturbations (Baker, 1972; Ford, 1975; Holm et al., 1977). Ces études apportent des connaissances sur la dynamique des espèces de sous-bois. Elles demeurent cependant limitées puisqu'elles ont comme postulat que ces espèces sont nuisibles.

1.1.4 Les années 1980 et le mouvement environnementaliste

Le mouvement environnementaliste prend de l'ampleur au cours des années 1980. Une transformation de la relation entre l'humain et la nature s'opère. L'humain prend conscience de son impact sur l'environnement, qu'il est dépendant de la nature et que la destruction de cette dernière pourrait entraîner sa propre destruction. Les environnementalistes désirent un retour à une vision holistique des écosystèmes forestiers. Plusieurs rejettent la technique et la science de type réductionniste qu'ils qualifient « de racine du mal » (Valcke, 1972). Prenant sa source dans le mythe de Frankenstein du 19^e siècle, une distinction est faite entre l'artificiel (les écosystèmes créés par l'homme) et la nature. La nature, anciennement lieu de sauvagerie, remplace maintenant dieu comme matière de divination (Oldeman, 1990).

Sensible à ce mouvement, l'écologie forestière cherchera à intégrer la vision holistique et les préoccupations sociales dans sa démarche scientifique. À l'aide de nouvelles méthodes d'analyses multivariées, elle cherchera à tester de façon expérimentale les théories avancées par l'approche holistique. Nous assisterons à un retour vers l'étude des facteurs autogéniques et le développement de nouveaux champs d'études reliés à

l'intérêt pour la biodiversité et la dynamique du sous-bois. À son tour, l'écologie servira de base scientifique aux revendications des environnementalistes. Le lien existant entre ce mouvement et cette discipline sera si fort jusqu'à occulter aux yeux de la population la différence entre la profession d'écogiste et les valeurs environnementalistes.

Le succès du livre de J.E. Lovelock publié en 1979 « La terre est un être vivant. L'hypothèse Gaïa » est représentatif de ce retour vers une vision holistique tant désiré par les environnementalistes (Lovelock, 1986). L'analogie établie entre la terre et un organisme vivant découle de la philosophie organiciste retrouvée dans l'œuvre de Clements. Lovelock met l'accent sur les interactions et le pouvoir de régulation homéostatique des composantes de l'écosystème Terre. Tous les organismes participent au grand réseau de la vie. En ce sens, même les plus petits organismes ont un rôle à jouer.

1.1.4.1 Études sur les facteurs autogéniques

Se basant sur le concept de niche écologique développé dans les années 1960, les facteurs autogéniques sont remis à l'étude avec Connell et Slatyer (1977). Selon ces derniers, les interactions entre espèces lors d'une succession végétale peuvent être résumées en 3 processus : l'inhibition (interaction négative), la tolérance (interaction neutre) et la facilitation (interaction positive). Ce concept est similaire à celui de réaction de Clements (Clements, 1916). Au cours des 20 dernières années, plusieurs études ont cherché à appliquer ce concept aux relations existant entre la végétation de sous-bois et la régénération lors d'une succession végétale (ex: Walker & Chapin, 1987; Gill & Marks, 1991; Berkowitz, 1995). Récemment, certains écologistes ont suggéré une application plus large du processus de facilitation (voir la revue de la littérature de Brooker et al., sous-presse). Ainsi, le processus de facilitation, qui ne jouerait qu'un rôle marginal lors d'une succession végétale, serait un facteur clé régulant la composition d'une communauté stable, en dehors d'un processus successional (Brooker et al., sous-presse). Les études mettant l'emphase sur le processus de facilitation accordent de l'importance à la végétation de sous-

bois dans le fonctionnement de l'écosystème, notamment en démontrant que celle-ci favorise le développement des espèces arborescentes (*nurse plant*). Une cohabitation est souhaitable, même du point de vue du rendement des espèces arborescentes. Le processus de facilitation est à la base de l'idée d'espèces compagnes en foresterie.

1.1.4.2 Études sur la phase d'établissement des espèces arborescentes

Au cours des années 1980 un nombre grandissant d'études s'intéressent à la phase d'établissement, notamment sous l'impulsion de Grubb (1986) et son concept de niche de régénération. De nombreuses études sur la germination et la croissance des semis d'arbre en milieu naturel sont donc menées (MaGuire & Forman, 1983; Gill & Marks, 1991; Simard, Bergeron & Sirois, 1998). Ces études prennent en compte la végétation de sous-bois en tant qu'environnement des semis. La végétation de sous-bois est représentée comme jouant un rôle majeur dans la phase d'établissement des semis puisque façonnant leur micro-environnement.

1.1.4.3 Biodiversité

Le développement du concept de biodiversité est fortement lié à la popularité croissante du mouvement environnementaliste. Le public et la communauté scientifique sont préoccupés par l'extinction d'espèces (Barbault, 1997). Les préoccupations sur la biodiversité amènent une modification importante dans notre perception de la forêt. On passe d'une vision d'exploitation d'une ressource vers une approche écosystémique. Les écologistes cherchent à donner une valeur écologique à toutes les composantes de l'écosystème forestier (Gilliam, Turrill & Adams, 1995; De Leo & Levin, 1997; Bengtsson et al., 2000). Il devient alors important de connaître la dynamique de l'ensemble des espèces, pas seulement par rapport à leurs relations avec les espèces commerciales, mais à titre de composante de l'écosystème forestier. La popularité de ce concept amène le développement de nouveaux sujets d'études portant sur la végétation de sous-bois,

notamment l'impact des coupes et des interventions sylvicoles sur la biodiversité (voir à ce sujet la revue de la littérature de Battles et al., 2001).

Dans les années 1980, les écologistes s'intéressent à la biodiversité principalement en terme de composition. Les écologistes traitent la diversité à l'échelle alpha (nombre d'espèces présentes dans un échantillon d'une communauté particulière) à l'aide des indices de Simpson et de Shannon (Pielou, 1965), et à l'échelle de diversité beta (variation en composition et en espèces entre 2 communautés adjacentes) à l'aide de coefficients de similarité (Legendre & Legendre, 1998). Les espèces rares sont aussi inventoriées et étudiées (Berg et al., 1994; Jolls, 2003) et un statut particulier leur est accordé (ex: Bouchard et al., 1983; Société de la faune et des parcs du Québec, 2000). Plus récemment, les écologistes se sont intéressés également à la diversité Gamma (d'une région géographique ou écologique donnée), à la diversité structurelle (niveau d'organisation et d'assemblage) et fonctionnelle (processus) (Noss, 1990). On prend conscience que les interventions humaines n'affectent pas seulement certaines espèces, mais également l'équilibre entre les espèces, l'écologie des communautés et le paysage dans son entier (Angelstam, 1997). La diversité alpha apparaît alors comme un outil limité pour évaluer l'effet de l'humain sur les écosystèmes (Chapin et al., 2000; Haeussler et al., 2002).

1.1.4.4 Études sur la végétation de sous-bois

Avant les années 1980, les études sur la végétation de sous-bois étaient principalement des études démographiques (ex: Tappeiner, 1971; Wilson & Fischer, 1977; Hibbs, 1979). La dynamique de la végétation de sous-bois était rarement étudiée à l'échelle de la communauté (White, 1985). Quelques articles publiés dans les années 1980 permettent d'apprécier l'éventail et la diversité des traits biologiques des espèces de sous-bois (Bierzychudek, 1982; Collins, Dunne & Pickett, 1985; Givnish, 1987). L'intérêt pour la biodiversité, pour le stade juvénile des espèces arborescentes et pour les facteurs autogéniques amène une volonté grandissante d'intégrer la végétation de sous-bois dans

l'étude des communautés. Le nombre d'études portant spécifiquement sur la végétation de sous-bois augmente. Certaines études s'intéressent à la dynamique de la végétation de sous-bois sous l'angle de sa relation avec la canopée (Veblen, Veblen & Schlegel, 1979b; Ehrenfeld, 1980; Hicks, 1980; Woods & Whittaker, 1981; MaGuire & Forman, 1983; Collins, Dunne & Pickett, 1985; Beaudet & Messier, 2002). D'autres études s'intéressent à la réaction de la végétation de sous-bois à la succession forestière (De Grandpré, Gagnon & Bergeron, 1993; Mabry & Korsgren, 1998), aux trouées (Collins, Dunne & Pickett, 1985; Moore & Vankat, 1986) et à l'impact des facteurs environnementaux sur la végétation de sous-bois à l'échelle des microsites (Beatty, 1984), et à l'échelle du paysage (Brosofske, Chen & Crow, 2001). Certaines études traitent également de l'impact de la végétation de sous-bois sur les conditions abiotiques en sous-bois (Aubin, Beaudet & Messier, 2000; Shropshire et al., 2001; Bartemucci, Messier & Canham, 2006). Flinn et Vellend (2005) ont recensé plus de 100 articles scientifiques portant sur le seul sujet de la colonisation de la flore forestière suite à l'abandon de terre agricole durant les 20 dernières années.

1.1.5 Place accordée à la végétation de sous-bois dans les études actuelles

En 1994, Matlack soulignait notre « monstrueuse ignorance » de la dynamique de la végétation de sous-bois et du besoin criant de recherche dans ce domaine (Matlack, 1994). Nous pouvons, je crois, affirmer que la communauté scientifique a répondu à cet appel. Notre connaissance de la végétation de sous-bois, qui demeurait essentiellement descriptive à la fin des années 1990 est maintenant beaucoup plus solide comme en démontre les revues de la littérature portant sur la végétation de sous-bois publiées récemment (ex: Flinn & Vellend, 2005; Hart & Chen, 2006). La dernière décennie de recherche a démontré tout à la fois le rôle déterminant de la végétation de sous-bois dans la dynamique forestière et la sensibilité de certaines de ses composantes aux perturbations anthropiques.

1.1.5.1 La végétation de sous-bois comme facteur déterminant dans le fonctionnement de l'écosystème

Suite à l'augmentation de nos connaissances sur la végétation de sous-bois, des études ont pu démontrer le rôle déterminant de la végétation de sous-bois dans le fonctionnement des écosystèmes forestiers. Par exemple en forêt boréale scandinave, Nilsson et Wardle (2005) qualifient la végétation de sous-bois de « forest ecosystem driver ». Ils ont démontré que la composition de la végétation de sous-bois de cet écosystème était un facteur déterminant pour la régénération arborescente, les propriétés du sol et la succession forestière. Ces auteurs soulignent qu'il reste beaucoup à apprendre sur le rôle de la végétation de sous-bois dans le fonctionnement de l'écosystème.

1.1.5.2 Sensibilité de la végétation de sous-bois aux perturbations humaines

Suite à l'anthropisation du domaine forestier et aux problématiques de conservation qui en découlent, les écologistes ont cherché à développer des outils de suivi des impacts des interventions humaines sur la qualité des écosystèmes. Le concept de santé de l'écosystème (Costanza, Norton & Haskell, 1992), profondément ancré dans la vision holistique de Clements, a ainsi vu le jour. Ce concept est basé sur l'idée que l'écosystème est une entité biologique fonctionnant et structurée comme un organisme (De Leo & Levin, 1997). Conçu pour servir de cadre d'évaluation de l'état d'un écosystème, ce concept a connu une certaine popularité. Cependant, il est fortement teinté d'anthropomorphisme, ne tient pas compte du caractère dynamique des écosystèmes, de même que du caractère flou de son assemblage (De Leo & Levin, 1997).

Aujourd'hui, le concept d'intégrité écologique a pris le pas sur celui de biodiversité et de santé (Karr & Dudley, 1981; Glenn, Webb & Cole, 1998). Ce concept, défini librement comme la capacité d'un système à maintenir une communauté comparable à celle d'un habitat naturel de la région, a l'avantage de prendre en compte le caractère complexe

et dynamique des écosystèmes (De Leo & Levin, 1997). La végétation de sous-bois n'y est pas prise en compte à titre d'espèce comme c'était le cas pour la biodiversité, mais plutôt dans son assemblage. Bien que conceptuellement adéquat, l'évaluation de l'intégrité écologique demeure difficilement réalisable sur le terrain. Théoriquement, pour y parvenir, il faudrait pouvoir quantifier les structures écologiques et les processus qui définissent le fonctionnement naturel d'une forêt, et ce à différentes échelles spatiales et temporelles. Dans la pratique, nous assumons qu'il y a atteinte à l'intégrité écologique d'un écosystème lorsque une espèce ou un élément structurel clé a disparu. De même, la comparaison à un état de référence est un point central du concept d'intégrité écologique. Cependant, il est de plus en plus difficile de trouver dans certaines régions des habitats naturels représentatifs avec l'augmentation de l'impact de l'homme sur le domaine forestier. En ce qui a trait à la végétation de sous-bois, sa caractérisation se bute également à la grande variation en espèces existant entre des écosystèmes similaires.

Déjà présent dans les travaux de Clements et de Braun-Blanquet au début du siècle, le concept d'espèces indicatrices acquiert une popularité toute particulière au courant des années 1990. Source d'une multitude de recherches (voir à ce sujet la revue de la littérature de Niemi & McDonald, 2004), il fut intégré par de nombreux pays, incluant le Canada et les Etats-Unis, dans leur programme de suivi des écosystèmes. Utilisé avec la faune, l'avifaune, et les insectes, ce concept fut également appliqué à la flore (ex: McLachlan & Bazely, 2001). Bien que l'objet de nombreuses critiques, notamment quant à la possibilité limitée de trouver des espèces indicatrices pouvant s'appliquer à une large région ou conditions de stations (Prendergast & Eversham, 1997), cette approche demeure populaire auprès du public et des agences gouvernementales. Dans le milieu scientifique, les espèces de sous-bois servent d'indicateurs de la qualité d'un site (Cserep, Standoval & Vanicsek, 1991; Strong et al., 1991; Meilleur, Bouchard & Bergeron, 1992) et de la conservation ou de la restauration de l'intégrité écologique d'un site (Nantel, Gagnon & Nault, 1996; Angelstam, 1998; McLachlan & Bazely, 2001).

L'approche par groupes fonctionnels est un indicateur plus holistique récemment développée en Europe. Prenant ses fondements dans les travaux de Grime (1979) et de Noble et Slatyer (1980), cette approche permet de généraliser la réponse des communautés végétales aux changements environnementaux et aux perturbations (Lavorel et al., 1997). Elle aborde la végétation de sous-bois sous l'angle de son rôle dans le fonctionnement de l'écosystème via ses traits écologiques (Walker & Chapin, 1987; Tilman et al., 1997). Cette approche est particulièrement adaptée à l'évaluation des impacts des activités humaines sur les écosystèmes.

1.1.6 Vers une intégration de la dynamique du sous-bois dans notre compréhension des écosystèmes forestiers

Compte tenu de sa diversité, il existe toujours relativement peu d'études portant sur la dynamique de la végétation de sous-bois. Notre connaissance du sous-bois demeure essentiellement descriptive. Nous manquons par exemple d'études à long terme ou sur une large échelle dépassant les disparités locales. Traditionnellement, les écosystèmes forestiers ont été principalement caractérisés en terme de leur strate arborescente, avec peu d'attention pour la végétation de sous-bois (McCarthy, 2003; Nilsson & Wardle, 2005). Par exemple au Québec, le ministère des Ressources naturelles n'inclus toujours pas l'échantillonnage des espèces de sous-bois dans leurs placettes permanentes. La canopée était considérée comme dominant les strates inférieures, non seulement physiquement, mais également dans les processus majeurs régissant l'écosystème (McElhinny et al., 2005). Ce qui se passait sous la strate arborescente était difficile à caractériser, sans valeur économique et considéré comme ayant peu d'importance pour le fonctionnement de l'écosystème.

Cette revue de la littérature a permis de discerner quatres facteurs pouvant avoir contribué à ce manque de connaissance sur la végétation de sous-bois. Sur le plan méthodologique : 1) les difficultés inhérentes à la caractérisation de la végétation de sous-

bois, et 2) la disponibilité d'outils ou de méthodes afin d'être en mesure de prendre en compte la diversité végétale. Sur un plan plus philosophique : 3) notre conception de la place de l'homme dans la nature, et 4) notre approche scientifique face à la complexité : réductionniste ou holistique ?

1.1.6.1 La caractérisation de la végétation de sous-bois

La végétation de sous-bois est complexe à étudier de par sa diversité et la multiplicité de ses interactions. Les études portant sur le sous-bois demandent un échantillonnage fastidieux. Par exemple, McCarthy, Small et Rubido (2001) ont démontré que le nombre de quadrats utilisé dans la majorité des études était généralement trop petit pour décrire la richesse en espèces, réduisant ainsi l'interprétation des résultats de ces études ainsi que notre capacité à tirer des conclusions claires quant à la dynamique de la végétation de sous-bois. De plus, la grande diversité de la végétation de sous-bois, les disparités régionales dans la distribution des espèces, ainsi que la forte corrélation entre les caractéristiques physiques ou régionales et l'historique d'utilisation, font que les résultats des études sur cette végétation demeurent souvent difficilement généralisables.

1.1.6.2 Limite des méthodes statistiques traditionnelles

Jusqu'à tout récemment, l'approche statistique traditionnelle ne permettait pas de prendre en compte les multiples interactions et la diversité du sous-bois. Comme le soulignait Margalef en 1975: « I stress that diversity has nothing to do with simple statistics, but with the expression of the dynamic properties of a complex system ». Ce manque d'outils a longtemps limité les écologistes forestiers. Cependant, les avancements dans le domaine des statistiques, notamment les analyses multivariées, apportent des outils pour l'étude de systèmes plus complexes et permettent donc d'intégrer la végétation de sous-bois. Par exemple, les approches directes d'analyses fonctionnelles telles que la méthode du 4^e coin utilisée au chapitre 3, permettent d'analyser en une seule étape les matrices floristique, environnementale et de traits biologiques, offrant ainsi une analyse

globale de l'impact de l'environnement sur les processus de l'écosystème (Dray & Legendre, soumis).

1.1.6.3 Notre conception de la place de l'homme dans la nature

Malgré la force du mouvement environnementaliste, nous concevons toujours la forêt comme une ressource à exploiter. Notre conception de la place de l'homme dans la nature nous fait apprécier celle-ci pour ce qu'elle a à nous offrir. La grande majorité des espèces de sous-bois n'ont pas de valeur monétaire directe et donc peu d'intérêt pour notre société.

1.1.6.4 Vision réductionniste ou holistique ?

À mon avis, un mouvement de balancier entre une approche réductionniste et une approche holistique d'aborder la complexité de la nature anime la recherche en écologie forestière. L'approche réductionniste nous a permis de développer de solides connaissances de phénomènes quantifiables, principalement au niveau de la dynamique des populations. Cependant, cette approche demeure limitée en ce qui a trait à l'étude du fonctionnement global des écosystèmes et des communautés.

L'approche holistique possède une propriété intégrative qui permet d'aborder différemment ces questions. Le paradigme actuel de s'inspirer des processus naturels, le concept d'intégrité écologique et l'intérêt grandissant pour le fonctionnement des écosystèmes sont selon moi de nature holistique, ce qui rend leur étude et application plus difficile dans notre cadre actuel d'analyse. Mais un changement de mentalité et les avancées récentes en statistiques nous permettent aujourd'hui d'appréhender la forêt de façon plus holistique et ainsi faire un pont entre Héraclite et Parménide.

1.2 Rôle de la végétation de sous-bois dans le fonctionnement des écosystèmes forestiers

Notre connaissance du rôle de la végétation de sous-bois, bien que toujours fragmentaire, a grandement augmenté au cours de la dernière décennie, démontrant tout à la fois le rôle déterminant de cette végétation dans la dynamique forestière et sa sensibilité aux perturbations humaines. Le rôle de la végétation de sous-bois est ici abordé sous l'angle de cinq attributs ou processus importants des écosystèmes forestiers : la stabilité, les interactions, la structure, la productivité et la chaîne alimentaire.

1.2.1 La stabilité

La végétation de sous-bois joue un rôle dans la stabilité de l'écosystème principalement par sa grande diversité structurelle, fonctionnelle et en composition. En forêt tempérée, la végétation de sous-bois représente la majeure partie de la diversité en espèces vasculaires (Flinn & Vellend, 2005). Bien que controversées (ex: May, 1975), plusieurs études ont démontré une relation existante entre la diversité en espèces et la stabilité d'un écosystème, soit théoriquement (De Leo & Levin, 1997; Peterson, Allen & Holling, 1998; Bengtsson et al., 2000; Drever et al., 2006) ou de façon empirique (Franck & Mc Naughton, 1991; Tilman & Downing, 1994; Naeem, 1998). La diversité augmente la probabilité d'inclure une espèce ou groupe d'espèces possédant un rôle clé dans l'écosystème (Chapin et al., 1997; Walker, Kinzig & Langridge, 1999). La présence de cette espèce augmenterait la stabilité de l'écosystème en réduisant les risques de grands changements dans les processus de l'écosystème en réponse à des variations dans les conditions environnementales (Tilman, Wedin & Knops, 1996; Chapin et al., 1997; Walker, Kinzig & Langridge, 1999; Drever et al., 2006). Le maintien de la diversité permettrait la conservation de la productivité de l'écosystème ainsi que des nombreux services écologiques qu'il nous procure (Vitousek et al., 1979; De Leo & Levin, 1997).

1.2.2 Les interactions

La végétation de sous-bois joue un rôle déterminant durant la phase d'établissement des semis d'arbre par ses interactions (Grubb, 1986; Gill & Marks, 1991; Puettmann, Krueger & Saunders, 2002). Ces interactions lors d'une succession végétale peuvent se résumer en 3 processus : la facilitation, l'inhibition et la tolérance (Connell & Slatyer, 1977). Dans le processus d'inhibition, la présence d'une espèce empêche la maturation, la croissance ou l'établissement d'une autre. De nombreuses études ont exploré ce type d'interaction entre les espèces arborescentes et la végétation de sous-bois (ex: Jobidon, 1995; Mallik, 2003). Dans le processus de facilitation, une espèce favorise l'établissement, la croissance ou le développement d'une autre espèce, généralement en modifiant les conditions environnementales. Ce processus, autrefois moins bien documenté que la compétition, fait maintenant l'objet d'un regain de popularité (Brooker et al., sous-presse). La littérature présente des exemples variés de facilitation, telles les espèces fixatrices d'azote (Walker & Chapin, 1987), le « nurse plant effect » où la présence d'arbustes favorise la survie et la croissance de semis d'arbre (Morgan, 1991; Gómez-Aparicio et al., 2004) ou le sumac qui favorise l'établissement des espèces climaciques en diminuant l'abondance des espèces herbacées (Werner & Harbeck, 1982). Le troisième processus, la tolérance, est plus difficile à démontrer. Généralement, lorsqu'il n'y a pas de tendance claire d'inhibition ou de facilitation, on dit qu'il y a tolérance (Gill & Marks, 1991). La facilitation ou l'inhibition peuvent être soit directe (les changements causés à l'environnement physique favorisent ou nuisent) ou indirecte (ont un impact à travers les activités d'un organisme qui lui est associé; Gill & Marks, 1991). La facilitation indirecte rejoint l'idée d'une facilitation par un tiers de Grubb (1986) où la présence d'une troisième espèce peut influencer le succès relatif d'établissement entre deux espèces.

Ces trois processus peuvent également se produire simultanément. Walker et Chapin III (1987) soulignent la multiplicité des interactions intervenant entre deux espèces. Pour

illustrer leur propos, ils présentent l'exemple de l'aulne et de l'épinette en Alaska. Ainsi, l'aulne favorise la croissance de l'épinette en enrichissant le sol et en fixant l'azote atmosphérique (facilitation directe). Cependant, le fort couvert de l'aulne inhibe la croissance de l'épinette (inhibition directe). Mais la présence du couvert d'aulne réduit la susceptibilité au broutage (facilitation indirecte). L'impact d'une espèce sur une autre peut être complexe et ne pouvoir se résumer à l'intérieur du concept de Connell et Slatyer (1977). Prenons l'exemple présenté par Puettmann, Krueger et Saunders. (2002) sur l'impact d'un couvert herbacé sur l'occurrence et l'intensité du broutage par le cerf en plantation. La présence de végétation réduit le broutage des semis en servant d'écran visuel (facilitation indirecte). Cependant, la composition de la végétation a aussi un impact sur le broutage, celui-ci devenant plus important si le semis est entouré d'espèces appréciées par les cerfs (ex : framboisier). Aussi, le couvert herbacé, en influençant la croissance (en hauteur et latérale) et la vigueur des semis, influence leur susceptibilité au broutage de même que leur taux de survie. Il existerait même des processus de facilitation indirecte entre deux espèces compétitrices (Brooker et al., sous-presse). Les interactions entre les plantes sont donc maintenant de plus en plus perçues dans un cadre plus large dépassant celui de la succession végétale, comme une balance complexe d'une série d'interactions positives et négatives (Brooker et al., sous-presse).

1.2.3 La structure

La structure de la biomasse aérienne de la végétation de sous-bois, tout particulièrement des arbustes, est très diversifiée. Elle joue un rôle régulateur sur de nombreux facteurs en sous-bois dont la disponibilité en lumière, la température et l'humidité (Grubb, 1986; Constabel & Lieffers, 1996; Aubin, Beaudet & Messier, 2000; Bartemucci, Messier & Canham, 2006). La structure de la végétation de sous-bois influence de façon différentielle l'établissement, la croissance, la germination et la mortalité des espèces, dont les semis d'arbre qui formeront la canopée de demain (MaGuire & Forman, 1983; Grubb, 1986; Cornett, Puettmann & Reich, 1998). La structure de la végétation de

sous-bois affecte également de nombreux autres processus tels que la dispersion des semences (Gill & Marks, 1991) et l'herbivorie (Boucher et al., 2004). Moins connue, la structure de la biomasse souterraine de la végétation de sous-bois influence notamment la disponibilité en eau et en éléments nutritifs (Kolb & Steiner, 1990; Muller, 2003; Nilsson & Wardle, 2005).

1.2.4 La productivité

La végétation de sous-bois possède généralement une production de la biomasse bien moins importante que celle des espèces arborescentes. Cependant, la végétation de sous-bois ne suit pas le même patron d'accumulation de la biomasse en fonction du temps que les arbres. L'acquisition des ressources et le recyclage des éléments nutritifs par cette végétation est plus rapide que celui des arbres (Nilsson & Wardle, 2005). Par exemple en forêt boréale suédoise, la productivité nette des arbustes de sous-bois représente plus de 50 % de celle des arbres (Nilsson & Wardle, 2005). La végétation de sous-bois constitue donc une part non négligeable du total des flux d'éléments nutritifs dans de nombreux écosystèmes forestiers (Peterson & Rolfe, 1982; Zak et al., 1990; Nilsson & Wardle, 2005).

La phénologie et la nature éphémère d'une proportion importante de leurs tissus, confèrent aux herbacées des caractéristiques particulières (Muller, 2003). À titre d'exemple, le « vernal dam hypothesis » (Muller, 2003) fait référence à l'habileté de certaines herbacées, notamment les printanières en érablière, d'immobiliser dans leur biomasse des éléments nutritifs qui autrement auraient été lessivés. La quantité, la qualité, de même que le taux de décomposition de la litière de la végétation de sous-bois influencent notamment les propriétés physico-chimiques, l'activité microbienne, la température, l'humidité du sol, la qualité du substrat et la présence de mycorhizes (Yarie, 1980; Facelli & Pickett, 1991; Gill & Marks, 1991; Nilsson, Wardle & Dahlberg, 1999; Baskin & Baskin, 2001; Nilsson & Wardle, 2005). Ceci a un impact direct sur la disponibilité en microsites favorables à l'établissement de nombreuses espèces herbacées et

arborescentes (Ehrenfeld, 1980; Cornett, Puettmann & Reich, 1998; Simard, Bergeron & Sirois, 1998; Baskin & Baskin, 2001). L'association particulière de certaines espèces de sous-bois avec des mycorhizes joue également un rôle notable sur la productivité de l'écosystème (Allen & Allen, 1990; Whigham, 2004).

À court terme, la réponse vigoureuse de certaines espèces de sous-bois suite à une perturbation est reconnue pour diminuer la productivité des espèces commerciales (Jobidon, 1995). Cependant, du point de vue de l'écosystème, cette revégétalisation réduit le lessivage et favorise la rétention des ressources à l'intérieur de l'écosystème (Bormann & Likens, 1987). Ce rapide recyclage permet une redistribution des éléments nutritifs et préserve la fertilité des sols ainsi que la productivité à long terme (Marks, 1974; Hooper & Vitousek, 1998). Également, certaines espèces telles l'aulne et les légumineuses peuvent contribuer à l'enrichissement du sol en fixant l'azote atmosphérique (Chapin, 1980).

1.2.5 La chaîne alimentaire

Les espèces de sous-bois servent également de nourriture, d'habitats et de ressource pour la faune (Keenan & Kimmins, 1993). Elles sont un maillon important de la cascade trophique. La diversité en plantes vasculaires favorise la diversité d'autres organismes tels les insectes (Murdoch, Evans & Peterson, 1972; Haddad et al., 2001). La composition et la structure de la végétation de sous-bois influencent notamment l'activité des pollinisateur, la dispersion et la prédation des semences, de même que la présence des pathogènes (Thompson, 1986; Gill & Marks, 1991). Une large fraction des multiples relations de mutualisme existant entre la végétation de sous-bois et d'autres organismes demeure cependant encore méconnue.

1.3 Caractéristiques biologiques des espèces et fonctions spécifiques dans l'écosystème

La végétation de sous-bois est diversifiée, notamment en ce qui concerne les caractéristiques biologiques et les stratégies de ses espèces. Cette diversité leur permet de se partager les ressources disponibles (Hooper & Vitousek, 1997). Par exemple, certaines espèces profitent des ouvertures de la canopée suite à la sénescence d'un arbre (Ehrenfeld, 1980; Collins, Dunne & Pickett, 1985; Canham, 1989) tandis que d'autres espèces croissent et fleurissent au printemps avant le débourrement des arbres (Givnish, 1987). Cette différenciation permet une complémentarité dans l'utilisation des ressources (Hooper & Vitousek, 1997). Cette complémentarité s'exprime dans l'espace (structure), dans le temps (phénologie) et dans les préférences (ex : éléments nutritifs). La sensibilité des espèces aux perturbations anthropiques ainsi que leur rôle dans le fonctionnement de l'écosystème varient également selon cette différenciation. Je présenterai ici les groupes d'espèces généralement définis dans la littérature pour la forêt décidue de l'est de l'Amérique du nord, leurs principales caractéristiques biologiques, leur réponse aux perturbations humaines ainsi que leur rôle spécifique dans l'écosystème.

1.3.1 Espèces résidantes versus espèces en transition

Une première distinction peut être faite selon que les espèces sont en transition ou résidantes (Gilliam & Roberts, 2003). Les espèces résidantes sont les herbacées et arbustes de sous-bois qui demeurent en permanence dans cette strate. Les espèces en transition sont les arbustes et semis d'arbre qui ont le potentiel d'émerger de cette strate (d'atteindre la canopée). Je présenterai ici seulement les espèces résidantes.

1.3.2 Espèces de milieux ouverts

1.3.2.1 Caractéristiques

Les espèces de milieux ouverts se régénèrent rapidement suite à une perturbation, par propagation clonale, à l'aide de banque de graines ou à l'aide d'un mécanisme de dispersion des semences à longue distance (ex : anémochorie). Ces espèces possèdent des adaptations physiologiques leur permettant une croissance rapide en pleine lumière (Collins, Dunne & Pickett, 1985). Une large proportion de ces espèces est exotique, possède une courte longévité ainsi qu'une production importante de petites semences (During et al., 1985; Newsome & Noble, 1986).

1.3.2.2 Rôle

Ces espèces fixent les conditions initiales de la succession. Leur développement permet une revégétalisation rapide, favorisant ainsi la résilience de l'écosystème (Marks, 1974). En possédant une croissance rapide et production de litière importante, elles permettent un cyclage rapide des éléments nutritifs. Suite à une perturbation, ces espèces sont en interaction avec les semis d'arbre. Cette relation est souvent décrite en terme de compétition, mais elle peut également se traduire par une facilitation (voir section précédente). Ces espèces jouent également un rôle important dans la diversité structurelle. Bien que les espèces exotiques sont potentiellement nuisibles pour les espèces indigènes, celles associées aux milieux ouverts sont rarement envahissantes en forêt (Hendrickson, 2002).

1.3.2.3 Réaction aux perturbations

Les perturbations sont nécessaires pour le maintien de la population de ces espèces. Elles sont généralement favorisées par les activités humaines tel l'aménagement sylvicole (Nyland, 1996), et la fragmentation du paysage (Charbonneau & Fahrig, 2004).

1.3.3 Espèces forestières associées aux trouées

1.3.3.1 Caractéristiques

Une large proportion des arbustes de sous-bois est associée aux trouées. Ils se reproduisent généralement par propagation clonale et sont très plastiques. Les attributs de leur population fluctuent selon le cycle des perturbations (ex: érable à épis; Aubin, Messier & Kneeshaw, 2005). Les herbacées associées aux trouées peuvent être divisées en 2 groupes. Les « fugitives », associées aux grandes trouées, possèdent une bonne dispersion et une importante production de semences. Les « mouvantes », associées aux petites trouées, ont une banque de semences et produisent moins de semences (Collins, Dunne & Pickett, 1985; During et al., 1985).

1.3.3.2 Rôle

Cette végétation sert de régulateur. Elle assure une résilience et une résistance, et est ainsi un facteur de stabilité de l'écosystème (Marks, 1974). Elle influence directement l'établissement des semis en structurant le patron lumineux, en modifiant la disponibilité des éléments nutritifs par les caractéristiques de sa litière et en créant des micro habitats favorables de façon différentielle selon l'espèce. Elle possède un impact indirect notamment par son interaction avec la faune et les insectes.

1.3.3.3 Réaction aux perturbations

Ces espèces sont généralement favorisées par les activités humaines (Collins, Dunne & Pickett, 1985; Jobidon, 1995; Royo & Carson, 2006).

1.3.4 Espèces forestières

1.3.4.1 Caractéristiques

Pour leur part, les espèces exclusivement forestières maximisent l'utilisation des ressources en maintenant une biomasse souterraine importante, en possédant une association avec des mycorhizes et en ayant une croissance lente (Collins, Dunne & Pickett, 1985; Graae & Sunde, 2000; Whigham, 2004). Les herbacées forestières tolérantes à l'ombre ont généralement une période juvénile longue et une période de reproduction étendue sur de nombreuses années (Bierzychudek, 1982; Whigham, 2004). Les semences sont peu nombreuses mais grosses, ce qui permet la germination en condition ombragée et de percer la litière (Leishman & Westoby, 1994; Eriksson, 1995; Whigham, 2004). Leurs semences sont généralement dispersées à courte distance par la gravité, les insectes ou les petits mammifères (Bierzychudek, 1982; Whigham, 2004). Il y a très peu d'espèces annuelles.

Certaines de ces espèces sont exclusives aux habitats d'intérieurs ou aux forêts naturelles non aménagées. Leur croissance lente, leur faible production de semence et leur dispersion limitée (barochore ou myrmécochore) en font des espèces sensibles aux perturbations (Bierzychudek, 1982; Meier, Bratton & Duffy, 1995; Bellemare, Motzkin & Foster, 2002; Jolls, 2003; Godefroid, Rucquoij & Koedam, 2005).

1.3.4.2 Rôle

Cette végétation est diversifiée. Elle est fréquemment associée à des mycorhizes (Whigham, 2004). Les relations existant entre les espèces forestières et les herbivores, les pathogènes, les prédateurs de semences et les vecteurs de dispersion sont méconnues.

1.3.4.3 Réaction aux perturbations

Certaines espèces forestières associées aux habitats d'intérieur sont reconnues comme sensibles aux perturbations humaines, principalement à la discontinuité forestière (Wulf, 1997; Herault & Honnay, 2005; Vellend et al., 2006), à la compétition avec les espèces de milieux ouverts (Meier, Bratton & Duffy, 1995) ainsi qu'à des modifications des propriétés du sol et de la micro topographie (Beatty, 2003; Flinn, 2006; Flinn & Marks, 2007).

1.4 Approche de la thèse

Évaluer l'intégrité écologique d'un écosystème demeure un défi pour les écologistes. Théoriquement, pour y parvenir, il faudrait pouvoir quantifier les structures écologiques et les processus qui définissent le fonctionnement naturel d'une forêt, et ce, à différentes échelles spatiales et temporelles. Dans la pratique, nous présumons qu'il y a atteinte à l'intégrité écologique d'un écosystème lorsqu'une espèce ou un élément structurel clé a disparu.

L'intégrité écologique, c'est la capacité d'un écosystème à supporter et à maintenir une communauté en équilibre, intégrée et en constante adaptation, d'organismes ayant une composition, une diversité et une organisation fonctionnelle comparables à celles des habitats naturels de la région, et ce, dans l'échelle de variabilité naturelle de ce type d'écosystème (modifié de Frego, 2007; Karr & Dudley, 1981). Ce concept est largement intégrateur puisqu'il inclut notamment l'âge de la forêt, la continuité forestière, le patron de perturbation et la biodiversité (Frego, 2007).

Une comparaison à un état de référence est nécessaire. Tout état de référence est implicitement basé sur un échelle de temps et d'espace et doit prendre en compte la variabilité naturelle d'un écosystème ainsi que ses sources de variation (White & Walker,

1997). L'état de référence peut provenir d'une reconstitution historique (même lieu, temps différent) ou à partir d'information contemporaine provenant d'un site de référence (lieu différent, même temps; White & Walker, 1997).

La reconstitution historique demande un effort considérable de recherche afin de documenter l'état pré-perturbation anthropique. Elle permet de retracer assez précisément la composition de la strate arborescente. Cependant, il est beaucoup plus difficile de statuer sur les autres composantes de l'écosystème forestier telle la végétation de sous-bois.

Le choix d'une forêt naturelle comme état de référence a l'avantage de permettre d'y mesurer la variable qui nous intéresse, avec l'échelle de précision désirée. Cependant, elle comporte également certains biais. Ainsi, il est de plus en plus difficile de trouver des forêts naturelles dans certaines régions suite à l'anthropisation du domaine forestier. Ces stations ne représentent bien souvent qu'un échantillon de la variabilité spatiale et temporelle originale. Les forêts naturelles rémanentes sont souvent de petites superficies, localisées dans des sites non représentatifs et/ou dans un contexte spatial pouvant altérer les caractéristiques de l'écosystème (White & Walker 1997).

Une évaluation globale de l'intégrité écologique se heurte donc à son caractère intégrateur et au choix d'un état référence, mais également à la grande diversité des écosystèmes, aux disparités régionales dans la distribution des espèces, à la forte corrélation entre les caractéristiques physiques ou régionales et l'historique d'utilisation, ainsi qu'à la difficulté d'établir un dispositif expérimental regroupant l'ensemble des facteurs (incluant des forêts témoins représentatives) à l'intérieur d'une seule région.

Nous avons choisi dans le cadre de cette thèse d'évaluer l'intégrité écologique d'une station par une comparaison de l'assemblage de son sous-bois à celui de forêts naturelles non aménagées servant de référence pour le caractère naturel des forêts de ce domaine. Nous avons choisi des forêts anciennes identifiées par le groupe de travail sur les écosystèmes forestiers exceptionnels du Ministère des Ressources naturelles du Québec

comme forêts naturelles non aménagées. Ces forêts anciennes sont des écosystèmes forestiers ayant atteint un âge avancé et ayant conservé leur caractère naturel. Ainsi, elles ont subi peu d'interférences humaines et possèdent une dynamique propre établie historiquement avant l'arrivée des Européens (Leduc & Bergeron, 1998). Contrairement à la grande majorité des forêts anciennes du biome, celles que nous avons choisies étaient localisées dans une matrice forestière et étaient représentatives de leur région en terme de condition de sol et de topographie.

Tout en ne représentant qu'un échantillon de la variabilité spatiale et temporelle originale, la dynamique de perturbation des forêts anciennes feuillues est représentative du long cycle de perturbation naturelle de la forêt feuillue du Québec méridional. Dans cette optique, les forêts anciennes sont un état de référence adéquat pour les forêts matures. Afin d'obtenir un état de référence propre à la dynamique de peuplements immatures, une comparaison additionnelle à une chronoséquence naturelle a été ajoutée afin de prendre en compte les stades de développement (voir chapitre 4).

Afin d'obtenir une évaluation globale libre des problèmes liés aux disparités régionales et de raréfaction des forêts naturelles, nous avons choisi de mettre l'accent sur les traits biologiques des espèces plutôt que sur la composition en espèces. Nous proposons dans cette étude une approche combinant deux niveaux d'analyse de l'assemblage de la communauté végétale de sous-bois : la structure et les groupes fonctionnels.

1.4.1 Groupes fonctionnels

Depuis quelques années, plusieurs études ont utilisé une approche dite par groupes fonctionnels (ex: Lavorel et al., 1998). Les traits biologiques des espèces sont utilisés comme alternative à la classification taxonomique, afin d'étudier l'impact des perturbations sur les communautés végétales (Gachet, Véla & Tatoni, 2005). Tout d'abord mené en milieux ouverts (Lavorel et al., 1998; Hadar, Noy-Meir & Perevolotsky, 1999; Barbaro et al., 2000), cette approche a récemment été utilisée pour caractériser la végétation en forêt

(Graae & Sunde, 2000; Herault & Honnay, 2005), dans les haies (Deckers et al., 2004; Roy & de Blois, 2006) et en plantation (Ramovs & Roberts, 2005; Gachet et al., 2007). L'approche par groupes fonctionnels permet de regrouper les espèces ayant développé des stratégies adaptatives convergentes, en présentant des processus similaires d'allocation des ressources entre leurs différentes fonctions vitales en fonction de l'environnement (Smith, Shugart & Woodward, 1997). L'hypothèse sous-jacente est que les processus importants d'un écosystème sont le produit de processus s'opérant au niveau des populations qui le composent, et que ceux-ci sont, quant à eux, la conséquence des traits biologiques des espèces (Peet, 1992). La définition d'un « groupe fonctionnel » varie selon les auteurs, selon que les espèces soient groupées uniquement en fonction de leurs traits (groupe émergent), de leurs traits et de leur réponse à un gradient environnemental (groupe réponse), ou de leur fonction dans l'écosystème (groupe effet; Lavorel et al., 1997).

Quel que soit le point de vue adopté, l'utilisation de groupes fonctionnels permet de s'affranchir de la taxonomie et de fournir un portrait synthétique de la communauté végétale. Basée sur les traits écologiques des espèces liés aux grands processus de l'écosystème, cette approche permet de dégager le rôle que sa végétation tient dans le fonctionnement de l'ensemble (Gitay & Noble, 1997; Hadar, Noy-Meir & Perevolotsky, 1999; Bond & Midgley, 2001). L'étude d'un écosystème complexe soumis à de nombreux régimes de perturbation est ainsi grandement facilitée (Gitay & Noble, 1997). Le recours aux groupes fonctionnels offre également la possibilité de comparaisons inter-régionales pouvant révéler des patrons d'organisation difficiles à détecter autrement à cause de différences de composition floristique causées par les disparités régionales et permet de s'affranchir des barrières biogéographiques, à différentes échelles spatiales (Tsuyuzaki & del Moral, 1995; Cramer, 1997; Leemans, 1997; Graae & Sunde, 2000).

1.4.2 Structure verticale

Nous avons combiné à cette approche la structure verticale de la végétation de sous-bois. La structure est produite par le développement de la végétation, mais façonne aussi les processus écologiques de la forêt, notamment en conditionnant le milieu abiotique (Spies, 1998). Cette variable peut être le premier indice d'une modification du fonctionnement de l'écosystème (Spies, 1998). Bien qu'il soit reconnu que les communautés végétales possèdent une stratification verticale multiple et variable (Terborgh, 1985), les études traitant de la structure verticale des communautés végétales en terme d'occupation de l'espace sont rares (Harcombe & Marks, 1977; Onaindia et al., 2004). La plupart des études s'intéresse en effet à la structure en terme d'abondance relative et de la distribution spatiale des arbres (il s'agit donc de la structure du peuplement au sens forestier du terme).

1.5 Lieu de l'étude

Nous avons choisi comme lieu d'étude le domaine de l'érablière du Québec méridional. Ces forêts possèdent une grande diversité se reflétant dans le large éventail de stratégies et de traits physiologiques, morphologiques et phénologiques qui caractérisent les espèces de ce domaine (Bierzychudek, 1982; Givnish, 1982; Collins, Dunne & Pickett, 1985; Neufeld & Young, 2003). L'enjeu de la préservation de leur intégrité écologique est une question cruciale puisqu'il s'agit d'une zone au capital écologique élevé soumis à une forte pression anthropique. Plusieurs espèces de sous-bois sont menacées de disparition locale ou régionale (ex : *Panax quinquefolium* L.; Nantel, Gagnon & Nault, 1996) tandis que la proximité de zones urbaine ou agricole favorise la propagation d'espèces exogènes potentiellement envahissantes (ex : *Alliaria petiolata*; Luken, 2003). L'évaluation de leur intégrité écologique est également un défi puisque cette zone a été fortement influencée par l'humain et qu'il ne reste que peu de forêts naturelles (Villeneuve & Brisson, 2003). Non seulement est-il possible d'y retrouver un large gradient d'historiques d'utilisation du

territoire, mais celui-ci varie régionalement et selon les caractéristiques physiques du milieu (Pan et al., 1999). Dans les régions propices à l'agriculture, l'homme est le principal agent structurant la dynamique forestière depuis plus de 200 ans (de Blois, Domon & Bouchard, 2001; Brisson & Bouchard, 2003). Les forêts de ces régions sont principalement des îlots résiduels de forêts secondaires en matrice agricole ou péri-urbaine. Plusieurs originent de friches et possèdent un agencement d'espèces altéré ainsi qu'une faible régénération arborescente (Singleton et al., 2001; Flinn & Vellend, 2005; Benjamin, Cogliastro & Bouchard, 2006; D'Orangeville, accepté). De grands massifs forestiers se trouvent dans d'autres régions, où la principale perturbation anthropique est l'exploitation forestière industrielle. Des forêts naturelles peu perturbées par l'homme peuvent être trouvées dans certaines zones difficiles d'accès de ces massifs. Les plantations occupent également une part de plus en plus importante du paysage forestier de ce domaine.

1.6 Structure de la thèse

Cette thèse apporte une connaissance globale de l'impact des interventions humaines sur l'intégrité écologique de nos forêts par l'utilisation d'une approche basée sur la végétation de sous-bois à titre de force structurante de l'écosystème forestier. Ancrée dans la vision holistique décrite précédemment, elle synthétise la complexité des écosystèmes pour n'en retenir que ce qui affecte les grands processus. Chacun des chapitres, rédigés sous forme d'article scientifique, porte sur un aspect différent de l'impact de l'homme sur le domaine forestier. Les annexes contiennent la liste des sources utilisées dans le développement de la base de données TOPIQ, la liste des stations géoréférencées et les spectres biologiques des stations utilisées au chapitre 2.

Chapitre 2.

How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach.

Isabelle Aubin, Sophie Gachet, Christian Messier et André Bouchard

Ecoscience 14 (2): 259-271

L'objectif de ce chapitre est d'évaluer l'intégrité écologique des érablières du Québec méridional par une comparaison de l'assemblage de leur sous-bois. Pour y parvenir, nous comparons le sous-bois de forêts ayant un historique d'utilisation varié à celui de forêts anciennes non aménagées servant de référence pour le caractère naturel des forêts de ce domaine. Puisque les activités humaines affecteraient les espèces différemment selon leurs traits biologiques, il serait possible d'associer des ensembles de traits à un type particulier d'intervention humaine, ou, de la même façon, à des forêts naturelles non aménagées. La répartition des traits biologiques retrouvés dans l'assemblage d'un sous-bois reflèterait donc l'historique des perturbations humaines. L'occurrence dans une station donnée d'espèces possédant des traits associés aux perturbations humaines indiquerait le degré auquel cette station a été altérée de son état naturel et pourrait servir d'indicateur de son intégrité écologique.

Chapitre 3.

Uses of two plant functional approaches to evaluate natural restoration along an old field-deciduous forest chronosequence

Isabelle Aubin, Marie-Hélène Ouellette, Pierre Legendre, Christian Messier et André Bouchard

Journal of Vegetation Science (soumis pour publication le 10 octobre 2007)

L'objectif principal de ce chapitre est de déterminer le potentiel de restauration écologique des friches agricoles via l'étude de leur flore de sous-bois. La question centrale de ce chapitre est : est-ce que la flore de sous-bois peut se restaurer naturellement dans ces

friches ? Et si c'est le cas, à quel stade de développement de la strate arborescente les processus de revégétalisation se produisent-ils ? Ces questions sont cruciales pour le domaine de la restauration écologique puisque ces friches sont traditionnellement considérées comme possédant peu de valeur tant écologique que commerciale et font face à de fortes pressions de conversion. Afin de mieux comprendre les processus de restauration naturelle, ce chapitre examine également les différences interspécifiques dans le potentiel de restauration de la flore de sous-bois. Pour y parvenir, ce chapitre définit la réponse de la végétation, identifie les espèces forestières sensibles et analyse leur rétablissement via l'étude de leurs traits fonctionnels le long d'une chronoséquence de friches issues de pâturage. L'hypothèse sous-jacente est qu'il serait possible de déterminer le succès de rétablissement d'une espèce selon ses traits biologiques. Si c'était le cas, il serait possible d'identifier des groupes d'espèces se rétablissant naturellement de ceux nécessitant une intervention, ce qui faciliterait grandement les activités de restauration. Finalement, deux types d'analyses basés sur les traits fonctionnels des espèces ont été comparés afin de déterminer leur capacité à synthétiser de façon adéquate le potentiel de restauration de ces friches.

Chapitre 4.

Can plantations develop understory biological and physical attributes of natural forests?

Isabelle Aubin, Christian Messier et André Bouchard

Biological Conservation (soumis pour publication le 15 août 2007).

Les plantations occupent une part grandissante du paysage forestier québécois. À l'aide des attributs fonctionnels et structurels du sous-bois comme indicateurs, l'objectif de ce chapitre est de déterminer si les plantations peuvent éventuellement développer les caractéristiques de forêts naturelles. Les questions posées sont celles-ci : Les plantations peuvent-elles devenir un habitat viable pour la flore de sous-bois ? Si c'était le cas, est-ce que leur potentiel varierait selon le type de plantation ? Est-ce que la plantation d'une strate

arborescente accélère le développement de la flore de sous-bois ? Plus spécifiquement, nous analysons le développement de la végétation de sous-bois en termes de ses traits biologiques, de sa structure ainsi que des conditions environnementales en sous-bois. Nous comparons ensuite le sous-bois de plantations de feuillues et de conifères à différents stades de développement, à des stations non plantées et des forêts matures naturelles.

Chapitre 2

How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach

Ce chapitre a fait l'objet d'une publication:

Aubin, I., Gachet, S., Messier, C., et A. Bouchard. 2007. How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach. *Ecoscience* 14 (2): 259-271

Abstract

Evaluating forest ecological integrity remains a major challenge for ecologists. We analyzed understory vegetation using an approach that combined plant functional types and vertical stratification to evaluate the effects of human disturbances on the ecological integrity of sugar maple-dominated stands of southern Québec. Ecological integrity was evaluated by the divergence of understory species assemblages from those observed in comparable unmanaged forest. Multivariate analyses of biological traits revealed 13 emergent groups that share common traits associated with a similar life history strategy. Responses of these groups, of specific traits, and of understory structure to different human disturbance were tested. Nine of the 13 emergent groups varied in occurrence or diversity among disturbance types. Analyses also revealed a set of traits specifically associated with unmanaged old growth forest, indicating that species possessing these traits may be sensitive to human disturbance. Overall, the understory vegetation assemblage was found to be relatively stable among all human disturbances investigated. However, our results suggest some issues of possible long-term conservation concern given a continuation of human disturbances: (i) an increase of species associated with open environment, including exotic species; (ii) a decrease of spring geophytes; (iii) a decrease of certain shade tolerant forbs; and (iv) a modification of understory structure by the development of a dense sapling stratum.

Keywords: old growth, plant biological traits, second growth, single-tree selection harvest, understory flora, vertical structure.

Nomenclature: Gleason & Cronquist (1991)

Introduction

Despite the increasing human-induced transformation of forests all around the world, evaluating forest ecological integrity, defined broadly as the capability of a system to maintain a community comparable to that of a natural habitat of the region (Karr & Dudley, 1981), remains a challenge for ecologists. In essence, the challenge centers on quantifying ecological structures and processes that define the ‘natural’ functioning of a forest at different spatial and temporal scales (De Leo & Levin, 1997). Often, we assume a forest has lost its ecological integrity when the disappearance of key structural elements or species can be identified. This identification requires an adequate control or reference point of the natural state as well as the determination of what constitute key elements to monitor.

In this study, we used understory functional and structural attributes to evaluate ecological integrity. Understory flora may be a suitable key element with which to monitor ecological integrity because of its great diversity as well as its important role in ecosystem functioning (George & Bazzaz, 2003; Gilliam & Roberts, 2003; Nilsson & Wardle, 2005). Moreover, because of life history characteristics of its component species, the understory stratum is likely more sensitive to disturbances or to changes in environmental conditions than the overstory (Bratton, 1994; Moffatt & McLachlan, 2004; Flinn & Vellend, 2005).

Numerous studies in northern hardwood forests have addressed the impact of human disturbances on understory species composition (see Roberts & Gilliam, 2003) and diversity (see Battles et al., 2001). However, the substantial variation in their conclusions illustrates the site-specific nature of floristic responses to disturbance (Gilliam & Roberts, 2003; Moffatt & McLachlan, 2004). This highlights the difficulties in evaluating ecological integrity across a vast region or range of stand conditions that arise from the great diversity of forest understories, regional differences in species distributions and strong correlations between physical or regional characteristics and land use history. Therefore, to allow generalization, several authors have suggested emphasising functional traits rather than taxonomic differences when analyzing plant community responses to disturbance (McCarthy, 2003; Moffatt & McLachlan, 2004). Over the last decade, classifications based on plant functional types (PFT) have been widely used to study vegetation processes (e.g. Smith, Shugart & Woodward, 1997). More recently, PFT have been

used for understanding ecosystem responses to land-use change (e.g. Verheyen et al., 2003; Kolb & Diekmann, 2005). While the definition of PFT depends on the authors, generally, PFT are species groups that have evolved convergent life history strategies by developing similar processes of resource allocation among their various vital functions in relation to prevailing environmental factors (Smith, Shugart & Woodward, 1997).

We evaluated assemblages of understory species in sugar maple (*Acer saccharum*) stands, a dominant forest type of the northern hardwood biome. These forests have a high diversity that is reflected in the broad range of life-history strategies and physiological, morphological and phenological traits that characterize the shrubs and herbs of these forests (Bierzychudek, 1982; Collins, Dunne & Pickett, 1985). From a conservation perspective, sugar maple forests have been and will very likely continue to be subjected to numerous human pressures. They contain many understory species threatened with local or regional extinction (e.g. *Panax quinquefolius* and *Allium tricoccum*; Nantel, Gagnon & Nault, 1996) and, due to their proximity to major urban or agricultural areas, are increasingly faced with potentially invasive exotic species (e.g. *Alliaria petiolata*; Luken, 2003).

Sugar maple forests are highly heterogeneous in their land use history. Regional variation in land use is frequently related to biophysical characteristics (Pan et al., 1999). For example, in flat, productive regions, forests are typically residual fragments of second growth forests embedded in an agricultural or peri-urban matrix. In remote or hilly regions, sugar maple forests can occur in extensive tracts where the principal disturbance is forest harvesting. While stands with little history of human disturbance are found in these tracts, such stands are extremely rare in the agricultural matrix (Villeneuve & Brisson, 2003). This regional variation complicates the design of a sampling strategy that encompasses forests subjected to all of the possible types of human disturbance as well as unmanaged forests.

Because it is based on universal vegetation traits rather than on site-specific vegetation composition, PFT are independent of biogeographic barriers and offer the possibility of inter-regional comparisons (Tsuyuzaki & del Moral, 1995; Cramer, 1997; Leemans, 1997; Graae & Sunde, 2000; Verheyen et al., 2003). This approach may reveal patterns of organization that are difficult to detect using an approach based solely on differences of floristic composition, as such differences can arise from regional variation in climate or geology. In other words, a PFT

approach makes it possible to compare ecosystems that differ in composition but possess similar underlying ecological processes and functions.

Our objective was to evaluate the ecological integrity of sugar maple forests by comparing the understory of forests with a varying history of human disturbance as well as unmanaged old growth forests that represent natural states. As human disturbances are likely to affect species differently according to their particular biological traits (McIntyre, Lavorel & Tremont, 1995; Roberts & Gilliam, 2003), it may be possible to associate certain sets of traits with particular human disturbances (Table 2.1) or, conversely, with natural unmanaged forests. The extent to which a given assemblage possesses the former trait set can reflect its history of human disturbance. Moreover, the abundance in a given stand of species possessing these ‘human-disturbance’ traits indicates the degree to which the stand has been altered from its unmanaged state and may provide a surrogate measure of its ecological integrity.

In our study, PFT were combined with measures of vertical stratification of the understory vegetation to provide a more complete portrait of vegetation assemblages than that garnered by using functional types alone. Structure is the result of vegetation development and can greatly influence several ecological processes by, for example, modifying aspects of the abiotic environment such as light and moisture availability (Spies, 1998). Moreover, structural changes can provide the first indication of a modification in ecosystem functioning (Spies, 1998).

Tableau 2.1. Literature review of biological traits associated positively (+) or negatively (-) with human disturbance types sampled in the present study.

Disturbance type	Biological traits
<i>Forested matrix</i>	<ul style="list-style-type: none"> + Short geophytes ¹² + Insect pollinated species ¹⁴ + Gravity or animal-dispersed perennial species ¹²
Old growth forest	<ul style="list-style-type: none"> + Perennial, native species ³ + Geophytes and hemicryptophytes ¹³ + Ant or gravity-dispersed species with large seed size ^{7, 18} + Species with low seed production and with limited dispersal ¹³ + Species with large storage organ ^{22, 23} + Shade tolerant species ^{13, 22, 24} + Saprophyte species ¹¹
Recent single-tree selection harvest *	<ul style="list-style-type: none"> + Annuals ^{10, 21} + Shade intolerant and mid-shade tolerant species ⁵ + Species with seed bank ⁸ + Species dispersed by wind or animal ingestion ^{10, 18} + Species with strong vegetative propagation ⁸ + Summer or fall flowering species ²¹ - Shallow rooted herbs ¹⁹ - Slow growing species ¹⁹ - Species with long juvenile period ¹⁹ - Saprophyte species ¹¹ - Low seed production and limited dispersal ¹⁹
Old single-tree selection harvest*	<ul style="list-style-type: none"> + Tall herb ¹⁹ + Woody species ^{1, 10} + Species dispersed by animal ingestion ¹⁰ + Species reproducing by vegetative propagation ¹⁰

<i>Agricultural matrix</i>	+ Exotic species ⁴ + Wind, animal and bird-dispersed species ^{16, 20} - Species dispersed by gravity, explosive discharge or ants ^{12, 20} - Insect-pollinated species ¹⁵ - Low stature species ¹⁵ - Species with heavy and short lived seeds ¹⁵
Undisturbed forest	+ Chamaephytes and – therophytes ⁹ + Species with large seed size ⁹ dispersed by gravity or ants ^{2, 9} + Shade tolerant species ⁵ + Species with early and short flowering time ⁹
Maple syrup production stands	- Tree seedlings and saplings ²⁵
Second growth forest of old pasture origin	+ Short life-span species ⁶ + Wind pollinated species ⁶ + Species with long distance seed dispersal ^{2, 6, 17} , by humans or animal adhesion ⁹ + Species with seed bank ² + Woody species ² + Late flowering species ⁹ - Species with limited seed dispersal ^{2, 3, 17}

From : 1. Angers et al. (2005); 2. Bellemare, Motzkin & Foster (2002); 3. Bossuyt, Hermy & Deckers (1999); 4. Charbonneau & Fahrig (2004); 5. Collins, Dunne & Pickett (1985); 6. Diaz et al. (1999); 7. Froborg & Eriksson (1997); 8. Gilliam & Roberts (2003); 9. Graae & Sunde (2000); 10. Halpern (1989); 11. Haeussler et al. (2002); 12. Herault & Honnay (2005); 13. Hermy et al. (1999); 14. Jolls (2003); 15. Kolb & Diekmann (2005); 16. Mabry, Ackerly & Gerhardt (2000); 17. Matlack (1994b); 18. McLachlan & Bazely (2001); 19. Meier, Bratton & Duffy (1995); 20. Moffat & McLachlan (2004); 21. Moore & Vankat (1986); 22. Olivero & Hix (1998); 23. Rogers (1982); 24. Scheller & Mladenoff (2002); 25. Whitney & Upmeyer (2004).

* Studies reviewed for harvesting are clear cuts. We assumed selection cutting would have a similar but reduced impact on forest flora.

Methods

We examined 30 maple-dominated stands of the Great Lakes-St. Lawrence forest region (Rowe, 1972) in southern Québec, Canada. These stands were located in two contiguous regions that differ in physiography and land use history: the Upper St. Lawrence and the Outaouais. Mean annual temperature in both regions ranges between 2.5 to 5°C and precipitation between 900 and 1000 mm. The growing season typically lasts 190-200 d in the Upper St. Lawrence and 170-190 d in the Outaouais (Robitaille & Saucier, 1998).

The Upper St. Lawrence region is located in southernmost Québec ($45^{\circ}01'$ – $45^{\circ}08'N$; $73^{\circ}58'$ – $74^{\circ}21'W$). Agriculture dominates the region on the vast expanses of clay deposits originating from the post-glacial Champlain Sea. Isolated forest fragments cover 28% of the region, principally on moraine ridges and other land unsuitable for agriculture (Bouchard & Brisson, 1996; Robitaille & Saucier, 1998). Upper St. Lawrence vegetation dynamics and land use history has been the subject of numerous studies (Simard & Bouchard, 1996; Bouchard & Domon, 1997; Pan et al., 1999; De Blois, Domon & Bouchard, 2001). Before the 19th century, the region was sparsely populated by a few groups of Native Americans (Simard & Bouchard, 1996). European settlement after 1820 brought intense forest exploitation, first for wood and potash production and subsequently for agriculture. Some forests remained on private lands unsuitable for agriculture and were used for firewood or maple syrup production (Brisson & Bouchard, 2003). As agricultural activities changed in the 20th century, many fields were abandoned and allowed to reforest (Bouchard et al., 1989). This history has altered tree composition in this region: a climax of human origin, sugar maple-hickory forests, has replaced pre-colonial climax of sugar maple-beech-hemlock forest (Bouchard & Domon, 1997; Doyon, Gagnon & Bouchard, 1998).

The Outaouais region extends west of the Upper St. Lawrence ($45^{\circ}43'$ – $46^{\circ}06'N$; $75^{\circ}00'$ – $75^{\circ}51'W$). This sparsely inhabited area contains extensive forests on glacial tills with rocky outcrops (Robitaille & Saucier, 1998). Ninety-five percent of the region is forests (Robitaille & Saucier, 1998), with 75 % of these in public ownership (MRNFP, 2003) and where the dominant disturbance is industrial forestry. Until the latter half of the 20th century, harvesting consisted principally of targeted extraction of large diameter pine, oak and spruce along waterways. During

the 1960s and 1970s, most of the area experienced selective, “diameter-limit” harvests. Presently, single-tree selection dominates the silvicultural regime, a system that removes approximately 30% of the basal area across all size classes every 20-30 y (Bédard & Majcen, 2003). A few unmanaged forests with very little history of direct human influence remain.

Description of study plots

Twelve stands were chosen in the Upper St. Lawrence region: four stands exploited for maple syrup production, four second-growth stands originating from abandoned pastures and four stands without recent human disturbance. From previous studies conducted in the region, we can assess that almost all these stands were entirely or partially cut in the 19th and/or first part of the 20th century (Brisson, Bergeron & Bouchard, 1988). Vegetation dynamics after pasture and agriculture have been studied extensively in the region (De Blois & Bouchard, 1995; Benjamin, Domon & Bouchard, 2005). These studies were used to identify stands originating from the abandonment of pasture or agriculture. Old field stands had at least one visible sign of past agricultural use (e.g. fence or large tree with a broad, open-grown crown). Syrup production stands were easily identified by presence of sap-collecting tubes. Undisturbed stands had no visible signs of pasturing, tree harvesting or other human activities, either in the field or on aerial photographs. We assumed these stands were never cleared for pasture or agriculture and had no important human disturbances at least for the second part of the 20th century.

We selected 18 stands in the Outaouais region: six old growth stands, six stands harvested by single-tree selection 12 y ago (1990-1991), and six stands recently harvested (2000-2001) by single-tree selection. Old growth stands were documented by the Exceptional Forest Ecosystems Working Group (Villeneuve & Brisson, 2003). Table 2.2 presents the principal characteristics of these study stands.

Stands were selected to reduce as much as possible any differences in edaphic conditions, aspect and drainage. In addition to the studies mentioned above, information concerning the land use history of our study stands was compiled from the following sources: field observations, aerial photo-interpretation (1964-1966, 1975-1983), and meetings with officials from the provincial forest ministry in the Outaouais region as well as private land owners in the Upper St. Lawrence region.

Tableau 2.2. Characteristics of sampled stands. No significant differences were detected in the diversity indices between the two regions and among disturbance types ($P > 0.05$, one-way ANOVA).

Code	Disturbance type	N plots	Basal area m ² /ha	Tree stem density n/ha	% PPFD ⁱ at 200cm / soil level	Diversity indices ⁱⁱ		
<i>Upper St. Lawrence region – Agricultural matrix</i>								
UND	No recent disturbance	4	38	752	1.9 / 1.3	21.5	3.350	0.758
ACE	Maple syrup production	4	34	581	3.7 / 2.2	18.3	2.992	0.716
PAS	Origin from pasture abandonment	4	36	672	2.3 / 1.4	21	3.344	0.770
<i>Outaouais region – Forested matrix</i>								
OGF	None (old growth)	6	28	447	3.9 / 2.5	12.5	2.687	0.762
OSH	Single-tree selection (1990)	6	20	369	2.4 / 1.5	16	2.898	0.744
RSH	Single-tree selection (2000-2001)	6	20	403	17.1 / 5.3	19	3.089	0.750

ⁱ % PPFD : percentage of above-canopy photosynthetic photon flux density. ⁱⁱ Diversity indices: S: species richness; H': Shannon's diversity index; J: evenness.

Field sampling

Sugar maple dominated all of the study sites, representing > 25% of the basal area and the total tree stem density. American beech (*Fagus grandifolia*), American basswood (*Tilia americana*) and ironwood (*Ostrya virginiana*) were the most frequent companion tree species. None of the stands showed signs of recent fire, windthrow or other natural disturbances. In each stand, a 25-m radius plot was centred on plots previously surveyed by Carignan (2005) or Angers et al. (2005). To avoid edge effects, all plots were located at least 200 m away from any openings.

We determined floristic composition using linear vegetation surveys. In each plot, 52 circular points (15-cm radius) were systematically sampled along four 25-m transects. Species detected within a sampling point received an occurrence value of 1, for a possible score of 52 when a species was present in all points. Species present in the plot but not in any of the sampling points received an occurrence value of 0.5. The occurrence frequency (%) of a given species was the proportion of points in a plot where the species occurred. To describe vertical structure, we sampled the vegetation as described above every 50 cm in height, from the soil surface to the top of the understory (see Aubin, Beaudet & Messier (2000) for further details). We sampled the plots three times from May to September 2003 to obtain data for all species present during the growing season. Grasses, sedges and hawthorns (*Crataegus* spp) were not identified to species.

The following forest cover data were collected for each plot: tree composition, basal area (m^2/ha) and stem density (stem/ha) measured for all stems with diameter at breast height (DBH) > 5 cm. The percentage of above-canopy photosynthetic photon flux density (% PPFD) was measured at each of the 52 sampling points, both at the ground level and at two meters above the ground, using a line-quantum sensor (LI-COR, Lincoln, Nebraska, USA). All light measurements were taken under completely overcast sky conditions following the methods of Messier & Puttonen (1995) and Gendron, Messier & Comeau (1998).

Data base of biological traits (TOPIQ)

The elaboration of plant functional types (PFT) required the characterization of a set of carefully chosen biological traits for each of the species inventoried. Although several data bases of biological traits exist (e.g. Kleyer, 1999; Gachet, Véla & Tatoni, 2005), none was available for Québec flora. We thus created a Québec-specific data base, Traits Of Plants In Québec (TOPIQ). The data base structure was based on the model of Grime, Hogson & Hunt (1988), using traits associated with regeneration and establishment. Due to the large number of species, we considered only traits for which information was available from published sources or herbarium specimens. Traits were chosen from a comprehensive literature review, with validation i.e. several sources were needed to include a given trait for a given species; contradictions among sources were settled by experts. A complete list source is given in Annexe I. Thirteen categorical traits were used in the present study, resulting in a total of 51 classes after expansion into binary form for analysis (Table 2.3).

Tableau 2.3. Biological traits of understory plants in sugar maple forests as compiled from the literature.

Trait	Code	Description
Raunkier life form	RA	mg: mega or meso-phanerophyte (≥ 8 m in height); mc: micro or nano-phanerophyte (25 cm to 8 m); ch: chamaephyte (herb or shrub, bud between 1 mm to 25 cm above ground); h: hemicryptophyte (herb with bud at the ground surface); g: geophyte (herb with underground bud); t: therophyte (annual)
Life cycle	PER	1: annual; 2: biennial; 3: perennial
Principal means of reproduction (39)	REP	se: seeds only; ms: vegetative propagation possible but mostly by seeds; ve: mostly by vegetative propagation
Foliage persistence	PFO	0: no; 1: yes

Trait (continued)	Code	Description
Foliage structure	SFO	<i>For phanerophytes:</i> ms: spread out stem; me: erect stem; mu: multi-stemmed <i>For other life forms:</i> No stem: r: rosette or semi-rosette; g: graminoid; e: erect leaves With stem: el: erect leafy stem; de: decumbent stem; um: umbrella-shaped stem; vi: vine Non-leafy stem: nl: saprophyte
Physical defences	DEF	0: no; 1: yes
Flowering phenology	FPH	sp: spring; su: summer; sf: summer-fall
Pollination vector (35)*	POL	a: abiotic; b: biotic; n: no pollination or vector; na: non applicable (e.g. pteridophytes)
Seed dispersal vector*	DI	w: wind (anemochorous); ez: animal ingestion (endozoochorous); an: insect, mostly ant (myrmecochorous); bi: bird ingestion (avichorous); hd: human dispersal: (anthropochorous); ex: ballasts or explosive discharge (ballistichorous)
Seed size	SE	1: < 0.1 mm; 2: 0.1 to 1.99 mm; 3: 2 to 2.99 mm; 4: 3 to 4.99 mm; 5: 5 to 40 mm
Seed dormancy (67) *	DO	nd: non dormant; sc: physical dormancy; dp: physiological or morphophysiological dormancy
Light requirement (9)	LI	s: shade tolerant; m: mid tolerant; i: intolerant
Status in Quebec	ST	0: native; 1: exotic

In parentheses: number of missing values. *For these traits, a species may have more than one class.

Data analysis

Plant Functional Types - emergent groups

PFT used in this study are emergent groups, i.e. species are grouped according to their biological traits (Lavorel et al., 1997). To develop emergent group and test for their responses to human disturbance, we conducted a three step analysis. First, a Correspondence Analysis (CA) was done on the data matrix of plant biological traits (214 species x 51 classes) to create a overall portrait of life-history strategies and trait associations for flora in sugar maple forests (results not shown). Second, to delineate emergent groups, a Ward type ascending hierarchical classification was done on the axis scores of this CA (Euclidean distance, weighted by 1). The cut-off was determined by visual inspection of the dendrogram in accordance with our botanical knowledge. Third, we examined the relative occurrence of these groups in the human disturbance types. To do this, a matrix of species groups' occurrence was calculated as the product of the species data matrix (214 species x 30 plots, with percent occurrence data of each species) and the binary matrix of emergent groups (214 species x 13 emergent groups). This new matrix was standardized by dividing the occurrence of each group by the total occurrence for all groups in each plot. Differences in the relative occurrence of species groups among disturbance types were analysed using a one-way ANOVA followed by a multiple comparison Bonferroni test in cases where significant effects of disturbance type were detected. Bonferroni test is based on Student's *t* statistic and correct the significance level for multiple analyses.

Plant Functional Types – individual traits

As emergent groups may be too general to reveal differences among species at the trait level, individual biological traits were also related to human disturbance types. A matrix of the prevalence of each trait in each plot was created by multiplying the plant species data matrix by the traits data matrix. This new matrix was standardized by dividing the occurrence of each class by the total occurrence for all classes in each plot. This biological spectra matrix (30 plots x 51 classes) comprises the relative abundance of species of a plot with a particular trait. A Principal Component Analysis (PCA) was done on this matrix to compare the distribution of classes among the different disturbance types.

Vertical understory stratification

We used the matrix of occurrence of species groups as determined for individual strata to examine the vertical occupancy of different groups. The impact of human disturbance on the development of understory vertical strata was also tested. Total species occurrence by vertical strata of 50 cm was analysed using a one-way ANOVA and a multiple comparison Bonferroni test.

In addition to these analyses, the following indices were calculated for each plot: species richness, Shannon's diversity index (Whittaker, 1972) and species evenness (Magurran, 1988). The functional diversity, or the richness of each emergent group, was also calculated. A one-way ANOVA followed by a multiple comparison Bonferroni test were done to verify for index differences among the disturbance types.

Where necessary, we performed a natural log transformation on the dependent variables to ensure normality and homoscedasticity. A significance level of 0.05 was used. The XLStat program (Addinsoft, 2006) was used for all analyses.

Results

A total of 142 species was recorded in the Upper St. Lawrence while 163 species were recorded in the Outaouais, with 91 species in common. No significant differences were detected in the diversity indices between the two regions and among disturbance types (Table 2.2).

Emergent group identification

Cluster analysis allowed 13 emergent groups to be delineated (Table 2.4). The following traits characterized the groups: (1) annuals (therophytes); (2) exotic, wind-dispersed (anemochorous) hemicryptophytes with a high proportion of biennials and rosette-form species; (3) exotic hemicryptophytes dispersed mainly by animal ingestion (endozoochorous), which were perennial species with a decumbent or vine form; (4) native, wind-dispersed hemicryptophytes with a high proportion of late-flowering species; (5) native hemicryptophytes dispersed by animal ingestion or bird (avichorous) with a decumbent form; (6) spring geophytes mainly dispersed by ants (myrmecochorous) or animal ingestion; (7) shade-tolerant herbs mostly wind-dispersed and containing particular sub-groups such as the *Orchidaceae*. Pteridophytes, with distinct biological traits, separated by the analysis into (8) ferns and (9) the genus *Lycopodium*; (10) the genus *Viola*. Finally, the phanerophytes separated into three groups: (11) trees dispersed by wind; (12) trees or vines dispersed by birds; and (13) shrubs dispersed by birds.

Tableau 2.4. Characteristic biological traits of the identified emergent groups computed from a cluster analysis done on the axis scores of a Correspondence Analysis on the biological traits data matrix.

Group	Characteristic trait										REP	Characteristic species	n
	RA	PER	PFO	SFO	DEF	FPH	POL	DI	SE	DO			
Annuals													
t	1	0	el, r	0	su	b	-	2, 4	dp	i	0	se	<i>Bidens frondosa</i>
													13
Exotic wind-dispersed hemicryptophytes													
h	2, 3	0	r	-	su	b, n	w	-	dp	i	1	-	<i>Cirsium arvense</i>
													18
Exotic hemicryptophytes dispersed by animal ingestion													
h	3	0	de, vi	0	su	b	ez	3	sc,	i, m	1	-	<i>Hieracium pratense</i>
													18
Native wind-dispersed hemicryptophytes													
h	3	0	el, r	0	su, sf	b	w	2, 3	dp	-	0	ve	<i>Trifolium pratense</i>
													5
Animal or bird-dispersed decumbent hemicryptophytes													
h	3	0	de	1	sp, su	b	ez, bi	3	dp	-	0	ve	<i>Vicia cracca</i>
													5
Spring geophytes													
g	3	0	um	0	sp	b	ez,	4	dp	s, i	0	ve,	<i>Medeola virginiana</i>
													26
							an					ms	<i>Uvularia grandiflora</i>

See Table 2.3 for code definitions. Codes in italic indicate that this class is present but in lower proportion.

Responses of emergent groups to human disturbances

The disturbance types differed in the relative occurrence of emergent species groups (Table 2.5). Old growth forests had the lowest proportion of exotic, wind-dispersed hemicryptophytes and trees or vines dispersed by birds. Undisturbed forests were not significantly different from old growth stands. Undisturbed stands possessed the highest proportion of spring geophytes. Maple syrup production forests possessed a higher proportion of trees or vines dispersed by bird than old growth stands but are not significantly different from undisturbed stands. They had the lowest occurrence of shrubs. Old pasture stands had a significantly higher proportion of trees or vines dispersed by birds than old growth stands and a significantly higher proportion of shrubs than undisturbed stands. Stands partially harvested 12 y ago were not significantly different than old growth stands. They possessed the lowest proportion of spring geophytes. Recently partially harvested stands had a significantly higher proportion of exotic, wind-dispersed hemicryptophytes and of native decumbent hemicryptophytes dispersed by animals or birds than old growth stands.

Functional diversity (richness in each emergent group) differed among disturbance types (Table 2.5). Old growth stands possessed the lowest diversity of annuals, of exotic, wind-dispersed hemicryptophytes, of animal- or bird-dispersed decumbent hemicryptophytes, and of trees. Undisturbed stands had a higher diversity in bird-dispersed trees or vines than old growth forests. Undisturbed stands had the highest spring geophytes diversity. Maple syrup production and old pasture stands had a higher diversity of trees or vines dispersed by birds than old growth but were not significantly different than undisturbed stands. These stands had no *Lycopodium* species. Old growth, undisturbed and old pasture stands had no exotic hemicryptophytes dispersed by animal ingestion. The older partially harvested stands possessed a significantly higher diversity of trees dispersed by wind than old growth and the highest diversity of *Lycopodium*. Recently partially harvested stands were the most distinct from the old growth because of their significantly higher diversity of annuals, of exotic, wind-dispersed hemicryptophytes, of native, decumbent hemicryptophytes dispersed by animals or birds, and of trees dispersed by wind. They possessed the lowest diversity in spring geophytes.

Tableau 2.5. Mean relative occurrence ($O\%$) of emergent groups and functional diversity (r : richness of each emergent group) among disturbance types. UND: undisturbed; ACE: maple syrup production; PAS: old pasture; OGF: old growth; OSH: old harvested; RSH: recent harvested stands.

	Groups	P	UND	ACE	PAS	OGF	OSH	RSH
	O %	r	O %	r	O %	r	O %	r
Annuals	-	*	0.1	0.3 ab	1.3	1.3 ab	0.2	0.50 ab
Exotic wind-dispersed h.	*	**	0.6 ab	1.5 ab	0.7 ab	1.5 ab	0.6 ab	1.8 ab
Exotic animal-dispersed h.	-	-	0.0	0.0	0.1	0.3	0.0	0.0
Native wind-dispersed h.	* i	*i	5.6	4.3	6.0	6.3	4.2	3.8
Animal / bird-dispersed decumbent h.	***	**	3.1 a	3.3 a	3.4 a	6.3 ab	0.9 a	2.8 a
Spring geophytes	*	*	34.4 b	11.8 b	24.6 ab	11.5 ab	19.3 ab	9.3 ab
Shade herbs	-	-	5.1	5.0	2.3	4.3	3.4	3.5
Ferns	-	-	6.1	5.0	3.8	5.5	0.6	1.8
<i>Lycopodium</i>	-	*	0.1	0.3 ab	0.0	0.0 a	0.0	0.0 a
<i>Viola</i>	-	-	0.7	1.0	0.8	1.3	0.5	0.5
Wind-dispersed trees	-	***	38.6	7.3 ab	48.9	8.0 ab	55.7	8.5 ab
Bird-dispersed trees / vines	***	***	2.4 abc	2.8 bc	5.2 c	3.0 bc	3.9 bc	3.8 c
Shrubs	*	-	3.3 a	6.3	2.8 a	4.5	10.8 b	7.3

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; - $P > 0.05$; ⁱbut Bonferroni test $P > 0.05$. For each emergent group (row) a different letter indicates a significant difference at $P < 0.05$ (one-way ANOVA followed by a multiple comparison Bonferroni test). See Table 2.4 for a detailed description of the groups.

Responses to human disturbances at the trait level

Figure 2.1 presents the ordination of all the study plots ($n = 30$) and species' biological traits contributing the most to build the axes ($n = 31$ on a total of 51) along the two PCA axes of the biological spectra matrix. The eigenvalues of the first two axes were 15.88 and 10.13, corresponding respectively to 29% and 19% of the total variance observed. The primary axis of variation distinguished between recently partially harvested stands on the left and old growth stands, a more or less homogeneous group to the right. The secondary axis of variation separated the two study regions, with Outaouais plots mostly located near the top of axis F2. The primary variation (Axis 1, Figure 2.1) reflects principally a gradient of flowering phenology, life cycle, provenance, seed characteristics and plant form classes. The secondary axis of variation (Axis 2, Figure 2.1) highlights differences in the principal mean of reproduction, seed dispersal, pollination vector, plant form classes and leaf persistence.

The PCA elucidated differences in how classes of traits are represented among the disturbance types. Old growth stands possessed a high proportion of spring flowering species (FPH_sp), species capable of vegetative propagation but that reproduce mostly by seeds (REP_ms), myrmecochorous species (DI_an), species with graminoid form (SFO_g) or saprophytes (SFO_nl). Old field stands possessed a large proportion of species reproducing either solely by seeds (REP_gr) or by strong vegetative reproduction (REP_ve), wind-dispersed species (DI_w) and no saprophyte species (SFO_nl). Recently partially harvested stands had a large proportion of hemicryptophytes and therophytes (RA_h, t), of exotic species (STA), of summer flowering species (FPH_su), species with small seeds (SE_2, 3), species with physical defences (DEF) and species with rosette form (SFO_r). No saprophyte species (SFO_nl) was found in old field stands. Maple syrup production stands had a large proportion of species reproducing by seed (REP_se) and dispersed by wind (DI_W). Stands partially harvested 12 y ago had a large proportion of spring flowering (FPH_sp) perennials (PER_3) and tree saplings (SFO_ms). Little difference in the representation of traits was found for undisturbed stands.

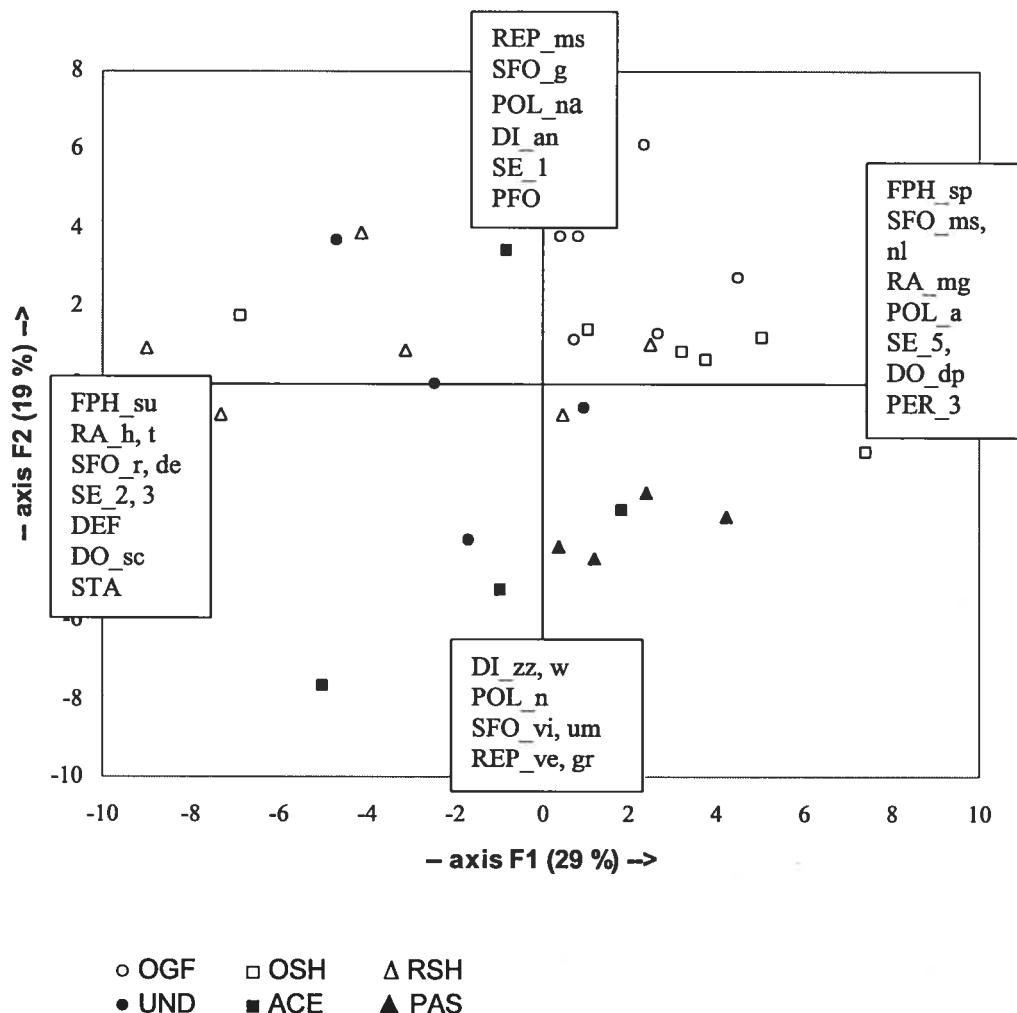


Figure 2.1. Principal Components Analysis (PCA) diagram (axes 1 and 2) of the biological spectra matrix (plots x traits). Indicated are study plots (see Table 2.2 for code definitions) and biological traits contributing strongly to build the axes (see Table 2.3 for code definitions).

Vertical stratification and human disturbance

In general, the recurring pattern of vertical stratification of the understory vegetation observed for all types of stands was the presence of a low stratum (0-50 cm) that was well-developed and diversified, strata between 50-200 cm that had little vegetation and a high stratum (≥ 250 cm) that was moderately developed but not very diversified (Figure 2.2). The vertical stratification was quite similar among disturbance types. The only significant difference was that stands partially harvested 12 y ago possessed an understory high stratum more developed than recently harvested and undisturbed stands (ANOVA $P = 0.006$).

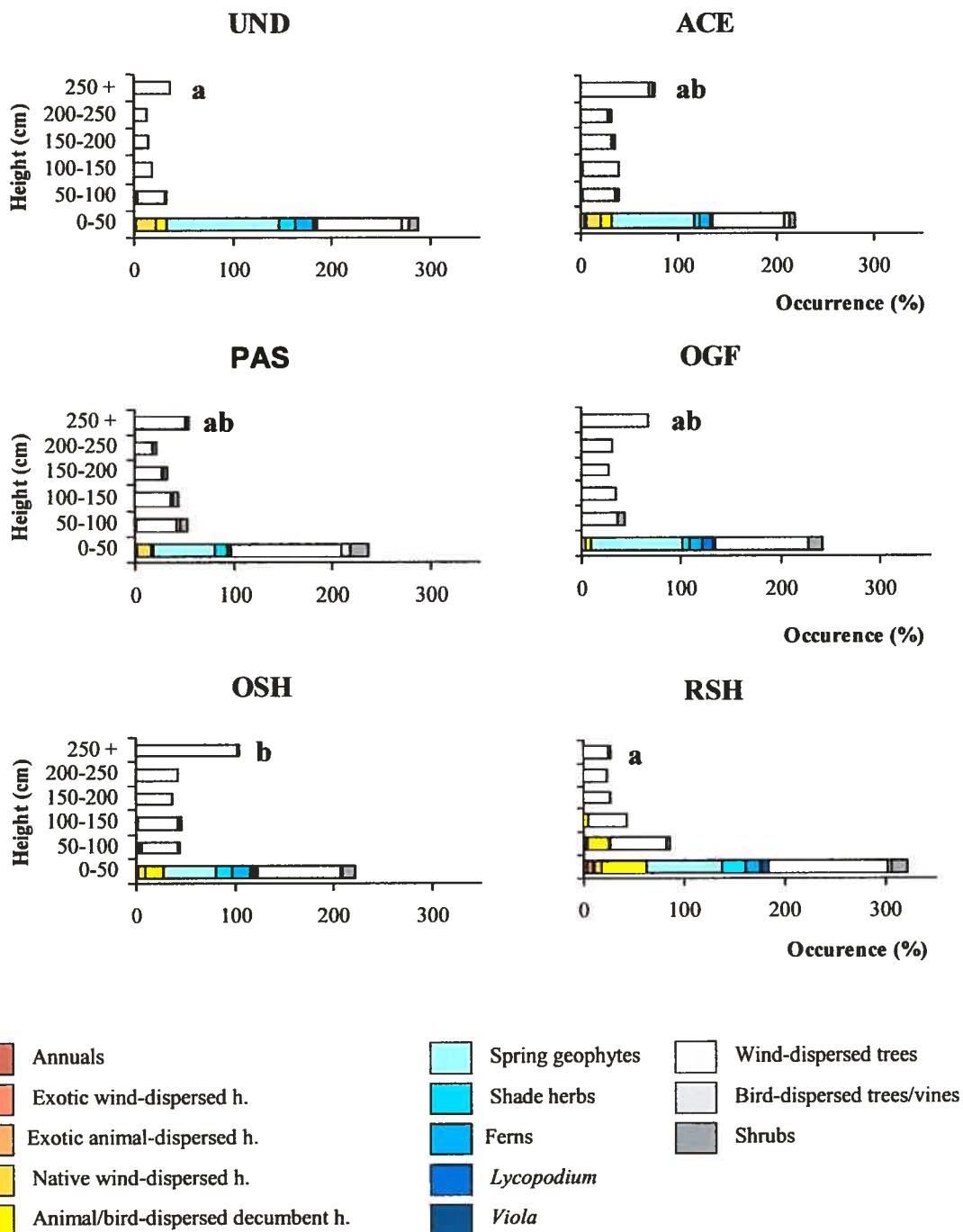


Figure 2.2 Vertical stratification of the vegetation by emergent groups for each type of human disturbance. UND: undisturbed; ACE: maple syrup production; PAS: old pasture; OGF: old growth; OSH: old harvested; RSH: recent harvested stands. For the stratum 250 cm and more, a different letter indicates a significant difference among disturbance type at $P < 0.05$ (multiple comparison Bonferroni test). No significant difference was found for the lower strata. See Table 2.4 for a detailed description of the groups.

Discussion

Biological traits and ecosystem functioning

Plant functional groups developed in this study were objectively constructed from a classification of the principal biological traits of the flora in sugar maple forests of Québec. These 13 groups possessed a set of common traits that can be associated with a similar life history strategy and particular roles in the ecosystem (Mooney, 1997). These groups outline different life history strategies as well as responses and adaptations to disturbance.

First, annuals and the two groups of exotic species were associated with open environments. These species were almost exclusively shade intolerant, of short longevity, capable of long distance seed dispersal and associated with recently harvested stands where ground-level light is plentiful (Table 2.2). Second, native, wind-dispersed species and animal- or bird-dispersed, decumbent hemicryptophytes comprised species with various light requirements. While the wind-dispersed group was mainly composed of open field species and seems adapted to the agricultural landscape of the Upper St. Lawrence, the latter group was associated with recently harvested stands. Third, the spring geophytes, the ferns and allies, and viola groups were mostly shade tolerant species and thus can be considered as shade forbs. Adaptations, such as foliage/stem form, phenology or saprophytic nature, allow these plants to tolerate the deep summertime shade prevalent in the understory of sugar maple forests (Collins, Dunne & Pickett, 1985; Givnish, 1987; Neufeld & Young, 2003). Many of these species have low colonisation capacity and are recognized as sensitive to human disturbances (Bierzychudek, 1982; Meier, Bratton & Duffy, 1995; Flinn & Vellend, 2005). Even the pteridophytes, which produce spores that can travel long distances, need specific microsites for establishment and therefore possess limited capacity for colonisation (Flinn, 2005). It was surprising that three of the five shade forbs did not vary in occurrence according to human disturbance type. The lack of significant difference for the fern group – despite their reduced presence in old pasture stands relative to undisturbed or old growth stands – may be explained by the large variability among stands. For the shade forbs and viola groups, phylogeny may explain the unresponsiveness to disturbance type. These groups are composed of species with convergent traits due to phylogeny but which differ in life history. This

relatively frequently occurring problem with emergent group classification (Lavorel et al., 1997) highlights the need to combine emergent group classification with trait level analyses.

Finally, the three phanerophyte groups, which contain shrubs, tree seedlings and saplings, occupy the upper strata of the understory. They serve as a “sapling bank” (Wilson, 1993) for the tree stratum and contribute strongly to understory structure (Harcombe & Marks, 1977). The phanerophyte groups possess regeneration and dispersal strategies that differ from all the above groups (Gilliam & Roberts, 2003), being almost all native species adapted for long-distance seed dispersal. The phanerophytes responded positively to human disturbance, corroborating the findings of Royo and Carson (2006) who documented that increases in canopy disturbance generally favour the development of a dense phanerophyte stratum.

Human effects on understory assemblages

We used an approach combining PFT and vertical stratification of the understory vegetation to evaluate the effects of human disturbance on the ecological integrity of sugar maple stands. Ecological integrity of a forest was evaluated by the divergence of its understory assemblage from that observed in comparable unmanaged old growth forest - the most natural stands available in the region (Villeneuve & Brisson, 2003). Even though they are subjected to indirect influences such as air pollution and population increases in deer and exotic earthworms, these forests show relatively little direct human influence. Unlike most of the old growth of eastern deciduous forest which are located in human-dominated matrix (Foster, Orwig & McLachlan, 1996; McCarthy, 2003), old growth stands in Outaouais are embedded in a large forested matrix far from urban centres and are representative of the regional forest in terms of soil characteristics and topography. It therefore seems reasonable to assume these forests be considered the best extant reference we can actually find. To prevent a potential bias due to regional differences, we also evaluated undisturbed stands for the Upper St. Lawrence region.

Although understory vegetation assemblages were generally similar across all the disturbance types (Figure 2.2), some distinctions can be made. In old growth stands, the shade forbs were predominant. Moreover, despite the presence of gaps, a relatively open canopy and a diversified structure in the tree stratum characteristic of old growth stands, the diversity and occurrence of open environment groups were low. Corroborating what is generally reported in the

literature (Table 2.1), our analyses at the trait level revealed the following traits are associated with old growth stands (Figure 2.1): spring flowering native perennial species, with ant-dispersed large seeds or saprophyte species with small seeds. Species that possess these traits, such as spring geophytes and some shade forb, may therefore be potentially sensitive to human disturbance.

Stands recently harvested by single-tree selection had an understory assemblage that differed most from that of old growth. Annuals, exotic species, and animal- or bird-dispersed decumbent hemicryptophytes had a higher occurrence and richness in these stands than in old growth. Certain shade forb described as sensitive to harvesting by Moola & Vasseur (2004), such as the saprophyte species and *Oxalis montana*, were absent. The apparent lack of difference between stands partially harvested 12 y ago and old growth stands, in conjunction with our observation that shade forb absent in recently harvested selection stands were present in the older harvested selection stands, suggest the understory eventually recovers from such partial harvesting treatment.

Although the canopy was not entirely closed in the older partially harvested stands, a dense sapling layer of wind-dispersed tree species above 250 cm greatly reduced light transmission to the forest floor. Therefore, structural changes in the understory following logging may lead to the partial exclusion of species groups associated with open environments, as these groups were infrequent in the older partially harvested stands. Moreover, occurrence of spring geophytes in these older harvested stands was lower than in all other stand types. As suggested by Meier, Bratton & Duffy (1995), spring geophytes may be affected by a strong post-logging response of tree seedlings and saplings. While several authors have documented a re-establishment or persistence of most species after logging, many have also observed a decline of certain forbs following clear cuts (Halpern, 1989; Elliott et al., 1997; Ruben et al., 1999; Roberts & Gilliam, 2003; Moola & Vasseur, 2004). Clear cutting apparently reduces populations of the more rare herb species (Meier, Bratton & Duffy, 1995; Jolls, 2003). Single-tree selection, by harvesting only part of the canopy, possibly has a lower impact on the forest flora than clear cutting. For example, Reader & Bricker (1992) did not detect negative impacts on forest flora two, five and nine y after selective harvests in deciduous forests.

Corroborating previous studies (see Table 2.1), we observed that former pastures tend to have less of species groups with limited colonization capacity, such as the spring geophytes and the pteridophytes. Species in second growth forests regenerating after agriculture abandonment are either good colonizers, capable of maintaining a persistent seed bank in the soil, or able to survive in a non-forested environment (Graae & Sunde, 2000; Bellemare, Motzkin & Foster, 2002). But occasional long distance seed dispersal is of noticeable importance for the colonisation of species with short distance dispersal vector (Cain, Damman & Muir, 1998). The initial floristic composition in these forests resulting from cattle grazing, which acted as a “selective agent” (*sensu* Hadar, Noy-Meir & Perevolotsky, 1999), was still apparent in the now mature maple forests. For example, the shrub group – which contains species avoided by cattle such as prickly ash (*Zanthoxylum americanum*) – had its highest occurrence in these stands.

Activities associated with maple syrup production affect structural diversity, particularly by eliminating tree species other than sugar maple and by cutting saplings (Messier & Beaudet, 2000; Whitney & Upmeyer, 2004; Lenière & Houle, 2006). Surprisingly, the low observed structural diversity of the tree stratum was not reflected in the understory assemblage of sampled syrup production stands as we found a high occurrence of seedlings and saplings of trees or vines dispersed by birds. Few differences were found between this forest type with either old growth and undisturbed forests, perhaps due to the large variation observed in syrup production stands arising from inter-stand differences in management practices.

Undisturbed stands were quite similar to old growth stands. These stand types had the highest occurrence of spring geophytes. The undisturbed stands located in the Upper St. Lawrence region had more exotic species than old growth stands located in the Outaouais, presumably because of land-use history and the nature of the dominant regional matrix. Most, if not all, forests in the Upper St. Lawrence have had episodes of human disturbance (De Blois, Domon & Bouchard, 2001) and legacies of these influences remain in the presence of certain groups of species of open environments. Moreover, the Upper St. Lawrence forests are located within an agricultural matrix that affects species differently according to their biological traits (Table 2.1). Conversely, the Outaouais remains generally forested with a considerably less frequent, intense and extensive history of human disturbance. The forested matrix has a buffering effect against the

introduction of species of open environments and favors the reintroduction of existing forest species after disturbance (Ruben et al., 1999; Charbonneau & Fahrig, 2004).

Undisturbed stands of the Upper St. Lawrence and old growth stands of the Outaouais showed little evidence of regional variations in PFT groups. The generally higher occurrence and diversity of wind dispersed hemicryptophytes and of tree and vines dispersed by birds in the Upper St. Lawrence are quite likely attributable to landscape context and land-use history. The higher occurrence of *Lycopodium* in the Outaouais region might be attributable to a regional difference in climate. However, it may also be related to nurse log availability as *Lycopodium lucidulum*, which is the most abundant *Lycopodium* species in our study, is known to need this specialized microhabitat for its establishment (Scheller & Mladenoff, 2002).

Long-term consequences for plant communities

A principal finding of this study is the remarkable stability of understory vegetation in sugar maple forests. It appears that the majority of understory forest plants are well-adapted to the range of human disturbances we studied. After 200 y of human disturbance, sugar maple forests still possess an understory community that appears to keep its ability to recover from human disturbance. However, results suggest some possible issues of conservation concern in the long term. An increase in the frequency, extent and severity of human disturbances may affect the understory assemblage of these forests by: (i) increasing the occurrence of groups associated with open environments, including exotic species; (ii) decreasing the diversity and occurrence of spring geophytes; (iii) decreasing the occurrence of certain shade forb such as saprophytes and (iv) modifying understory structure by an increased development of phanerophytes, thereby modifying the understory abiotic conditions and potentially negatively affecting recruitment of species in the lower strata. These modifications in the understory assemblage could eventually alter the natural character of the understory of sugar maple forests over the long term.

Conclusion

The use of plant functional types provides a synthetic view of vegetation response to disturbance. By allowing comparisons of similar ecosystems in different regions, this approach offers a new methodological framework that can be applied to the study of human effects on

vegetation processes as well as to many aspects of forest management. For instance, this approach provides an avenue for monitoring human effects on ecological integrity even where it is difficult to find unmanaged forest to serve as a reference state.

The northern hardwood forest of southern Québec is now seriously degraded from a market value perspective in terms of tree stem quality (Coulombe et al., 2004). However, our study shows that the understory has kept its functionality till now. Possessing a functional understory is a determining factor in ensuring the long-term establishment and survival of the trees that will dominate the system in the future. As such, all studied forests seem to conserve their potential for a natural recovery of the tree stratum in the long term.

From these results, it appears that disturbed forests remain valuable from the perspective of conserving biodiversity and ecological integrity. It is thus still possible to respond to the urgent need for increasing protected areas in southern Québec by including a proportion of these disturbed forests into our conservation strategy.

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Chapitre 3

Use of two plant functional approaches to evaluate natural restoration along an old field-deciduous forest chronosequence

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Aubin, I., Ouellette, M.H., Legendre, P., Messier, C., et A. Bouchard. Use of two plant functional approaches to evaluate natural restoration along an old field-deciduous forest chronosequence. *Journal of Vegetation Science*.

Abstract

With the goal of evaluating the potential of pasture to recover an understory flora similar to mature maple forests, changes in trait dominance and forest herb recovery were studied along a chronosequence which extended from active pasture to mature northern hardwood forest of pasture origin. Two plant functional type approaches were used to synthesize species responses to succession: (i) a frequently used approach based on co-occurrence of traits (emergent groups), and (ii) a new version of a direct functional approach at the trait level (the fourth-corner method). Clear associations between traits and stand developmental stages emerged from both approaches. Ferns, tree seedlings and spring geophytes dispersed by ants groups were associated to mature stands. At the trait level, mature forests were associated with native spring-flowering shade-tolerant geophytes dispersed by ants. The presence of species possessing these traits was thus considered as an indicator of understory flora recovery. A forest understory began to develop in the tall shrub-dominated stand stage. The young tree stand stage possessed a rich understory although it only had a few species with limited dispersal capacity. Sensitive forest herb species were found to comprise a varying recovery capacity. These differences seem in part related to their potential to survive in a non-forested environment. Our study indicates that abandoned pastures of the northern hardwood biome have a good potential for natural restoration. Conversion of these lands to other functions will lead to an irremediable loss in biodiversity. We suggest restoration activities according to the developmental stage of the land.

Keywords : ecological restoration, emergent group, forest herbs, fourth corner method, understory vegetation

Nomenclature: Gleason and Cronquist (1991)

Introduction

In the last century, modernization of agriculture resulted in the abandonment of many agricultural lands. While natural revegetation often occurs rapidly on these lands, the resulting understory communities are generally considered as biologically impoverished relative to the original forest because of their (i) altered composition and poor richness of species with high conservation value (Singleton et al., 2001; Flinn & Vellend, 2005), and (ii) low forestry potential (Benjamin, Cogliastro & Bouchard, 2006; D'Orangeville, accepté). In part because of negative societal perceptions of abandoned farmlands (Hunziker, 1995; Benjamin, Bouchard & Domon, Accepted), these lands are often converted into agricultural fields or into plantations by rapid afforestation.

Vegetation development in abandoned farmlands has been widely studied in the temperate biome (see Flinn & Vellend, 2005). However, decreasing forested area in the biome and the pressure to convert these lands into other uses begets new questions of conservation concern. In this respect, determining the potential of abandoned farmlands to develop into a functional forest ecosystem has become a central question. Do natural revegetation processes in these lands allow the development of a community with ecological values comparable to a natural ecosystem? Or, in other words, are these lands valuable from an ecological restoration perspective?

Answers to these questions are not straightforward, in particular because of the varying nature of abandoned farmlands. Abandoned farmlands being a transitional stage, vegetation development greatly varies in time and space, from herb-dominated communities to communities dominated by shrubs and pioneer trees (Benjamin, Domon & Bouchard, 2005; Flinn & Vellend, 2005). Abandoned farmlands also vary according to their land-use history, with succession on former pasturelands being quite different than that on cultivated fields or hay meadows (Stover & Marks, 1998; Benjamin, Domon & Bouchard, 2005; Flinn & Vellend, 2005).

Among abandoned farmlands with various land use histories, pasturelands hold particular potential for natural revegetation. This potential arises in part because they generally not have been plowed with modern heavy machinery and thus have preserved biological legacies (*sensu* Franklin et al., 2000) such as their original micro-topography (Beatty, 2003) and relict populations of forest herbs (Stover & Marks, 1998). Additionally, pasturelands also present high heterogeneity in drainage and soil properties that generally favor diversity (Beatty, 2003; Flinn & Marks, 2007).

From an ecological restoration perspective, knowledge of the possible course and time scale of natural vegetation succession is particularly essential (Prach et al., 1999; Hobbs & Harris, 2001), for instance to determine during which successional stage it is best to introduce selected species (e.g. rare forest herbs) or eradicate undesirable species (e.g. invasive exotics). Despite this research need, studies that specifically address questions of understory flora development on former pastures remain quite rare (e.g. Stover & Marks, 1998). The studies that are available regarding the herb stratum in old fields primarily concern croplands and typically focus on herb stratum impacts of woody species development (e.g. Gill & Marks, 1991) or deal with only a short segment of the succession (e.g. Myster & Pickett, 1994). Forest herb recovery is generally inferred from a comparison between ancient woodlands and recent ones (e.g. Wulf, 1997), or indirectly by the relationship between the establishment of selected species with forest age and distance to nearby forests (e.g. Matlack, 1994b).

In fact, the high diversity and broad range of life history strategies of understory species of the northern hardwood forests as well as the site-specific nature of understory composition limit our capacity to develop a broad characterization of compositional changes induced by succession using a traditional taxonomic approach. A plant functional trait (PFT) approach can synthesize species responses into general vegetation strategies. It gives valuable insight into the mechanisms of community development because the potential of a species to establish or persist in any given environmental conditions are largely determined by its ecological traits (Lavorel et al., 2005). A PFT approach therefore

allows elucidating the relationship between species strategies as defined by a set of traits and species responses to environmental changes. This approach may substantially increase our understanding of forest herb recovery as well as aid in identifying species traits that impede or delay recovery.

Two different PFT approaches were used in the study. The first, termed emergent groups, involves identifying groups of species that share similar traits (Lavorel et al., 1997); it has been widely used to study ecosystem responses to human-induced change (e.g. Verheyen et al., 2003; Kolb & Diekmann, 2005). Secondly, we used a new version (Dray & Legendre, submitted) of a direct functional approach at the trait level called the 4th-corner method (Legendre, Galzin & Harmelin-Vivien, 1997). This recent and innovative approach allows testing for the significance of the relationship between species traits and an environmental variable in a one-step analysis. Although these two PFT approaches differ in how they account for the relationship between the plant traits and environmental variables (Lavorel et al., 1997), they never have been used on the same data set to compare the type and precision of the information obtained.

Our primary goal was to evaluate whether natural revegetation in former pastures can be a successful strategy to restore an understory in a way comparable to natural forests. To capture the full range of succession and to determine specifically at which stage particular revegetation processes occur, we used a complete chronosequence from active pasture to mature forest of pasture origin. Our key questions were: To what extent does the understory flora recover on former pastures? And if so, at which stage does the understory converge toward those of a forest, as estimated by ecological traits? More specifically, this study: (i) characterized trait responses along a chronosequence of abandoned pastures that ranged from 10 to approximately 100 years since abandonment; (ii) identified sensitive forest herbs via their ecological traits and document their recovery; (iii) discussed the restoration potential of these old pasture lands; (iv) and compared two PFT approaches and their usefulness to synthesize species responses to various successional stages.

Methods

Study area

The study was conducted in Upper St. Lawrence Regional County Municipality ($45^{\circ}01' - 45^{\circ}08'N$; $73^{\circ}58' - 74^{\circ}21'W$) of southern Québec, Canada. The area is within the deciduous forest of the Great Lakes-St. Lawrence River forest region (Rowe, 1972). Regional mean annual temperature is $5^{\circ} C$, precipitation ranges between 900 and 1000 mm and mean annual growing season length is typically between 190 and 200 days (Robitaille & Saucier, 1998).

European settlement in the 19th century brought intense forest exploitation, first for wood and potash production and subsequently for agriculture (Simard & Bouchard, 1996; Domon & Bouchard, Accepted). In the last quarter of the 19th century, the study area was nearly completely deforested and transformed into different forms of agriculture (Domon & Bouchard, Accepted). As in many other agricultural regions in Eastern North America, the traditional rural landscape changed during the 20th century towards intensified agriculture, resulting in the progressive abandonment of many agricultural lands (Bouchard & Domon, 1997; Domon & Bouchard, Accepted). With time, vegetation developed in these abandoned lands, creating a patchwork of various field and forest types (Meilleur, Bouchard & Bergeron, 1994; Pan et al., 1999).

Actual and historical land uses are closely associated to geomorphological characteristics. The Upper St. Lawrence region lies on bedrock composed of sandstone, dolomite and shale of the Postdam and Beekmantown groups (Globensky, 1987). Surficial deposits originates from the post-glacial Champlain Sea and comprise two major types: (i) a moraine-type deposit in islets and ridges with stony soils principally covered by forests and abandoned old fields, and (ii) nutrient-rich marine clays, principally in the low lying areas that are covered by agricultural lands (Domon & Bouchard, Accepted). Mature mesic forests are generally dominated by sugar maple (*Acer saccharum* Marsh.) in association with bitternut hickory (*Carya cordiformis* (Wang.) K. Koch), ironwood (*Ostrya virginiana*

(Mill.) K. Koch), basswood (*Tilia americana* L.) and beech (*Fagus grandifolia* Ehrh.) (Bouchard & Brisson, 1996). After abandonment, young forests are dominated by gray birch (*Betula populifolia* Marsh), trembling aspen (*Populus tremuloides* Michx), ashes (*Fraxinus spp.*), red maple (*A. rubrum* L.) and white elm (*Ulmus americana* L.) (Brisson, Bergeron & Bouchard, 1988; Meilleur, Bouchard & Bergeron, 1994).

Study plots

As agricultural abandonment happened over time, stands in different successional stages are now found throughout the study area, from active pasture to secondary forest, providing a chronosequence that allows the study of natural revegetation. Five successional stages of the tree stratum were chosen based on the following structural and biological criteria: (PA) Active pasture stands where cows were still present; (LS) stands dominated by low shrubs (< 1.5 m) where pasture activity was abandoned; (TS) stands dominated by tall shrubs where a relatively closed shrub canopy < 6 m in height has developed; (YT) young tree-dominated stands with a fully developed canopy < 10 m in height; (MA) mature second growth forest with a canopy > 25 m in height composed of species characteristic of mature mesic forests.

Each stand stage was represented by a selection of six stands, for a total of 30 stands. Shrub stands were chosen from the work of Benjamin, Domon and Bouchard (2005) while young tree stands were identified using the work of Delage et al. (2005). Six active pasture stands were chosen in the vicinity of these stands. These stands all possessed old barbed wire, indicating their past agricultural use. We did not detect any evidence of plowing as no stone piles were found and rocks and pit-mounds were visible in the ground. We thus considered that they have never been plowed with modern heavy machinery. This classification was later validated by aerial photograph interpretation (1964-1966, 1975-1983), the studies of Benjamin, Domon and Bouchard (2005) and Delage et al. (2005), and by meeting private landowners; see Table 3.1 where the main characteristics of these study stands are described.

In each sampled stand, we set up 25-m radius plots at the approximate center of each stand. All plots were located at least 25 m away from roads and between 25 to 300 m from adjacent mature forest. All stands had stony soil and good drainage (Benjamin, Domon & Bouchard, 2005). Stands were selected to reduce any differences in edaphic conditions, aspect and drainage.

Field sampling

We determined floristic composition using linear vegetation surveys. In each plot, 13 circular points (15-cm radius) were systematically sampled along four 25-m transects for a total of 52 points per plot. Species within a sampling point received an occurrence value of 1, for a possible total score of 52 when a species was present in all points. Species present in the plot but not in any of the sampling points received an occurrence value of 0.5. The occurrence frequency (%) of a species for a plot was determined as the proportion of points in the plot where the species occurred. The plots were sampled three times from May to September 2003 to obtain data for all species present during the growing season. Grasses, sedges and hawthorns (*Crataegus* spp.) were identified to genus only.

Forest cover data were collected in each plot: tree composition, maximum tree height (m), basal area (m^2/ha), and density (stems/ha) of trees with diameter at breast height (DBH) > 5 cm. To characterize the understory environment, we quantified light availability and soil cover substrate for the 52 sampling points of each plot. The percentage of above-canopy photosynthetic photon flux density (% PPFD) was measured both at the ground level and at 2 m above ground, using a line-quantum sensor (LI-COR, Lincoln, Nebraska, USA). Light measurements were taken under completely overcast sky conditions following the methods of Messier and Puttonen (1995) and Gendron, Messier and Comeau (1998). We used the following categories of soil cover substrate types: grasses, herbs, deciduous shrub or tree leaf litter, conifer needles, mineral soil, rock and downed woody debris. The frequency of occurrence (%) of each substrate type was determined as the proportion of points in a plot where that substrate type occurred.

Tableau 3.1. Characteristics of the sampled plots.

Stand	Tree stratum						Understory stratum						Und. environmental conditions			
	Code	Class	Mean	Basal	Tree	Main tree species	Mean	Richness	% PPFD ⁱⁱ	at 200 cm	Grass	Leaves	Mineral	Rock	DWD	
	age yrs	max tree height m	area m ² /ha	stem density ^j n/ha		height cm	und.	n/plot	/ soil level							soil
Active pasture																
PA	0	.	0	0	.		36	34 ^d	100.0 ^a / 100.0 ^a	70 ^a	0 ^c	26 ^b	4	0 ^d		
Low shrub dominated stand																
LS	10 – 25	3	0.3	20	<i>Pinus strobus</i> <i>Ulmus americana</i> <i>Prunus serotina</i>		117	64 ^b	93.2 ^b / 31.7 ^b	71 ^a	8 ^c	16 ^c	2	3 ^c		
Tall shrub dominated stand																
TS	23 – 39	8	2.5	181	<i>U. americana</i> <i>Thuya occidentalis</i> <i>P. serotina</i>		356	73 ^a	29.2 ^c / 4.7 ^c	35 ^b	14 ^c	37 ^a	4	10 ^b		
Young tree dominated stand																
YT	28 – 60	14	14.5	743	<i>Fraxinus</i>		368	68 ^b	5.6 ^d / 2 ^c	47 ^b	21 ^{bc}	5	25 ^a			

* A different letter indicates a significant difference at $P < 0.05$ (one-way ANOVA followed by a multiple comparison Tukey test). DBH >

Species ecological traits

Information on the species ecological traits was obtained from the TOPIQ data base (Traits Of Plants In Quebec, see Aubin et al., 2007). Because of the lack of data and absence of distinct trends in exploratory analyses, some traits such as seed dormancy and pollination mode were discarded. Eleven categorical traits and two quantitative traits were used (Table 3.2).

Tableau 3.2. Plant biological traits compiled from the literature.

Trait	Code	Description
Raunkier life form	RA	mg: mega or meso-phanerophyte (≥ 8 m in height); mc: micro or nano-phanerophyte (25 cm to 8 m); ch: chamaephyte (herb or shrub, bud between 1 mm to 25 cm above ground)*; h: hemicryptophyte (herb with bud at the ground surface)*; g: geophyte (herb with underground bud)*; t: therophyte (annual)*
Life cycle*	PER	1: annual; 2: biennial; 3: perennial
Principal means of reproduction	REP	se: seeds only; ms: vegetative propagation possible but mostly by seeds; ve: mostly by vegetative propagation
Foliage persistence	PFO	0: no; 1: yes
Foliage structure	SFO	For phanerophytes: m: one stem; mu: multi-stemmed; vi: vine For other life forms*: No stem: r: rosette or semi-rosette; g: graminoid; e: erect leaves With stem: el: erect leafy stem; de: decumbent stem; um: umbel-shaped stem; vi: vine Non-leafy stem: nl: saprophyte

Trait (continued)	Code	Description
Physical defences	DEF	0: no; 1: yes
Flowering phenology	FPH	sp: spring; su: summer; sf: summer-fall*
Color of chasmogous flower	CFL	w: white; g: unattractive (green or brown); b: bright (red, yellow or blue); na: non applicable
Seed dispersal vector ⁱ	DI	w: wind (anemochorous); ez: mammal (zoochorous); mammal, carried externally (epizoochorous)*; an: insect, mostly ant (myrmecochorous)*; bi: bird ingestion (avichorous); hd: human dispersal: (anthropochorous)*; ex: ballasts or explosive discharge (ballistichorous)*
Seed size	SE	quantitative variable: 0.05 to 40 mm
Height	HT	quantitative variable: 10 to 3500 cm
Light requirement	LI	s: shade tolerant; m: mid tolerant; i: intolerant
Status in Quebec	ST	0: native; 1: exotic

ⁱ For the seed dispersal vector, a species can have more than one class * Omitted in the analysis of the woody species subset of EG groups

Data analyses

Two different PFT approaches were used in the study: a two-step analysis called emergent groups and a direct functional analysis called the fourth-corner analysis.

Indirect functional analysis - Emergent groups

The first step was to delineate emergent groups (EG) from the biological trait matrix using classification methods. EG were identified separately for the woody and herbaceous species following the hierarchical approach suggested by Lavorel et al. (1997) and McIntyre et al. (1999) and used by Deckers et al. (2004). As stated by McIntyre et al. (1999), some traits may be ecologically relevant to only some life forms and the variation of a trait may differ among life forms. Some classes of seed dispersal vector, life cycle, foliage structure, and flowering phenology traits were not present for the woody species (indicated with an asterisk in Table 3.2); so they were omitted from the classification of woody species. Raunkier's phanerophyte forms and life cycle were omitted for the herbaceous species classification.

To identify EG, a Gower similarity coefficient was calculated separately for the woody and herbaceous subsets of the biological traits matrix. This coefficient can be programmed to handle both missing values and mixed data (Legendre & Legendre, 1998). A Ward hierarchical classification was then computed for these similarity matrices. To verify the robustness of this classification, we qualitatively compared this classification with the result of a non-hierarchic clustering using K-means (Legendre & Legendre, 1998). The cut-off limit was determined subjectively after visual screening of the dendrogram and according to our botanical knowledge. To assess the impact of group number on the results, two cut-off levels were chosen for the herbaceous species subset.

The second step required assessing EG differences among stand stages. We examined the relative occurrence of EG in different successional stages using a matrix of the species group occurrences calculated as the product of the transposed species data

matrix (253 species x 30 plots, with percent occurrence data of each species) by the binary matrix of emergent groups (253 species x 13 or 15 emergent groups). This new matrix (30 plots x 13 or 15 emergent groups) was then standardized by dividing the occurrences of each group by the total occurrence for all groups in each plot. Differences in the relative occurrences of the species groups among stand stages were analyzed using one-way ANOVA followed by multiple comparison Tukey tests in cases where significant effects of stand stages were detected. A correction for multiple analyses was done and only the relationships that remained significant after Holm's (1979) correction were considered ($p \leq 0.05$).

Direct functional analysis – Fourth-corner analysis

We used a new version (Dray & Legendre, submitted) of the fourth-corner analysis (Legendre, Galzin & Harmelin-Vivien, 1997) to assess how individual species traits are related to stand stages. The fourth-corner analysis directly relates environmental variables (matrix **B**) to species traits (matrix **C**) by way of the species occurrences measured in the field (matrix **A**). This method allows statistical tests of the significance of the link between all combinations of species traits and environmental variables to be carried out (Dray & Legendre, submitted). The results are stored in a fourth matrix (**D**). Before the analysis, a Hellinger transformation (see Legendre & Gallagher, 2001 for details) was applied to the species occurrence matrix to standardize for the effect of decreasing occurrences along successional stages. Each statistic of **D** was tested for significance using permutation model 1 of the modified fourth-corner analysis of Dray and Legendre (submitted). This new version of the fourth-corner analysis allowed the use of quantitative data in the species data matrix instead of presence-absence data as in the original paper and program. The resulting probabilities were adjusted for multiple testing using Holm's procedure (1979).

Additionally, a multivariate regression tree (MRT; Segal, 1992; De'ath, 2002; Larsen & Speckman, 2004) was constructed to test whether understory developmental stages correspond to those of the tree developmental stages.

The R 3.0 package (Casgrain & Legendre, 2005) was used for the analysis. The mpart (2006) library of the R statistical language (R Development Core Team, 2006) was used to build the MRT, and the ‘fouthcorner’ R function from <http://biomserv.univ-lyon1.fr/~dray/software.php> was used for fourth-corner analysis.

Results

Species richness and discriminant species

Of the 253 species recorded in the sampled old fields, 190 (75%) were herbaceous and 63 (25%) were woody. Exotic species represented 23% of total species richness and were mainly herbs (56 of 59 species). Average plot species richness was 57. Species richness was highest in mid-successional stages, with tall-shrub-dominated stands possessing the highest richness overall (73, Table 3.1). Thirty-five species were widespread, being present in more than half of the plots. In contrast, 33 forest herb species described as characteristic of maple forests by Dansereau (1943) were found in our mature stands (Table 3.3). Of these 33 forest herbs, 10 species were unique to our mature forests. *Circea lutetiana*, *Sanguinaria canadensis*, *Smilacina racemosa* and *Trifolium grandiflorum* were found in all stand stages, except active pastures. *Erythronium americanum* was found in all stand stages, including one active pasture (Table 3.3).

Tableau 3.3. Mean occurrences and frequencies*of forest herbs among stand stages. PA: active pasture; LS: low shrub; TS: tall shrub; YT: young tree; MA: mature forest.

Species	EG	PA	LS	TS	YT	MA
<i>Actaea alba</i>	H6	.	.	0.2 (1)	1.4 (3)	0.8 (3)
<i>Actaea rubra</i>	H6	.	.	1.1 (3)	.	1.0 (5)
<i>Adiantum pedatum</i>	H5	.	.	.	0.6 (3)	0.3 (2)
<i>Allium tricoccum</i>	H6	0.3 (1)
<i>Aralia nudicaulis</i>	H6	0.2 (1)
<i>Arisaema triphyllum</i>	H6	.	.	.	0.5 (3)	0.3 (2)
<i>Asarum canadense</i>	H7b	.	.	.	0.5 (2)	0.3 (2)
<i>Athyrium filix-femina</i>	H5	.	.	.	1.6 (4)	0.5 (2)
<i>Cardamine diphylla</i>	H6	0.6 (3)
<i>Cardamine laciniata</i>	H6	0.3 (1)
<i>Caulophyllum thalictroides</i>	H6	.	.	.	0.3 (1)	7.5 (4)
<i>Circaeа lutetiana</i>	H3	.	0.3 (1)	0.5 (2)	5.4 (5)	10.1 (6)
<i>Claytonia caroliniana</i>	H7b	0.6 (1)
<i>Cystopteris bulbifera</i>	H5	0.2 (1)
<i>Dryopteris marginalis</i>	H5	.	.	0.3 (2)	0.6 (4)	0.2 (1)
<i>D. intermedia</i> and <i>carthusiana</i>	H5	.	.	0.8 (4)	1.8 (5)	0.2 (1)
<i>Erythronium americanum</i>	H7b	0.2 (1)	2.2 (1)	14.6 (4)	5.1 (4)	13.3 (5)
<i>Galium circaezans</i>	H6	0.2 (1)
<i>Hepatica acutiloba</i>	H7a	.	.	.	1.6 (2)	1.8 (2)
<i>Hydrophyllum virginianum</i>	H7a	.	.	.	0.2(1)	0.3 (1)
<i>Maianthemum canadense</i>	H6	.	.	0.6 (2)	1.8 (5)	2.7 (4)
<i>Mitchella repens</i>	H6	.	.	0.2 (1)	1.9 (3)	0.3 (1)
<i>Phryma leptostachya</i>	H3	0.2 (1)
<i>Polystichum acrostichoides</i>	H5	.	.	.	0.3 (3)	0.2 (1)

Species (continued)	EG	PA	LS	TS	YT	MA
<i>Polygonatum pubescens</i>	H6	.	.	.	0.3 (2)	0.2 (1)
<i>Sanguinaria canadensis</i>	H7b	.	0.2 (1)	0.3 (1)	0.8 (4)	1.8 (4)
<i>Smilacina racemosa</i>	H6	.	0.6 (1)	0.5 (2)	0.8 (4)	0.3 (2)
<i>Solidago flexicaulis</i>	H4	.	.	2.4 (4)	7.5 (4)	1.4 (4)
<i>Streptopus amplexifolius</i>	H6	0.2 (1)
<i>Trillium erectum</i>	H7b	.	.	.	0.2 (1)	0.3 (2)
<i>Trillium grandiflorum</i>	H7b	.	0.2 (1)	1.0 (2)	5.4 (4)	13.0 (5)
<i>Uvularia grandiflora</i>	H7b	.	.	.	0.2 (1)	0.3 (2)
<i>Viola pubescens</i>	H7b	.	.	1.6 (3)	4.8 (4)	5.1 (1)

In this table, forest herbs are vascular herbs found in mature stands sampled in our study, and described by Dansereau (1943) as characteristic of interior habitats of mature maple forests. *Frequency, as the number of stand where this species was found, is indicated in parenthesis.

Discriminant species were identified using a multivariate regression tree (MRT). The choice of the final MRT model was done by v-fold cross-validation. It explained 50.4% (SSE: 0.496) of the species variation in plots and corresponded perfectly to the five studied successional stages (Figure 3.1). The numbers under each node are the contributions to the R^2 , which is the percentage of variance explained by the model. The two shrub stages had the most similar composition (4.01%). *Fraxinus americana* was the discriminant species at the node separating these two stand stages (0.34%). These two shrub stages were then associated with active pasture with a contribution to the R^2 of 10.98%, with *Circium vulgare* (1.39%) and *Medicago lupulina* (0.96%) as the species discriminating between active pastures and the two shrub stands. Young tree and mature stands were associated at a contribution to R^2 of 6.54%; *Acer saccharum* (1.93%) was the discriminant species between these stand types. They are discriminated from younger stand stages with a contribution to $R^2 = 28.82\%$, for which *Acer saccharum* and Grass spp accounted for 4.52% and 2.39% respectively.

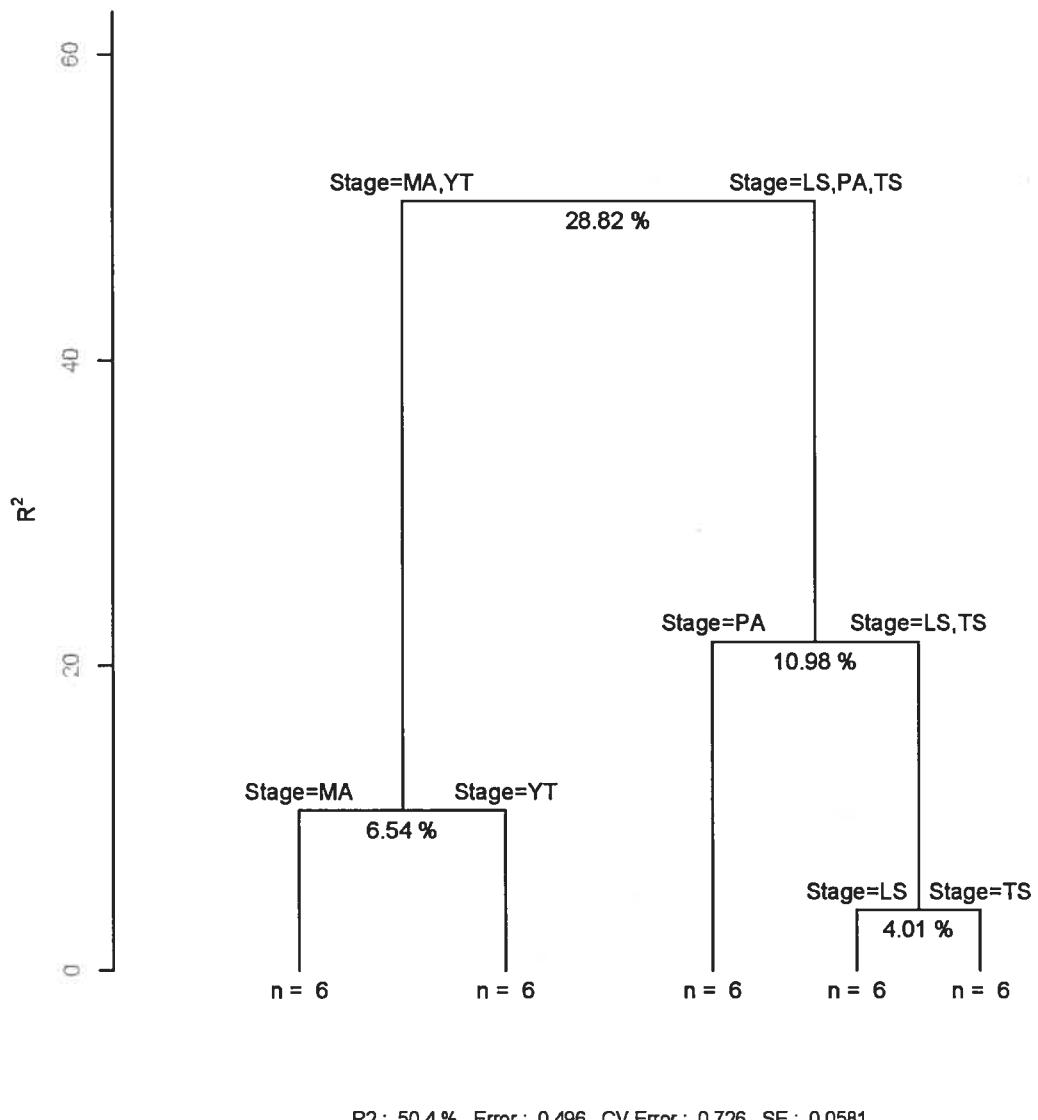


Figure 3.1. Multivariate regression tree model of the 30 plots. Numbers under each node indicate their individual contributions to R^2 , which is the percentage of variance explained by the model. The axe at the left shows the cumulative R^2 for the entire tree. PA: active pasture; LS: Low shrub; TS: Tall shrub; YT: young tree; MA: mature forest.

Emergent group identification

The cluster analysis allowed the determination of 4 groups for the woody species and 7 for the herbaceous species, both at a cutting level of $S = 0.82$. Woody species groups (Table 3.4) were characterized by the following traits: (W1) tall phanerophytes reproducing by large seeds mainly dispersed by mammals (zoochorous); (W2) wind-dispersed (anemochorous) phanerophytes; (W3) short mid- or shade-tolerant multi-stemmed phanerophytes producing seeds mainly dispersed by birds (avichorous). A fairly large proportion of these species possess physical defence (e.g. thorns); (W4) summer flowering bird-dispersed phanerophytes, mainly vines.

For the herbaceous species (Table 3.5), the following traits characterized the groups: (H1) exotic shade-intolerant summer flowering species, with erect leafy stems or in rosette form and dispersed by wind or mammals (this group contained all the biannuals); (H2) annuals that possess traits similar to H1 but are composed of both native and exotic species dispersed exclusively by wind; (H3) other summer flowering native perennials with erect leaf stems or decumbent form, dispersed mainly by mammals, with many species possessing physical defences; (H4) tall summer or late flowering native perennials dispersed by wind; (H5) ferns and allies, which have distinct biological traits, along with other shade-tolerant species with very small seeds (this group included a relatively large proportion of species with persistent foliage); (H6) shade-tolerant, spring-flowering native perennials dispersed by mammals; and (H7) short spring-flowering native perennials mainly dispersed by gravity (barochorous) or ants (myrmecochorous).

Tableau 3.4. Classification by species groups of woody species having similar biological traits computed from a cluster analysis using the biological traits data matrix (n = 63). Cut-off limit at S = 0.82.

Traits	Tall mammal-dispersed phanerophyte	Wind-dispersed phanerophyte	Short bird-dispersed multi-stemmed phanerophyte	Summer flowering bird-dispersed phanerophyte
	W1	W2	W3	W4
RA	mg	mg, (mc)	mc	mc, mg
REP	2	2 (3)	3, 2	3
PFO	(1)	0	0	0
FPH	sp	sp	sp	su
SFO	m	m, (mu)	mu	(vi)
CFL	-	-	-	w, g
DEF	0	0	(1)	0
DI	ez, (bi, w)	w	bi, (ez)	bi
LI	-	-	m, s	(m)
ST	0	0	0	0
HT	2336	1948	471	1025
SE	13.9	5.3	4.4	4.7
Sp	<i>Pinus strobus</i>	<i>Acer saccharum</i>	<i>Corylus cornuta</i>	<i>Vitis riparia</i>
	<i>Thuja occidentalis</i>	<i>Ulmus americana</i>	<i>Dirca palustris</i>	<i>Celastrus scandens</i>
	<i>Carya cordiformis</i>	<i>Ostrya virginiana</i>	<i>Cornus sericea</i>	<i>Rhus typhina</i>
n	11	22	22	8

See Table 3.2 for code definitions. Codes in parentheses indicate that this class is present but in lower proportion. Sp: characteristic species.

Tableau 3.5. Classification by species groups of herb species having similar biological traits computed from a cluster analysis using the biological traits data matrix ($n = 190$). Cut-off limits at $S = 0.82$ and $S = 0.72$ (in grey).

Traits	Exotic	At $S = 0.72$		Annual		Summer		Late		Fern and allies		Spring		Spring flowering		At $S = 0.72$	
		H1	H2														
RA	h	h				t		h		h, g		g, h		h, g		h	
PER	3 (2)	3	2, 3		1			3		3		3		3		3	
REP	-	3 (2)	1 (3)	1	-			3		3		3		3		3	
PFO	0	0	0	0	0			0		(1)		0		0		(1)	0
FPH	su	su	su	su	su			su, sf		su		sp		sp		sp	
SFO	(r, el)	r, el, de	r (el)	el, (r)	el, de			el, (r)		e		-		r (el, de)		-	
CFL	b	b (w)	b	w, b	w, b			w, b		na		-		b, w		b (w)	
DEF	0	0	(1)	0	(1)	0		0		0		0		0		0	
DI	w, ez	(ez)	w	w	(ez)	w		w, ex		ez (bi)		(an)		g (w)		an (ex)	
LI	i	i	i	i	-			(i)		(s)		s		-		s (m)	
ST	1	1	1	(1)	0			0		0		0		0		(1)	0
HT	110	71	152	156	122			156		67		102		46		5.5	35
SE	2.6	1.8	3.5	1.9	2.3			1.9		0.05		3.2		2.2		1.8	2.6
Sp	<i>Neptea</i>	<i>Cichorium</i>	<i>Erigeron</i>	<i>Rubus</i>	<i>Aster</i>			<i>Dryopteris</i>		<i>Arisaema</i>		<i>Aquilegia</i>				<i>Asarum</i>	
	<i>cataria</i>	<i>intybus</i>	<i>strigosus</i>	<i>idaeus</i>	<i>novae-</i>			<i>marginalis</i>		<i>triphyllum</i>		<i>canadensis</i>				<i>canadense</i>	

<i>Rumex</i>	<i>Lactuca</i>	<i>Chenopodium</i>	<i>Verbena</i>	<i>angliae</i>	<i>Adiantum</i>	<i>Medeola</i>	<i>Stellaria</i>	<i>Sanguinaria</i>
<i>crispus</i>	<i>serriola</i>	<i>album</i>	<i>urticifolia</i>	<i>Solidago</i>	<i>pedatum</i>	<i>virginiana</i>	<i>graminea</i>	<i>canadensis</i>
<i>Hypericum</i>	<i>Hieracium</i>			<i>canadensis</i>		<i>Smilacina</i>	<i>Veronica</i>	<i>Trillium</i>
<i>punctatum</i>	<i>caespitosum</i>	16	27	28	16	29	33	<i>grandiflorum</i>
n	41	21	20	33	15	18	18	15

See Table 3.2 for code definitions. Codes in parentheses indicate that this class is present but in lower proportion. Sp: characteristic species.

To test the robustness of this classification, we selected a cut-off level for the herbs at a similarity level of 0.72. This limit resulted in nine groups (Table 3.5). From a visual screening of the dendrogram and our botanical knowledge, this classification seems another ecologically relevant choice. The group of exotic species (H1) was thus split into: (H1a) short exotic perennials mainly dispersed by mammals, and (H1b) tall exotics dispersed by wind with large seeds (this group contained many biennials). Spring-flowering short perennials (H7) was split into: (H7a) wind- or gravity-dispersed species, comprising light-demanding hemicryptophytes of which many had persistent foliage; and (H7b) ant-dispersed species, comprising short shade-tolerant or spring ephemeral geophytes with a variety of shapes.

Responses of emergent groups to stand stages

Except for the summer-flowering perennials (H3) and the spring flowering short perennials (H7), all EG varied significantly in proportions among stand stages (Table 3.6). Exotics (H1), annuals (H2), and spring flowering mammal-dispersed perennials (H6) had a decreasing relative occurrence from active pasture to mature forests. Ferns (H5) and tall phanerophytes (W1, W2) increased in occurrence with stand stages. Late-flowering wind-dispersed perennials (H4) showed their highest relative occurrence in the two shrub stages (LS, TS), while short avichorous multi-stemmed phanerophytes (W3) and summer-flowering bird-dispersed phanerophytes (W4) had their highest occurrences in tall shrub and young tree stages (TS, YT).

In the 9-group classification of the herb matrix (Table 3.5), the two exotic subgroups (H1a and H1b) showed a similar trend across the chronosequence, with decreasing relative occurrences from active pastures to mature forests. In contrast, the two spring-flowering subgroups (H7a and H7b) showed a different response to stand stages. Relative occurrences of the wind- or gravity-dispersed subgroup (H7a) decreased significantly among stand stages while the relative occurrences of the ant-dispersed subgroup (H7b) increased significantly (Table 3.6).

Tableau 3.6. Mean relative occurrences of emergent groups among stand stages. PA: active pasture; LS: low shrub; TS: tall shrub; YT: young tree; MA: mature forest. Cut-off limits at $S = 0.82$ and $S = 0.72$ (in grey).

Emergent groups	<u>P</u>	Stand stage				
		PA	LS	TS	YT	MA
H1	***	40.2a	32.7b	11.5c	4.8d	1.8d
H1a	***	30.7a	25.1b	8.8c	3.6d	1.1d
H1b	***	9.5a	7.6b	2.7c	1.2d	0.7d
H2	***	10.6a	2.6b	1.0c	0.3c	0.3c
H3	-	3.9	6.8	7.5	6.9	5.0
H4	***	6.9d	18.4b	20.2a	12.8c	3.5e
H5	**	0.0b	0.0b	0.1b	5.0a	0.5b
H6	***	22.3a	17.2b	14.4c	9.7d	6.1e
H7	-	14.6	8.6	11.8	7.2	14.7
H7a	***	14.3a	7.6b	7.0b	2.8c	2.0c
H7b	***	0.3c	1.0c	4.8b	4.4b	12.7a
W1	***	0.0c	0.9b	1.3b	4.1a	4.8a
W2	***	0.2d	1.3d	6.4c	20.8b	50.5a
W3	***	1.1d	9.4c	21.0a	22.3a	11.1b
W4	***	0.1d	2.0c	4.6b	6.0a	1.7c

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; - $P > 0.05$

For each emergent group (row), a different letter indicates a significant difference at $P < 0.05$ (one-way ANOVA followed by a multiple comparison Tukey test). Detailed descriptions of the groups are found in Table 3.4 and 3.5.

Directly relating species ecological traits to stand stages

Based on the fourth-corner analysis, the relationship between stand stages and species ecological traits was globally significant for the large majority of the traits (Table 3.7). Except for physical defenses, foliage persistence and seed dispersion by mammals and wind, all traits varied significantly across the chronosequence. Seed size and plant height significantly increased along the chronosequence. In terms of the qualitative variables, the statistically significant ecological profile of species in active pastures was short light-demanding exotic herbs, mainly annuals, that reproduce principally by small seeds dispersed by humans (anthropochorous). For the low shrub stage, a positive correlation was found for short summer or late summer bright flowering biannual or perennial hemicryptophytes that have a rosette or erect leafy stem shape, are exotic, and are light-demanding and mainly dispersed by humans. For the tall shrub stage, a positive correlation was found with perennial mid-tolerant or light-demanding hemicryptophytes, phanerophytes or chamaephytes with a variety of foliage structure. Species in the tall shrub stage generally possessed large seeds dispersed by birds and could propagate vegetatively. Species in the young tree stage are native mid- or shade-tolerant spring-flowering perennials, mainly phanerophytes or geophytes, with a tree, shrub, vine or erect leafy stem foliage structure; they are dispersed by birds or by explosive discharge. Saprophytes were only found in this stand stage. Species traits associated to the mature forest stage were native spring-flowering shade-tolerant geophytes with an umbel-shape foliage structure and seeds dispersed by ants.

Tableau 3.7. Results of the fourth-corner analysis where species occurrence for each successional stage is related to species traits. For nominal traits, the first line of each cell indicates a pseudo-frequency while the first line indicates a Pearson correlation in the case of quantitative traits. The second line gives the probability results after 9999 random permutations. The sign indicates if the statistic is above (+) or under (-) the expected value (mean of the permutations results). PA: active pasture; LS: low shrub; TS: tall shrub; YT: young tree; MA: mature forest. Non significant results, at the 5% significance level after Holm's correction, are printed in italics.

		PA	LS	TS	YT	MA
Nominal traits						
		<i>10</i> –	<i>13</i> +	<i>13</i> +	<i>12</i> +	<i>7</i> –
<i>DEF</i>	<i>I</i>	<i>0.275</i>	<i>0.143</i>	<i>0.134</i>	<i>0.246</i>	<i>0.008</i>
		<i>2</i> –	<i>3</i> +	<i>6</i> +	<i>3</i> –	<i>1</i> –
<i>RA</i>	<i>ch</i>	<i>0.281</i>	<i>0.428</i>	<i>0.007</i>	<i>0.48</i>	<i>0.006</i>
		<i>1</i> –	<i>8</i> –	<i>10</i> –	<i>29</i> +	<i>25</i> +
	<i>g</i>	<i>0.001</i>	<i>0.002</i>	<i>0.022</i>	<i>0.001</i>	<i>0.001</i>
		<i>40</i> –	<i>80</i> +	<i>68</i> +	<i>53</i> –	<i>25</i> –
	<i>h</i>	<i>0.002</i>	<i>0.001</i>	<i>0.001</i>	<i>0.417</i>	<i>0.001</i>
		<i>2</i> –	<i>13</i> –	<i>21</i> +	<i>21</i> +	<i>10</i> –
	<i>mc</i>	<i>0.001</i>	<i>0.463</i>	<i>0.001</i>	<i>0.001</i>	<i>0.028</i>
		<i>0</i> –	<i>11</i> –	<i>20</i> +	<i>27</i> +	<i>18</i> +
	<i>mg</i>	<i>0.001</i>	<i>0.012</i>	<i>0.011</i>	<i>0.001</i>	<i>0.096</i>
		<i>9</i> +	<i>7</i> +	<i>5</i> –	<i>6</i> –	<i>3</i> –
	<i>t</i>	<i>0.027</i>	<i>0.218</i>	<i>0.196</i>	<i>0.402</i>	<i>0.021</i>

		PA	LS	TS	YT	MA
(continued)						
		46 –	84 +	62 +	36 –	18 –
LI	i	0.186	0.001	0.002	0.002	0.001
		9 –	29 +	42 +	43 +	19 –
	m	0.001	0.377	0.001	0.001	0.001
		1 –	9 –	25 –	59 +	45 +
	s	0.001	0.001	0.212	0.001	0.001
		18 +	27 +	17 +	13 –	9 –
REP	se	0.314	0.001	0.393	0.063	0.001
		10 –	27 +	33 +	37 +	26 –
	ms	0.001	0.492	0.015	0.001	0.407
		27 –	70 +	80 +	87 +	47 –
	ve	0.001	0.035	0.001	0.001	0.002
		4 –	10 –	13 +	17 +	7 –
PFO	I	0.001	0.462	0.086	0.001	0.021
		13 –	43 –	62 +	77 +	57 +
FPH	sp	0.001	0.046	0.003	0.001	0.072
		46 –	88 +	75 +	64 +	25 –
	su	0.003	0.001	0.002	0.195	0.001
		6 –	19 +	14 +	11 +	5 –
	sf	0.002	0.001	0.035	0.452	0.001

		PA	LS	TS	YT	MA
(continued)						
		9 +	7 +	6 –	6 –	3 –
PER	1	0.048	0.287	0.343	0.43	0.022
		9 +	14 +	6 –	3 –	2 –
	2	0.061	0.001	0.26	0.001	0.001
		37 –	102 +	118 +	129 +	76 –
	3	0.001	0.041	0.001	0.001	0.002
		35 +	51 +	30 +	12 –	6 –
ST	1	0.005	0.001	0.09	0.001	0.001
		1 –	12 –	24 +	26 +	19 +
SFO	ms	0.001	0.019	0.001	0.001	0.137
		1 –	9 –	13 +	16 +	8 –
	mu	0.001	0.369	0.017	0.002	0.183
		29 +	46 +	32 +	17 –	13 –
	r	0.303	0.001	0.055	0.001	0.001
		3 –	5 +	5 +	4 +	3 –
	g	0.2	0.141	0.251	0.401	0.168
		1 –	5 –	7 –	21 +	8 –
	e	0.001	0.054	0.217	0.001	0.484
		8 –	26 +	28 +	25 +	15 –
	el	0.001	0.032	0.01	0.053	0.015

		PA	LS	TS	YT	MA
(continued)						
		12 –	14 +	14 +	15 +	8 –
	de	0.362	0.254	0.193	0.121	0.005
		0 –	0 –	0 –	4 +	7 +
	um	0.004	0.006	0.026	0.077	0.001
		1 –	5 +	7 +	8 +	1 –
	vi	0.001	0.208	0.012	0.002	0.001
		0 –	0 –	0 –	2 +	0 –
	nl	0.493	0.499	0.497	0.008	0.506
		20 –	40 +	42 +	44 +	31 –
DI	ez	0.001	0.075	0.03	0.008	0.094
		9 +	8 +	5 –	4 –	1 –
	hd	0.001	0.007	0.272	0.074	0.001
		4 –	26 +	34 +	34 +	19 –
	bi	0.001	0.136	0.001	0.001	0.035
		23 –	56 +	50 +	62 +	28 –
	w	0.001	0.004	0.036	0.001	0.001
		2 –	9 –	11 +	11 +	13 +
	an	0.001	0.364	0.096	0.193	0.029
		3 –	6 –	10 +	18 +	8 –
	ex	0.001	0.09	0.226	0.001	0.257

		PA	LS	TS	YT	MA
(continued)						
		16 –	43 +	46 +	47 +	31 –
CFL	w	0.001	0.054	0.005	0.003	0.057
		7 –	14 –	22 +	27 +	14 –
	g	0.001	0.081	0.006	0.001	0.074
		32 –	61 +	55 +	46 +	30 –
	b	0.001	0.001	0.006	0.448	0.001
		0 –	5 –	7 –	18 +	6 –
	na	0.001	0.126	0.458	0.001	0.279
Quantitative traits						
		-0.11 –	-0.04 –	0.03 +	-0.01 –	0.11 +
SE		0.001	0.765	0.949	0.648	0.552
		-0.14 –	-0.09 –	0.03 +	0.07 +	0.11 +
HT		0.001	0.011	0.925	1	0.998

See Table 3.2 for code definitions.

Discussion

Clear patterns of trait associations with stand developmental stages emerged both at the trait level (Table 3.7) and the group level (Table 3.6). From these results, natural revegetation processes after old-field abandonment were characterized via species trait responses and synthesized in a schematic illustration (Figure 3.2). Changes in traits dominance in different stand stages and their impacts on natural revegetation processes are discussed below.

Traits associated to pioneer stages

A characteristic of vegetation succession in abandoned pasture is the selective pressure of grazing and trampling, which creates a particular initial floristic composition. Species avoided by cattle or with an adapted morphology possess a competitive advantage. Species responses to grazing are function of their architecture, morphology and phenology as well as to their palatability (Hadar, Noy-Meir & Perevolotsky, 1999). Corroborating other studies conducted in the Mediterranean biome (McIntyre, Lavorel & Tremont, 1995; Lavorel et al., 1998; Lavorel, McIntyre & Grigulis, 1999), we found the short-lived rosette-shaped species with small seeds to be associated with active pastures and low shrub stages. However, species with physical defences such as thorns, generally favoured by pasture activity (Stover & Marks, 1998), were not significantly associated to any stand stages (Table 3.7). In fact, many thorny shrubs such as hawthorn (*Crataegus spp.*) and prickly ash (*Zanthoxylum americanum* Mill.) were found throughout the studied stand stages, including mature forest originating from pasture. These species were likely present in low abundance in active pasture and rapidly invaded via vegetative propagation in the first stages of succession.

Many shrubs can acclimate to the shaded forest understory, waiting for disturbance to become dominant via clonal propagation (Hibbs & Fischer, 1979; Tappeiner et al., 2001; Aubin, Messier & Kneeshaw, 2005; Bartemucci, Messier & Canham, 2005). Shrubs with

thorns persist through succession while short-lived rosette species are present only in pioneer stand stages. The effect of these two set of species will thus be different. Short-lived rosette species affect revegetation processes limited to pioneer stages while thorny shrubs can influence understory function and structure throughout succession. A major impact of these shrubs is their regulatory effect on understory light availability and other environmental conditions (Aubin, Beaudet & Messier, 2000; Bartemucci, Messier & Canham, 2005). Their presence also increases the structural complexity of vegetation. High structural diversity can create variability in environmental conditions, and in this way favor floral diversity. High structural diversity also indirectly favors diversity by providing diverse habitat for fauna and insects that act as vectors for seed dispersal. Additionally, many of these shrubs bear fruits attractive to birds (e.g. hawthorn) and may therefore aid in the introduction of bird-dispersed species such *Smilacina racemosa* and *Actaea spp.*

Annuals and exotics were associated with pioneer stages, occupying nearly 50% of the relative occurrence in active pasture (Table 3.6). However, their relative occurrence decreased rapidly with canopy closure, totaling less than 3% in mature stands. Meiners, Pickett and Cadenasso (2002) observed a similar abundance of exotic species shortly after old field abandonment as in our study as well as a similar decline after canopy closure. However, they also noted the presence of shade-tolerant exotics such as the herb *Alliaria officinalis*, the shrub *Lonicera tatarica*, and the tree *Acer platanoides* in mature stands. Exotics in our study were mostly short-lived open-adapted species, confined to early succession stages. Although they do grow in the region, we found none of these species in our study sites. Shade-tolerant exotics represent a greater risk for the natural development of understory native flora than light demanding pioneer exotics because they can invade mature stands and displace native forest flora (Hendrickson, 2002).

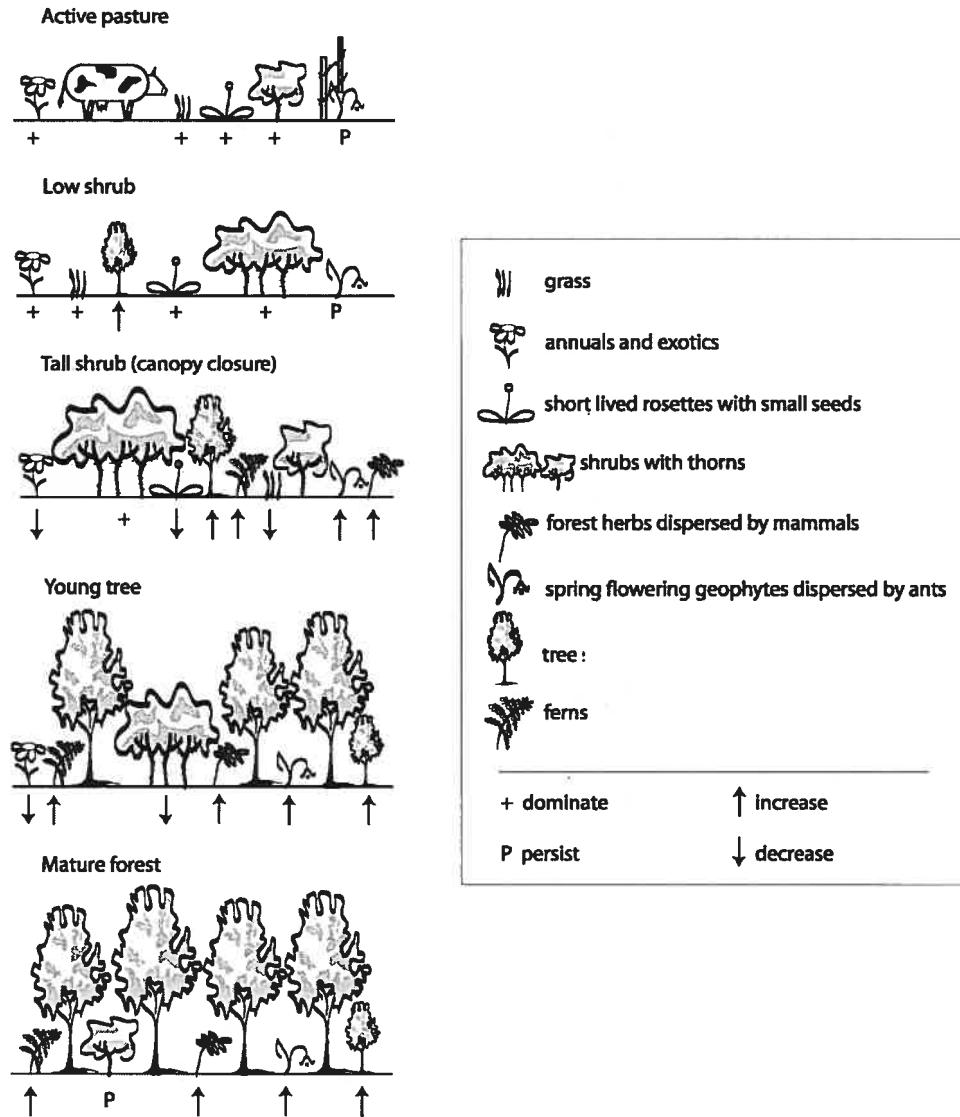


Figure 3.2. Schematic of natural revegetation in abandoned pasturelands. PA: active pasture; LS: Low shrub; TS: Tall shrub; YT: young tree; MA: mature forest.

Trait responses to canopy closure

The increasing abundance of woody species during the course of succession can greatly influence understory environmental conditions and species traits occurrence. In our study, canopy closure occurred approximately 30 years after land abandonment, during the tall shrub stand stage. Tall shrub-dominated stands have a canopy composed of a mix of shrubs and tree saplings of a low commercial value (Table 3.1; Cogliastro, Benjamin & Bouchard, 2006; D'Orangeville, accepté). Many shrub species that dominate these stands are perceived as impeding succession (Niering & Egler, 1955; Putz & Canham, 1992; Meilleur, Véronneau & Bouchard, 1994; Laliberté, Bouchard & Cogliastro, in press). However, this stand stage appears to be a key for understory development, representing a balance between field flora and forest understory assemblages and having the highest species richness we observed (Table 3.1). This stage has important features that favor the reestablishment of mature forest species. Canopy closure led to a sharp decrease in light availability, a decrease of grasses and an increase of bare soil and leaf litter substrate (Table 3.1) – conditions that provide a relative advantage to forest herbs. Last, the mixed shrub and sapling canopy in this stand stage creates high structural complexity and generally favors diversity.

Traits associated with mature forest

The understory of mature maple forest represents the reference conditions of a natural ecosystem for the region. As such, a comparison with plant traits associated with mature forest allows verifying whether flora of an abandoned pasture is changing from field to forest species assemblages. The trait-level analysis revealed that mature maple forests are typically associated with native spring-flowering shade-tolerant geophytes dispersed by ants. These traits are mainly those of the spring flowering ant-dispersed geophytes subgroup (H7b). Many studies have associated this set of traits to natural unmanaged forests or to ancient forests (Froborg & Eriksson, 1997; Bossuyt, Hermy & Deckers, 1999; Scheller & Mladenoff, 2002; Aubin et al., 2007). Species with these traits are generally slow

growing and possess a low capacity for colonization, making them particularly sensitive to human disturbance (Bierzychudek, 1982; Meier, Bratton & Duffy, 1995; Whigham, 2004). These herbs are thus considered as having a high conservation value and can be used as an indicator of natural forests in the deciduous temperate biome (Keddy & Drummond, 1996; Hermy et al., 1999; McLachlan & Bazely, 2001; Aubin et al., 2007). An increase in occurrence of this target group in a given stage is thus considered as an indicator of understory flora recovery.

To what extent do forest herbs recover in former pastures?

The shift in traits dominance observed along the successional stages indicates a convergence of the developing understory community toward that of a natural forest. Young tree-dominated stands showed a rich understory with diverse foliage structure and dominated by native spring flowering geophytes and woody species. This suggests good potential for natural recovery. However, the occurrence and richness of high conservation value species such as the spring-flowering ant-dispersed geophytes subgroup remains low.

At the species level, forest herb species showed a variable capacity for recovery, with some species found in young stages while others are being restricted to mature forests. Within the spring flowering herbs dispersed by ants, we observed important variations in recovery ability. Surprisingly, three species in this group (*Erythronium americanum*, *Trillium grandiflorum* and *Sanguinaria canadensis*) were found in the tall shrub and young tree stages (Table 3.3). *E. americanum* was even found in one active pasture. Typically, species that recover well after forest discontinuities are good colonizers, capable of maintaining a persistent seed bank in the soil, or able to survive in a non-forested environment (Bellemare, Motzkin & Foster, 2002). No persistent soil seed bank is reported for those species (Baskin & Baskin, 2001; Whigham, 2004). The principal agents of dispersion for these species, ants, can carry forest herbs for a mean distance of 1.38 m and occasionally up to 35 m, with a reported maximum yearly rate of transport of 1.6 m per year for *S. canadensis* (Matlack, 1994b; Cain, Damman & Muir, 1998). Ants are thus likely

not responsible for the reintroduction of these species in tall shrub stands, which range from 23 to 39 years old and are located from 50 to 225 m from a forest edge (Table 3.1). Cain, Damman and Muir (1998) emphasized the importance of occasional events of long distance seed dispersal for the colonization of species with short distance dispersal. However, in our study, these species were found in many young stands; it seems unlikely that so many occasional long distance events could occur. We thus propose that some of these species survived as relict population of the original forests in a non-forested environment. In addition to the individuals that we found in young stands, we frequently observed *T. grandiflorum*, *S. canadensis* and *E. americanum* in hedgerows, shrub thickets and along the fence in or closed to sampled pastures. These results and observations corroborate those of Stover and Marks (1998), who observed these species in a stand two years after pasture ended. The presence of shrub thickets or hedgerows may provide shelter for these long-lived perennials (Stover & Marks, 1998; Singleton et al., 2001; Bellemare, Motzkin & Foster, 2002). These three species, as well as *Allium tricoccum*, *Asarum canadense* and *Uvularia grandiflora* have been reported in hedgerows, although in reduced relative occurrence (Roy & De Blois, 2006). Bellemare et al. (2002) even observed a higher frequency of *S. canadensis* in post-agricultural forests than in primary forests.

The ability of these species to survive in a non-forested environment appears to be a key factor behind their recovery in post-agricultural stands. Many species of the spring flowering ant-dispersed geophytes sub-group are light demanding. Some of these species, such as *S. canadensis*, shows larger plants with strong clonal growth in high-light environments (Marino, Eisenberg & Cornell, 1997). Adapted to a stable environment, the species of this target group are long-lived and able to regress to a juvenile stage (Bellemare, Motzkin & Foster, 2002; Whigham, 2004). In this way, they may survive unfavorable conditions for many years. These species are particularly sensitive to changes in the forest floor, such as soil structure, hydrology, microbial ecology, competitive environment and forest floor microclimate (Moore & Vankat, 1986; Matlack, 1994a; Wulf, 1997; Flinn & Marks, 2007). However, individuals of these long-lived species can survive these harsh conditions as long as the soil is not disturbed. These individuals left as biological legacies

(sensu Franklin et al., 2000) play a major role in understory recovery. Being established, they serve as a source for new individuals via seeds and vegetative propagation when a site progressively recovers forest-like understory conditions following canopy closure.

Even when relict populations persist from the original forests, species of this target group will take centuries to recover to the occurrence of unmanaged natural maple forests as they grow very slowly (Singleton et al., 2001; Bellemare, Motzkin & Foster, 2002; Scheller & Mladenoff, 2002; Beatty, 2003; Flinn & Vellend, 2005; Flinn & Marks, 2007). In our study, species that were found exclusively in mature stands were also generally infrequent (Table 3.3). These infrequent species were geophytes dispersed by gravity or ants: *Allium tricoccum*, *Claytonia caroliniana*, *Cardamine spp.* (Table 3.3). Bellemare et al. (2002) observed a similar low frequency of these species in post-agricultural forests. The rarer herb species are generally reported as the most sensitive to disturbances (Meier, Bratton & Duffy, 1995; Jolls, 2003). These sensitive species would probably have been more frequent in unmanaged natural stands than in our mature stands originating from old pasture. In a study comparing understory assemblage in maple forests of different land use history, Aubin et al. (2007) have found forest originating from old pasture to be globally similar to unmanaged natural forests. However, former pastures tended to have less of species groups with limited colonization capacity, such as the spring geophytes and the pteridophytes. Accordingly, many studies have found second growth forests after agriculture abandonment to have less species with limited colonization capacity or requiring specific microhabitats (such as spring geophytes and ferns) than unmanaged natural stands (Matlack, 1994b; Bossuyt, Hermy & Deckers, 1999; Singleton et al., 2001; Bellemare, Motzkin & Foster, 2002; Flinn & Vellend, 2005).

Our data do not allow identifying what makes these infrequent herbs more sensitive than the three species of the target group found in young stands. These differences were not related to dispersal vector or other traits analyzed in this study. Other than dispersal constraints, other less-studied traits warrant more investigation, such as those related to

survival potential in non-forested environments. Additionally, specific environmental requirements such as the availability of particular microhabitats may explain the differences in recovery capacity for species possessing similar sets of traits (Flinn, 2007). A lack of knowledge regarding the ecological traits of many forest herbs impedes our understanding of their responses to different environmental conditions. In this study, using other important but insufficiently documented ecological traits such as seed longevity, potential mycorrhiza, nutrient caption and pH requirement could have substantially improved our understanding of understory recovery.

Except for individuals persisting from the original forest, forest herb recovery is highly dependant of seed dispersion (Verheyen & Hermy, 2004; Flinn & Vellend, 2005). Our results show different dispersal modes being optimal in specific stand stages and suggest the timing of a species establishment is related to its dispersal. Dispersal mode was a major trait of the emergent group delineation (Table 3.4 and 3.5). It was also closely associated with different stand stages at the trait level (Table 3.7). Human-dispersed species were principally found in active pasture and low shrub stages, bird dispersion was characteristic of tall shrub and young tree stages, while species dispersed by ants were associated with mature forests. Wind- and mammal-dispersed species were frequent in all stand stages and not significantly associated with any particular stand stage. While wind-dispersed species are favored in open environments such as agricultural landscapes, this dispersal mode is presumably less efficient in a forested environment (Matlack, 1994b; Takahashi & Kamitani, 2004). Dispersion by mammal ingestion is an effective means of colonization in post-agricultural lands (Matlack, 1994b; Bellemare, Motzkin & Foster, 2002). In accordance with this finding, many shade-tolerant forest herbs with seeds dispersed by mammals such as *Smilacina racemosa* and *Actaea* spp. were found relatively frequently in young stand stages (Table 3.3), indicating a good potential for natural recovery for these species. These species possess a good potential of recolonization in hedgerows (Roy & De Blois, 2006). Adhesion on fur (epizoochorous) has also been found to be a very effective means of propagation (Matlack, 1994b; Bellemare, Motzkin & Foster, 2002; Couvreur et al., 2004), so it was therefore unsurprising that *Circea lutetiana*, a

summer flowering forest herb with this dispersal mode, was found in all stand stages except active pastures (Table 3.3).

Ferns possess variable colonizing capacities (Flinn, 2007). For instance, *Polystichum acrostichoides* can successfully colonize young post-agricultural forests while *Adiantum pedatum* is typically restricted to primary forests (Bellemare, Motzkin & Foster, 2002). Specific environmental requirements such as particular microhabitats may explain this contrasting colonizing capacity for those species possessing a similar life history strategy and ecological traits (Flinn, 2006; Flinn, 2007). In our study, ferns were absent from pioneer stages but appeared after canopy closure in tall shrub stage. Ferns had their highest occurrence in the young tree stage (Table 3.3, Table 3.6). Ferns in our study area thus seem to generally possess a good potential for natural recovery in old pasture lands. The preservation of the pit and mound topography in former pastures likely facilitates their reestablishment as compared to plowed land (Flinn, 2005; Flinn, 2007).

Comparison of the indirect and direct trait-based approaches

Our simultaneous use of two different trait-based approaches provided a robust and comprehensive characterization of vegetation responses in the old field-deciduous forest chronosequence. We were interested in comparing these two approaches.

Emergent groups provide an easy way to construct objective classification of the flora from its principal biological traits. Each group is composed of species sharing a similar set of traits that can be associated with a similar life history strategy (Lavorel et al., 1997). The main utility of emergent group classification is to provide a coarse-scale portrait of plant communities. In themselves, emergent groups are purely descriptive and do not provide information on vegetation processes or ecosystem changes. A second step analysis is necessary to relate these groups with an environmental gradient. However, information may be lost if the two-step analysis is performed at too coarse of a scale. Although easy in implementation, a relevant emergent group classification is not in itself an easy task to accomplish. The not straightforward relationships among emergent groups and ecosystem

processes (Kleyer, 1999), effects of traits selection on the ecological relevance of groups (Kleyer, 1999; Pillar, 1999; Weiher et al., 1999), autocorrelation among traits (Kleyer, 1999; Lavorel, McIntyre & Grigulis, 1999) and phylogeny (Chazdon et al., 2003) are some of the problems in developing emergent group classification that may complicate the ecological interpretation.

Although arbitrary, the visual screening of the cluster diagram is the most common way to delineate the final partition. Statistical methods such as the efficiency criteria of Legendre and Legendre (1984) exist but are rarely used. The final number of groups in emergent group classification must be based on sound botanical knowledge. While the number should be small enough to provide information synthesis, ecologically relevant information may be lost if the classification is too coarse. The contrasting results we obtained with a seven- or nine-group classification of the herbaceous subset illustrates how critical group number is for emergent group classification (Table 3.5). Choosing seven groups rather than nine would have hidden the response of our target group, the spring flowering ant-dispersed geophytes (H7b), as this group would have been merged with the spring flowering wind- or gravity-dispersed hemicryptophytes (H7a). Although possessing similar traits, these two closely related groups respond in vastly different ways to succession (Table 3.6).

Emergent groups may be too general and hide trait-level differences. For instance, the 4th-corner analysis revealed a shift in seed size, light requirement, plant form and height along the chronosequence that was not easily shown by the emergent group classification. Particular associations between traits and stand stages can also be observed, such as the bird-dispersed species in the tall shrub and young tree stages.

Ecologists generally use emergent groups when referring to plant functional groups. However, they are searching for vegetation response to an environmental gradient. In this sense, new direct functional approaches that directly relate plant traits to environmental variable are far more accurate. These approaches can link floristic, traits and environmental matrices in one step analysis. The 4th-corner method has the particularity of giving a

statistical test for all combination of species traits and environmental variables (Dray & Legendre, submitted). An exhaustive and precise analysis of the relationships between species traits and environmental variables is thus obtained. However, this analysis does not at this time provide the possibility to develop group of species (which would be response groups sensu Lavorel et al., 1997). Work is needed to make these methods more accessible to ecologists and further research is needed in developing response groups.

Implications for restoration ecology

Our study illustrated that natural revegetation can be effective for the development of a functional understory in abandoned pastures of the northern hardwood biome. Forest flora in former pastures begins to develop with canopy closure approximately 30 years after abandonment. However, complete recovery may take centuries. In fact, it was likely still ongoing in 100-year-old mature stands of old pasture origin. Some rare herbs with poor colonization ability may never reestablish, particularly in a fragmented landscape. Surprisingly, some spring geophytes with limiting colonization capacity were found in pioneer stands. This finding highlights the crucial role that relict populations in a non-forested environment play in the recovery potential of post agricultural lands.

To accurately evaluate the potential of these lands to recover naturally, it is imperative to recognize the dynamic nature of these ecosystems as well as to include a relevant time span in our restoration goal. In the case where the development of a forest ecosystem is needed in a relatively short time scale, a sound knowledge of natural vegetation development is necessary to design restoration activities based on an appropriate windows of opportunity. Activities unlike these natural processes such as heavy site preparation and planting conifer species may lead toward novel pathways of vegetation development and irremediably impoverish the established flora.

Restoration activities should preserve the biological legacies and be tailored according to the developmental stage of the area in question. Before canopy closure, restoration activities should focus on the development of a tree or shrub stratum, taking

special care to preserve structural heterogeneity, soil properties and established flora. Canopy closure will create environmental conditions favorable to forest herb establishment while the heterogeneous structure will favor diversity, directly through habitat provision and indirectly via seed dispersal vectors. After canopy closure, restoration activities may include seeding or planting of high conservation value species with low dispersal capacity such as the spring flowering herbs dispersed by ants. Seeding has been successful for many forest herb species as long as the understory environmental conditions are favorable (Verheyen & Hermy, 2004; Flinn, 2007).

With the important loss of forest habitat that the deciduous temperate biome has incurred, conservation strategy in this region needs to include ecological restoration. Secondary forests such as these abandoned pastures may take a long time span to fully recover. However, these forests are viable habitats for native forest flora, and possibly for other ecosystem components closely associated with understory vegetation (e.g., fungi, insects and herbivores). Conversion of these lands for agriculture or via plantations using traditional practices that include heavy site preparation will lead to a perhaps irreversible loss of biodiversity.

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Chapitre 4

Can plantations develop understory biological and physical attributes of natural forests?

Ce chapitre a été soumis pour publication sous forme d'article:

Aubin, I., Messier, C., et A. Bouchard. Can plantations develop understory biological and physical attributes of natural forests? Biological conservation.

Abstract

With an increasing proportion of natural forests being replaced by plantations, there is a need to determine their potential to fulfill some ecological purposes other than just wood production. This study evaluated the extent to which deciduous and coniferous plantations develop understory attributes comparable to natural forests and unplanted old-field stands. A functional group approach was used to synthesise species responses in terms of their ecological traits. Multivariate analyses of ecological traits revealed 16 emergent groups that shared common traits associated with a similar life history strategy. Responses of these groups, understory structure, and understory environmental conditions to plantation types and stand stages were analysed and compared to natural forests. Clear associations of trait responses to stand developmental stages and plantation types emerged. Light-demanding and wind-dispersed species groups were associated with early successional stages while woody groups, ferns and ant-dispersed spring flowering herbs were associated with late successional stages. Analyses also revealed an indicator group associated with natural forest. The understory functional groups and environmental conditions of deciduous plantations converged toward those of natural forests. However, understory structure in deciduous plantations remained poorly developed and richness of the indicator group was low. Conifer plantations, presently the most common plantation type in northern hardwood biome, show a completely different pathway of understory development. Our results reveal a dichotomy between the development of the tree cover and the understory strata in plantations. Modifications to the current plantation management practices are proposed to help recreate or maintain as much natural understory biological and physical attributes as possible.

Keywords: deciduous and conifer plantations, ecological integrity, natural restoration, plant functional types, understory flora

Nomenclature: Gleason and Cronquist (1991)

Introduction

Around 60 000 km² of primary forest are lost or modified annually by human interventions around the globe (FAO, 2006). In many regions, this marked loss of natural forest has been offset by the rapid increase in forest lands that have been allocated to plantations (FAO, 2006). While plantations provide some tree cover and forest wood products, little is known regarding their potential to fulfill other ecological services typical of natural forest ecosystems such as the maintenance of biodiversity. The question has arisen therefore whether plantations can develop ecological attributes similar to natural forest ecosystems over time.

Conceptually, a natural forest is a complex adaptive system with a minimum level of tree cover, which is composed of living organisms and their abiotic environment, and not subject to agricultural practices (Kimmens, 1987; Gardner-Outlaw & Engelman, 1999). As such, forests exhibit connectivity among their components, are dynamic, and are self-organised into hierarchies and cycles (Levin, 1998; Holling, 2001). Natural forests are generally dominated by native species. Their complexity is expressed at three levels of diversity: compositional, structural and functional (Noss, 1990).

In contrast to a natural forest, a plantation is generally composed of one or several artificially established tree species, whose individuals are even-aged and regularly spaced (FAO, 2006). Plantations thus generally possess low compositional, structural and functional diversity, with relatively limited interactions among their components (Hunter, 1990; Hansen et al., 1991). Plantations are generally made of genetically improved native tree species or of fast-growing exotic species. Plantations are also managed on a relatively short rotation, which contrasts sharply with the longevity that characterizes natural forest components.

From the perspective of wood production, mono-specific plantations have been very successful, but from the perspective of creating diversified and resilient ecosystems, many current plantations have failed to achieve this goal (Whitehead, 1982; Kirby, 1988; Swindel

& Grosenbaugh, 1988). Plantations are generally less resistant to natural stresses, such as pests and diseases, and not self-sustaining (Hunter, 1990; Noss, 1990; De Leo & Levin, 1997).

Beyond these statements, what makes a forest a fully self-sustaining and functional ecosystem has remained difficult to grasp due to the intrinsic spatial and temporal complexity of such ecosystems. Consequently, ecologists have sought to develop integrative tools that can take into account the complexity of natural forest ecosystems without having put all the pieces of the puzzle together. The ecological integrity concept, which can be defined broadly as the capability of an ecosystem to maintain a community comparable to that of a natural habitat for a given region (Karr & Dudley, 1981), provides a valuable framework for evaluating heavily modified systems such as plantations.

This study aimed at evaluating to what extent plantations can be compared functionally to naturally established stands. To characterize the complexity of a natural forest ecosystem, we used understory community development in terms of its functional and structural attributes as indicators of the ecological integrity of the whole ecosystem. The understory flora is a suitable key element with which to evaluate ecological integrity of an ecosystem because of its high compositional, structural and functional diversity, its numerous interactions with different trophic levels, and its important role in ecosystem functioning (George & Bazzaz, 2003; Gilliam & Roberts, 2003; Nilsson & Wardle, 2005).

A plant functional type (PFT) approach was used in order to obtain a more synthetic view of the understory community that was free of differences found at the species level (Lavorel et al., 1997). Based on universal vegetation traits rather than on site-specific vegetational composition, the PFT approach has been shown to greatly facilitate large scale studies or inter-regional comparisons (Tsuyuzaki & del Moral, 1995; Cramer, 1997; Leemans, 1997; Graae & Sunde, 2000; Verheyen et al., 2003; Aubin et al., 2007) and has been frequently used for the characterization of vegetation responses to human-induced change (e.g. Verheyen et al., 2003).

We compared assemblages of understory species in conifer and deciduous plantations established in the northern hardwood forests of eastern Canada. From a conservation perspective, many northern hardwood forests are considered to have high value. They contain a rich understory with many rare species, of which several are being threatened with local or regional extinction (e.g. *Panax quinquefolius* and *Allium tricoccum*; Bouchard et al., 1983; Nantel, Gagnon & Nault, 1996) and, due to their proximity to major urban or agricultural areas, are increasingly faced with numerous human pressures.

Until recently, plantations in temperate deciduous regions of Europe and North America were almost exclusively composed of mono-specific conifer stands. Deciduous plantations are slowly gaining in popularity but they are still marginal (Cogliastro, Benjamin & Bouchard, 2006), representing less than 10 % of the planted trees in the deciduous zone of Quebec (MRNFP, 2006). Except for studies on vegetation competition, very few studies have been conducted on understory development in plantations. Most studies on understory flora in plantations have been conducted in boreal forests and only report about conifer plantations (Swindel & Grosenbaugh, 1988; Ramovs & Roberts, 2005; Newmaster et al., 2006; Gachet et al., 2007). These studies observed a generally low abundance and diversity of native forest herbs in plantations. In Europe, Herault, Honnay and Thoen (2005) compared understories of Norway spruce plantations with those of natural deciduous forests and found that conifer plantations were functionally totally different from natural deciduous stands. To our knowledge, studies from the temperate deciduous region of North America have neither characterized the understory development of coniferous plantations nor compared them with those of deciduous plantations.

The present study is also the first at our knowledge to use both a natural mature forest as a target system and a natural old field-deciduous forest succession as a temporal point of comparison. The use of two benchmarks provides a more accurate evaluation of understory development as well as helping to identify the global impact of tree planting and its associated activities on natural flora development.

Using ecological traits of the understory flora, together with structural and environmental conditions as indicators, we aim to assess if plantations can eventually develop understory attributes similar to natural forest ecosystem. To do so, we first characterized understory traits responses to stand development stage in order to determine traits associated to early vs. late successional stages. Second, we assess differential understory development between conifer and deciduous plantations to determine which plantation types is most likely to develop attributes similar to natural deciduous forests. Third, we evaluate if planting abandoned agricultural sites accelerate the development of a functional understory. From these results, we suggest modifications to the current management practices to promote the development of a functional understory in plantations.

Methods

Fifty-six plots were established within two areas of deciduous forest in the Great Lakes-St. Lawrence forest region (Rowe, 1972) of southern Quebec, Canada. The two areas were the Upper St. Lawrence ($45^{\circ}01'$ – $45^{\circ}08'N$; $73^{\circ}58'$ – $74^{\circ}21'W$) and Drummondville ($45^{\circ}52'$ – $46^{\circ}01'N$; $72^{\circ}09'$ – $72^{\circ}35'W$). Mean annual temperature across both areas is $5^{\circ}C$ and the growing season typically lasts 190 to 200 days (Robitaille & Saucier, 1998). Annual precipitation is slightly higher in the Drummondville area (1000-1100 mm) compared to the Upper St. Lawrence (900-1000 mm). Percent forest cover (including plantations) ranged from 28% for Upper St. Lawrence to 40 % for Drummondville (Robitaille & Saucier, 1998). Natural, mature mesic forests in both regions are normally dominated by *Acer saccharum* in association with *Fagus grandifolia*, *Tilia americana* and *Ostrya virginiana*, and also with *Carya cordiformis* in the Upper St. Lawrence. *Fraxinus americana*, *A. rubrum*, *Populus tremuloides* and *Betula populifolia* are found on disturbed sites (Meilleur, Bouchard & Bergeron, 1994; Brisson & Bouchard, 2003). As in many other agricultural regions of eastern North America, the traditional rural landscape has changed over the last century in favour of intensified agriculture, which has resulted in abandonment of many marginal agricultural fields (Bouchard & Domon, 1997; Domon & Bouchard,

Accepted). A proportion of these abandoned lands were converted in plantations, while others were left to regenerate naturally (Benjamin, Cogliastro & Bouchard, 2006).

Soil deposits in both regions originated from the post-glacial Champlain Sea. In the Drummondville area, the deposits are mainly sand and reworked till (Robitaille & Saucier, 1998). This region principally lies on slate, limestone and sandstone bedrock of the Bourret, Bulstrode and Melbourne formations, and of the Shefford group (Tremblay & Bourque, 1991). The Upper St. Lawrence region lies on a bedrock of sandstone, dolomite and shale of the Postdam and Beekmantown groups (Globensky, 1987). Superficial deposits in this region are of two major types: a morainal deposits in islets and ridges with stony soils on which forests and abandoned old fields are mainly found (including the sampled stands), and nutrient-rich marine clay deposits in the lowlands where agricultural lands are concentrated (Robitaille & Saucier, 1998; Domon & Bouchard, Accepted).

Description of study plots

Fourteen deciduous (DP) and 18 conifer (CP) plantations were surveyed. They were compared with 18 stands of a natural old field-deciduous forest succession, hereafter referred to as unplanted stands (UN). These stands were classified according to their stand stages (open, O; closed, C; mature canopy, M). They were additionally compared to 6 natural maple-dominated forests plots (NAT). Conifer plantations were composed of red pine (*Pinus resinosa*), while deciduous plantations were composed of mixed hardwoods (*Quercus rubra*, *Q. macrocarpa*, *Fraxinus americana*, *Betula alleghaniensis*, *Acer saccharum*, *Prunus serotina*, *Juglans cinerea* and *J. nigra*). Natural regeneration in the unplanted stands consisted principally of *Ulmus americana*, *Prunus spp.*, *Fraxinus spp.*, and *A. saccharum*.

Plantations were located in or nearby the “Forêt Drummond” in Drummondville region, while unplanted and natural maple forests were located in the Upper St. Lawrence region. Because it is based on universal traits rather than on site-specific vegetation composition, the plant functional group approach allows this type of inter-regional

comparison (Tsuyuzaki & del Moral, 1995; Graae & Sunde, 2000; Verheyen et al., 2003; Aubin et al., 2007).

We sampled six plots per stand type, except for mature deciduous plantations, where it was not possible to find more than two plots owing to the rarity of old deciduous plantations. All stands were selected on mesic, flat lands of old pasture origin. They all had visible signs of their past agricultural use, such as old fences or large trees with broad, open-grown crowns. For some stands, such as the older plantations, it was not possible to determine if they had also been previously used for crop production.

Site preparation for both deciduous and coniferous plantations included ploughing, harrowing, and drainage when necessary. Plastic mulches were installed for open and closed canopy deciduous plantations. Deciduous plantations received the most frequent and intensive silvicultural treatments, with pruning every 2-3 years in young stands, and thinning done every 10 years. In coniferous plantations, pre-commercial thinning and pruning had been done every 10 years, where 20% to 40% of the tree basal area was removed. Mechanical, manual and/or chemical release treatments have been periodically done on plantations when competitive vegetation was considered as impeding tree development.

Information on land use history for unplanted stands and natural forests came from chapter 3 and previous studies (Benjamin, Domon & Bouchard, 2005) while information on plantation stands was provided by officials from the provincial forest ministry and from local forest agencies. This information was later validated through air photograph interpretation (1964-1966, 1975-1983). The principal characteristics of the stands have been summarised in Table 4.1.

Tableau 4.1. Characteristics of sampled stands. The result of a two-way ANOVA on mean plot richness with stand types and stages are given at the bottom of the table (natural maple forests are excluded from this analysis).

Stand type	Code	N	Stand age ^a plots	Mean maximum tree height (m)	Mean basal area (m ² /ha)	Mean tree density ^b (stems/ha)	Richness*
Natural forest	NAT	6	100+	29	36.2	672	48
<i>Unplanted</i>							
Mature canopy	UN-M	6	32 – 60	14	14.5	743	68
Closed canopy	UN-C	6	23 – 39	8	2.5	181	73
Open canopy	UN-O	6	10 – 25	3	0.3	20	64
<i>Plantation - deciduous</i>							
Mature canopy	DP-M	2	50	19	20.4	508	39
Closed canopy	DP-C	6	14 – 17	12	11.9	1134	47
Open canopy	DP-O	6	10 – 15	8	1.6	243	57
<i>Plantation - conifer</i>							
Mature canopy	CP-M	6	53 – 65	24	39.8	625	51
Closed canopy	CP-C	6	15 – 24	17	30.8	1784	36
Open canopy	CP-O	6	7 – 10	5	0.1	9	45

^a Ages were provided by officials from the provincial forest ministry and local forest agencies for planted stands and by Benjamin, Domon and Bouchard (2005) and chapter 3 for unplanted stands. ^b DBH > 5 cm. *Type: < 0.001, Stage: 0.717, Type x Stage: 0.086

Field sampling

A 25-m radius plot was established at the approximate center of each stand. To avoid edge effects, all plots were located at least 25 m away from any openings. All plots were 40 to 800 m from a forested area (mainly early successional stands) which may serve as seed sources. These study plots were sampled three times from May to September 2003 for the upper St. Lawrence region, and from May to September 2004 for the Drummondville area, to obtain floristic data for all species present during the growing season.

We determined floristic composition using linear vegetation surveys. In each study plot, 52 circular points (15-cm radius) were systematically sampled along four 25-m transects. Species that were detected within a sampling point were given an occurrence value of 1, for a possible total score of 52 when a species was present at all points. Species that were present within the plot, but not at any of the sampling points, were assigned an occurrence value of 0.5. The frequency of occurrence (%) of a given species was the proportion of points within a plot where that species occurred. Grasses, sedges and hawthorns (*Crataegus spp.*) were identified to genus only. Planted tree occurrences were recorded separately. To describe vertical structure, we sampled the vegetation as described above every 50 cm in height, from the soil surface to the top of the understory vegetation (around 5 m.; see Aubin, Beaudet & Messier, 2000 for further details).

Forest cover data were collected in each plot for tree composition, maximum tree height (m), basal area (m^2/ha), and the density of individuals (stem/ha) with diameters at breast height (DBH) > 5 cm. To characterize understory environmental conditions, light availability and soil cover substrate were also quantified for the 52 sampling points of each plot. The percentage of above-canopy photosynthetic photon flux density (% PPFD) was measured both at the ground level and at two meters above the ground, using a line-quantum sensor (LI-COR, Lincoln, Nebraska, USA). All light measurements were taken under completely overcast sky conditions following the methods of Messier and Puttonen

(1995) and Gendron, Messier and Comeau (1998). Soil cover substrate type was assigned to one of the following categories: grasses, herbs, deciduous shrub or tree leaf litter, conifer needles, mineral soil, rock, downed woody debris and plastic mulch. The frequency of occurrence (%) of a given substrate type was the proportion of points in a plot where that substrate type occurred.

Species ecological traits

Information on species' ecological traits was obtained from TOPIQ data base (Traits Of Plants In Quebec see Aubin et al., 2007). Ten categorical traits and two quantitative traits were used in the present study (Table 4.2).

Tableau 4.2. Plant biological traits as compiled from the literature.

Trait	Code	Description
Raunkier life form	RA	mg: mega or meso-phanerophyte (≥ 8 m in height); mc: micro or nano-phanerophyte (25 cm to 8 m); ch: chamaephyte (herb or shrub, bud between 1 mm to 25 cm above ground); h: hemicryptophyte (herb with bud at the ground surface)*; g: geophyte (herb with underground bud)*; t: therophyte (annual)*
Principal means of reproduction (21)	REP	se: seeds only; ms: vegetative propagation possible but mostly by seeds; ve: mostly by vegetative propagation
Foliage persistence	PFO	0: no; 1: yes

Trait (continued)	Code	Description
Foliage structure	SFO	For phanerophytes: m: one stem; mu: multi-stemmed; vi: vine For other life forms*: No stem: r: rosette or semi-rosette; g: graminoid; e: erect leaves With stem: el: erect leafy stem; de: decumbent stem; um: umbel-shaped stem; vi: vine Non-leafy stem: nl: saprophyte
Physical defences (e.g., thorns)	DEF	0: no; 1: yes
Flowering phenology	FPH	sp: spring; su: summer; sf: summer-fall
Color of flower	CFL	w: white; g: unattractive (green or brown); b: bright (red, yellow or blue); na: non applicable
Seed dispersal vector ⁱ (28)	DI	w: wind (anemochorous); ez: mammal ingestion (endozoochorous); zz: animal, carried externally (epizoochorous)*; an: insect, mostly ant (myrmecochorous)*; bi: bird ingestion (avichorous); hd: human dispersal (anthropochorous)*; ex: ballasts or explosive discharge (ballistichorous)*; none: barochorous
Seed size	SE	quantitative variable:< 0.1 to 40 mm
Height	HT	quantitative variable: 6 to 3500 cm
Light requirement (9)	LI	s: shade tolerant; m: mid tolerant; i: intolerant
Status in Quebec	ST	0: native; 1: exotic

In parentheses : number of missing value. ⁱ For the seed dispersal vector, a species can have more than one class * Omitted in the analysis of the woody species subset emergent groups.

Data analysis

Identifying emergent groups

Emergent groups (i.e., groups of species having similar biological traits) were identified separately for woody and herbaceous species following the hierarchical approach suggested by McIntyre et al. (1999) and Deckers et al. (2004). Not all classes of seed dispersal vectors, life cycle, foliage structure and flowering phenology traits were present in the woody species and therefore, they were omitted from the classification of the woody species subset (indicated with an asterisk in Table 4.3). No trait was omitted for the herbaceous species subset, except for Raunkier's phanerophyte forms.

To identify emergent groups, a Gower similarity coefficient was calculated separately for the woody and herbaceous subsets of the biological traits matrix. This coefficient can be programmed to handle both missing values and mixed data (Legendre & Legendre, 1998). A Ward hierarchical classification was then computed for these similarity matrices. The cut off limit was determined subjectively after a visual screening of the dendrogram and according to our botanical knowledge.

Assessing differences among stand types

We examined the relative occurrence of these groups between stand types and among the different stand stages using a matrix of the species group occurrences calculated as the product of the transposed species data matrix (353 species x 56 plots, with percent occurrence data of each species) by the binary matrix of emergent groups (353 species x 16 emergent groups). This new matrix (56 plots x 16 emergent groups) was then standardised by dividing the occurrence of each group by the total occurrence for all groups in each plot. Differences in relative occurrences of the species groups among stand types (deciduous plantation, conifer plantation, and unplanted), and among different stand stages (open, closed and mature canopy) were analysed using two-way ANOVA. The natural maple forests (6 stands) were not included in this analysis.

In addition to these analyses, species richness and functional diversity (richness of each emergent group) were calculated and analysed using the same procedure. To globally compare the understory vegetation assemblage of each combination of stand type and stand stage (hereafter referred to as stand type x stage) with the natural maple forests as our natural habitat benchmarks, we performed principal components analysis (PCA) on the matrix of the relative occurrences of emergent groups.

Vertical understory stratification and understory abiotic conditions

We used the matrix of species occurrence, as determined for individual strata, to examine vertical occupancy of the understory vegetation. Development of vegetation structure was characterized for each stand type and stage. Total species occurrence by stratum was analysed using two-way ANOVA following the same procedure as for species group occurrences. Differences in pattern of vertical stratification among stand types and stages were analysed using a Friedman's test, where the randomised blocks were the different stratum.

Possible differences in understory environmental conditions (light and substrate) among stand types and stages were also analysed using the same procedure. To globally compare the understory abiotic conditions of each combination of stand types and stand stages with natural maple forests, we also performed PCA on environmental variables matrix.

When necessary, we performed a natural-logarithmic transformation on the dependent variables to ensure normality and homoscedasticity. A significance level of 0.05 was used. The XLStat programme (Addinsoft, 2006) was used for all analyses.

Results

Species richness

A total of 84 woody species and 269 herbaceous species were recorded. Mean plot richness significantly varied across stand types, but not among stand stages (Table 4.1). Unplanted stands had the highest mean plot richness (68 species), followed by deciduous plantations (50 species) and then coniferous plantations (44 species). Based on number of species, plantations possess a similar richness than natural maple forest (48 species). However, major differences were found in species traits. For instance, 80 exotic species were found in the sampled stands. While exotics represented less than 8 % of the average plot richness in natural maple stands, they represented 12 % in unplanted stands, 13% in deciduous plantations and 14% in mature coniferous plantations, and up to 38% in open canopy unplanted stands.

Emergent group identification

Cluster analysis allowed 6 emergent groups to be delineated for the woody species (Cut off limit at $S = 0.63$) and nine for the herbaceous species ($S = 0.77$). As grasses and sedges were not identified to species, they were assigned an a priori group. For woody species (Table 4.3), the first three groups were composed of micro-nanophanerophytes with multi-stemmed foliage structure reproducing mainly by vegetative propagation. These groups were: (W1) summer-flowering vines or shrubs dispersed by birds (avichorous); (W2) spring-flowering shrubs dispersed by birds or by mammal ingestion (endozoochorous); and (W3) low stature shrubs that were also spring flowering, but with small seeds dispersed by wind (anemochorous). The last three woody groups were composed of trees (megaphanerophytes) that reproduced predominantly by seeds: (W4) propagules dispersed by winds; (W5) propagules dispersed by bird or mammal ingestion; and (W6) coniferous trees.

Tableau 4.3. Classification by species groups of woody species having similar biological traits computed from a cluster analysis done on the biological traits data matrix ($n = 85$). Cut off limit at $S = 0.63$.

Traits	W1. Summer		Shrubs dispersed by bird	Shrubs dispersed by wind	W4. Trees		W5. Trees dispersed by mammal or bird	W6. Conifer trees
	flowering vines or shrubs	Shrubs dispersed			dispersed	by wind		
		by bird						
RAU	mc (mg)	mc	mc	mc	mg	mg	mg	mg
SFO	vi (mu)	mu	mu	(ms)	ms	ms	me (ms)	
REP	3 2	3	3	2 (3)	2	2	2	
LI	2	2	1	-	(2)	(2)	-	-
CFL	b g	b	b	g (b)	g	g	na	
DI	bi	bi ez	w	w	ez bi	ez bi	w ez	
ST	0	0	0	0	0	0	0	0
SE	4.35	4.27	1.79	6.70	20.53	20.53	4.25	
PFO	0	0	0	0	0	0	0	(1)
DEF	0	(1)	0	0	0	0	0	0
FPH	su	sp	sp	sp	sp	sp	sp	sp
HT	840	425	271	2317	2300	2300	2480	
Sp	<i>Parthenocissus</i> <i>quinquefolia</i>	<i>Ilex</i> <i>verticillata</i>	<i>Spiraea</i> <i>alba</i>	<i>Acer</i> <i>saccharum</i>	<i>Carya</i> <i>cordiformis</i>	<i>Pinus</i> <i>resinosa</i>		
	<i>Sambucus</i>	<i>Cornus</i>	<i>Myrica</i>	<i>Ulmus</i>	<i>Juglans</i>	<i>Abies</i>		
	<i>canadensis</i>	<i>sericea</i>	<i>gale</i>	<i>americana</i>	<i>cinerea</i>	<i>balsamea</i>		
n	10	30	8	18	8	10		

See Table 4.2 for code definitions. Codes in parentheses indicate that this class is present but in lower proportion. Sp: characteristic species.

For the herbaceous species (Table 4.4), the following traits characterized the groups. Exotic species were separated by the analysis into: (H1) exotic annuals, which were dispersed predominantly by mammal ingestion; (H2) exotic perennials, which were mainly wind-dispersed; (H3) summer-flowering species, which were mainly wind-dispersed and shade intolerant; (H4) summer-flowering species dispersed by mammal ingestion; (H5) late-flowering, wind-dispersed hemicryptophytes; and (H6) ferns and allies, which have distinct biological traits, along with other shade tolerant species with very small seeds (this group included a relatively large proportion of species with persistent foliage). The spring-flowering species were separated into: (H7) those dispersed by mammal ingestion or birds, which possessed the largest seeds and were shade tolerant; (H8) those that were dispersed by wind, carried externally by mammals (epizoochorous), or had no specialised vector (barochorous); and (H9) those propagules that were dispersed by ants (myrmecochorous), which were the shortest in height.

Tableau 4.4. Classification by species groups of herbaceous species having similar biological traits computed from a cluster analysis done on the biological traits data matrix ($n = 270$). Cut off limit at $S = 0.77$.

Traits	H1.	H2.	H3. Summer	H4.	H5. Late	H6. Ferns and allies	H7. Spring	H8. Spring	H9. Short	Grass and sedges
	Introduced	flowering	Summer	flowering	herbs	flowering	herbs	flowering	spring	flowering
annuals	perennials	herbs	flowering	herbs	dispersed by	herbs	dispersed by	herbs	herbs	herbs
			wind	dispersed	by wind	mammal or	dispersed by	wind or	dispersed by	
				by mammal		bird	gravity	ant		
RAU	t(h)	h	h(t)	h	h	h(g)	g, h	h(g)	h, g	h
SFO	-	(r)	el(r)	de, el	el, r	e	el, de	-	r, e	g
REP	1	(3)	-	3	-	3	3	3	3	3
LI	1	1	1 (2)	-	(1)	3	3	-	-	1 (2)
CFL	b (w)	b	b (w)	w	b	na	w, b	w, b	b, w	g
DI	(ez)	(w)	(w)	ez	w	w, ex	ez(bi)	(w zz), g	an(ex)	w (ez, an)
ST	1	1	0	0	0	0	0	0	0	(1)
SE	2.03	2.56	2.68	2.15	1.34	0.27	3.30	2.43	2.46	1.5
PFO	0	0	0	0	0	(1)	0	(1)	0	0
DEF	0	-	0	(1)	0	0	0	0	0	0
FPH	su	su	su	su	su, sf	su	sp	sp	sp	-
HT	96	94	131	144	143	116	114	82	29	-
Sp	<i>Chenopodium album</i>	<i>Cirsium arvense</i>	<i>Anemone virginiana</i>	<i>Rubus idaeus</i>	<i>Aster novae-</i>	<i>Dryopteris intermedia</i>	<i>Arisaema triphyllum</i>	<i>Cardamine diphylla</i>	<i>Sanguinaria canadensis</i>	<i>Poa pratensis</i>
	<i>Daucus carota</i>	<i>Sonchus asper</i>	<i>Chelone glabra</i>	<i>Gallium angliae</i>	<i>Osmunda claytoniana</i>	<i>Smilacina racemosa</i>	<i>Hydrophyllum virginianum</i>	<i>Asarum caudatum</i>	<i>Dactylis glomerata</i>	

<i>Galeopsis</i>	<i>Hieracium</i>	<i>Lactuca</i>	<i>Rubus</i>	<i>canadensis</i>	<i>Thelypteris</i>	<i>Aralia</i>	<i>Medeola</i>	<i>Viola</i>	<i>Carex</i>
<i>tetrahit</i>	<i>caespitosum</i>	<i>canadensis</i>	<i>occidentalis</i>	<i>Solidago</i>	<i>noveboracensis</i>	<i>racemosa</i>	<i>virginiana</i>	<i>pubescens</i>	<i>lurida</i>
n	18	43	65	19	18	26	20	41	19

See Table 4.2 for code definitions. Codes in parentheses indicate that this class is present but in lower proportion. Sp: characteristic species.

Responses of emergent groups to stand types

The assemblage of emergent groups differed according to their stand types and stages (Table 4.5). Twelve of the 16 emergent groups varied significantly among stand types or stages (Two-way ANOVA $p \leq 0.05$). Deciduous plantations had a high proportion of summer- or late-summer flowering herbs that were wind-dispersed (H3 and H5), as well as grasses and sedges. Conifer plantations possessed a high proportion of ferns (H6) and wind-dispersed shrubs (W3), together with the lowest occurrence of spring-flowering herbs dispersed by ants (H9). Unplanted stands possessed a higher proportion of summer-flowering vines and shrubs (W1), and bird-dispersed shrubs (W2) than did planted stands. Among stand stages (from open to mature canopy), we observed a general decrease in summer- or late summer- flowering herbs that were dispersed by wind (H3, H5), together with introduced perennials (H2) and grasses and sedges, while ferns (H6) and of bird-dispersed shrubs (W2) generally increased. Spring flowering herbs that were dispersed by ants (H9), summer-flowering vines and shrubs (W1) and wind-dispersed shrubs and trees (W3, W4) also progressively increased along stand stages in both unplanted stands and deciduous plantation stands.

Tableau 4.5. Mean relative occurrence (%) of emergent groups among stand types. The result of a two-way ANOVA with stand types and stages are given at the bottom of the table (natural maple forests are excluded from this analysis). Nat: natural maple forest; UN: unplanted; DP: deciduous plantation; CP: coniferous plantation; M: mature; C: closed; O: open canopy.

Stand types	Stages	H1	H2	H3	H4	H5	H6	H7	H8	H9	W1	W2	W3	W4	W5	W6	Grass
NAT		0.0	0.6	1.4	4.2	1.3	1.4	4.7	3.1	17.1	1.6	9.3	0.0	47.0	3.2	3.0	2.3
UN	M	0.3	3.0	4.5	5.0	4.2	3.6	7.2	4.1	5.0	6.3	20.3	0.9	16.4	1.7	8.8	9.2
	C	2.2	9.5	6.0	4.2	10.6	0.2	8.3	7.3	4.6	4.7	21.2	0.1	6.5	0.5	1.0	13.3
	O	6.5	25.5	9.9	3.3	11.9	0.2	7.9	7.7	1.1	2.1	9.8	0.0	1.3	0.5	0.4	11.9
DP	M	0.7	1.8	2.2	0.3	2.0	15.5	3.8	2.6	7.6	2.3	3.6	0.3	42.1	1.0	2.8	11.6
	C	1.6	8.0	21.0	18.8	8.2	6.5	0.2	6.5	0.4	1.0	1.3	0.1	4.1	1.6	0.0	20.6
	O	4.0	17.4	13.4	6.4	16.4	4.9	4.0	6.5	0.1	0.8	0.3	2.4	1.1	0.3	0.18	21.9
CP	M	2.6	3.6	1.9	11.6	1.9	28.0	13.1	13.6	0.0	1.0	2.7	1.4	11.6	0.7	1.2	5.6
	C	0.8	8.2	5.3	3.0	3.3	11.8	11.44	10.2	0.3	2.9	4.4	3.7	27.9	0.6	0.9	5.2
	O	0.4	14.6	10.9	6.6	10.3	4.9	9.4	4.9	0.2	1.3	2.8	8.7	3.8	0.0	1.3	19.9
ANOVA	d.f.	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F
Model	8	0.033	<0.001	<0.001	0.005	<0.001	<0.001	0.061	0.080	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.138	0.001
Type (T)	2	0.272	0.230	0.02	0.252	0.035	<0.001	0.007	0.078	<0.001	<0.001	<0.001	<0.001	<0.001	0.101	0.351	0.094
Stage (S)	2	0.075	<0.001	0.002	0.314	<0.001	0.002	0.918	0.635	<0.001	0.029	0.014	0.022	<0.001	0.080	0.013	0.011
T x S	4	0.043	0.334	0.025	0.006	0.287	0.108	0.671	0.058	0.008	0.069	0.065	0.040	<0.001	0.410	0.020	0.099
R2 ^a	.	0.19	0.42	0.44	0.27	0.46	0.44	0.15	0.13	0.43	0.41	0.69	0.41	0.48	0.1	0.44	0.35

^a Whole model. Detailed descriptions of the groups are found in Table 4.3 and 4.4. T x S: Type x Stage.

The two PCA axes of the species groups relative occurrence illustrates emergent groups repartition among the different study plots ($n = 50$) and in comparison with natural maple forests ($n = 6$, Figure 4.1). The first two axes that were extracted from principal components analysis of the species group relative occurrences explained 38% of the total variance (Figure 4.1). The first principal component (F1) represented a gradient of stand development, with open canopy stages (O) on the left and mature canopy (M) on the right. This successional gradient was reflected in the location of the emergent groups in the ordination biplot; pioneer species groups that were associated with open habitats (H1 to H5, and grass) were on the left hand side of axis F1, while spring-flowering ant-dispersed herbs (H9) and woody species (W) associated with natural and mature habitats were on the right. Conifer plantations (CP) tended to segregate from the other stand types along the second axis (F2), which otherwise did not show any clear pattern for the traits under study. Ferns and spring-flowering herbs that were dispersed by mammals or birds (H7), or by wind and gravity (H8), were located at the top of axis F2, while woody species and late-flowering herbs were at the bottom. The ordination of the PCA components showed that natural maple forest stands ($n = 6$) formed a tight, homogeneous grouping that was separate from the other study plots ($n = 50$), which in turn formed less distinct clusters. Natural maple forests had a high occurrence of woody groups (W) and of ant-dispersed spring-flowering herbs (H9), as well as a low occurrence of exotic groups (H1, H2), wind-dispersed summer- and late summer-flowering herbs (H3, H5), and grasses and sedges (GRASS). Unplanted mature canopy stands (UN-M) and deciduous plantation mature canopy stands (DP-M) had emergent group assemblages that were most similar to natural maple forests.

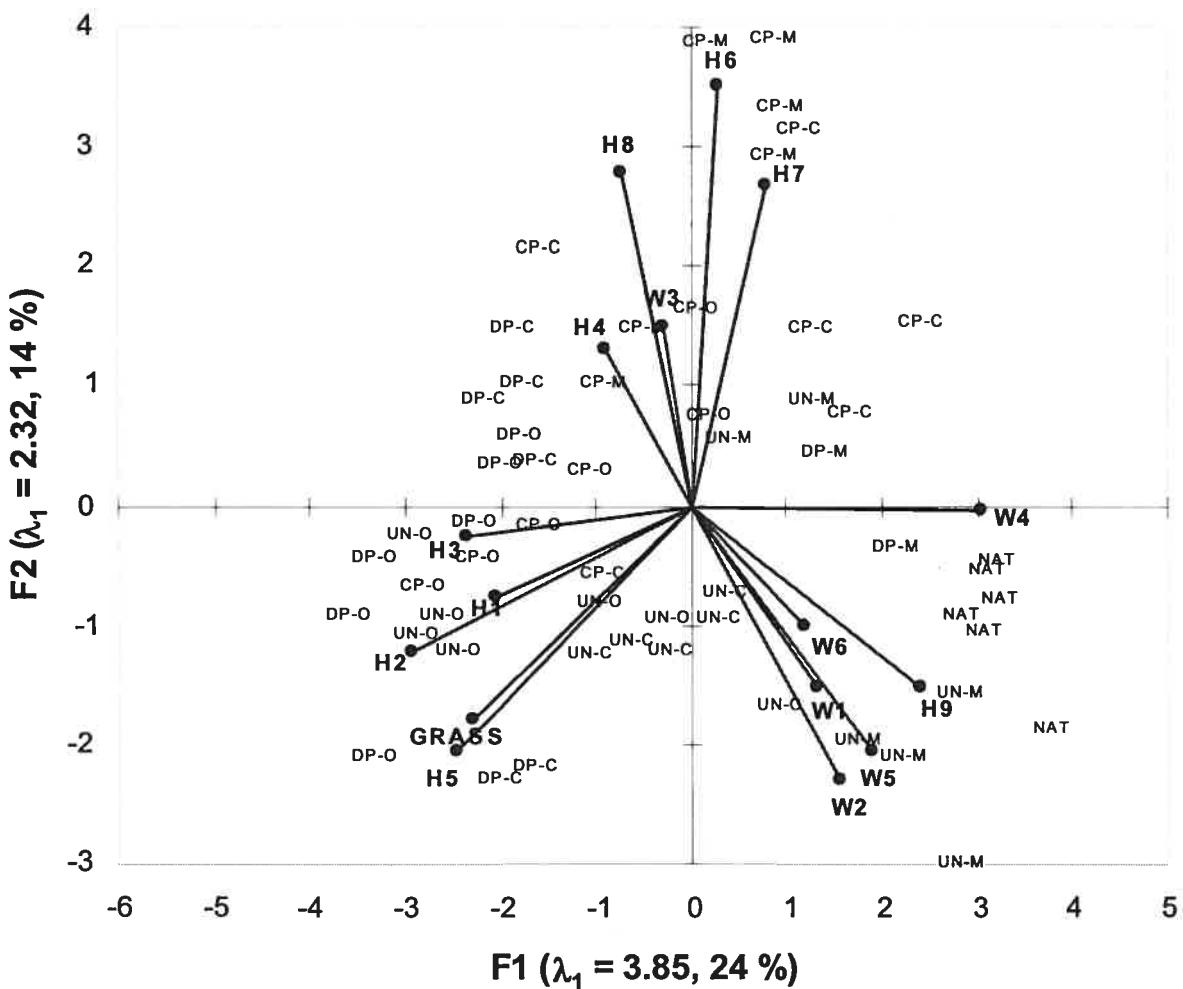


Figure 4.1. The first two axes of the PCA calculated on the emergent group relative occurrence matrix. Nat: natural maple forest; UN-M: unplanted mature canopy; UN-C: unplanted closed canopy; UN-O: unplanted open canopy; DP-M: mature deciduous plantation; DP-C: closed canopy deciduous plantation; DP-O: open canopy deciduous plantation; CP-M: mature conifer plantation; CP-C: closed canopy conifer plantation, CP-O: open canopy conifer plantation. See Table 4.3 and 4.4 for emergent group description.

Functional diversity (richness in each emergent group) also largely differed among stand types and stages (Table 4.6). Conifer plantations possessed a low diversity of introduced herbs (H1, H2), summer- or late summer-flowering herbs that were dispersed by wind (H3, H5), trees that were dispersed by mammals or birds (W5), but had a high diversity of shrubs that were dispersed by wind (W3). Deciduous plantations had a low diversity of spring flowering herbs that were dispersed by mammals or birds (H7). Unplanted stands were characterized by a low diversity of ferns (H6), but by a high diversity of spring flowering herbs that were dispersed by wind and gravity (H8) or by ants (H9), summer flowering vines or shrubs (W1) and bird-dispersed shrubs (W2). At all stages of stand development, we observed a general decrease in diversity, proceeding from open canopy to mature stands, for exotic species (H1, H2), late-flowering herbs (H5), and wind-dispersed shrubs (W3). Ferns (H6), spring flowering herbs that were dispersed by mammals or birds (H7) or by ants (H9), as well as trees (W4, W5, W6), increased through stand stages.

Tableau 4.6. Mean functional diversity (richness of each emergent group) among stand types. The result of a two-way ANOVA with stand types and stages are given at the bottom of the table (natural maple forests are excluded from this analysis). Nat: natural maple forest; UN: unplanted; DP: deciduous plantation; CP: coniferous plantation; M: mature; C: closed; O: open canopy.

Stand types	Stages	H1	H2	H3	H4	H5	H6	H7	H8	W1	W2	W3	W4	W5	W6	
NAT		0.0	1.3	3.2	2.8	1.8	2.5	4.7	5.3	5.8	3.0	6.2	0.0	4.3	2.0	
UN	M	1.0	3.2	7.8	4.5	4.0	5.5	6.3	5.2	4.2	5.0	7.3	1.0	6.2	1.8	
	C	3.2	11.2	9.8	3.7	7.0	1.3	2.8	6.5	3.3	4.8	9.0	0.2	4.3	1.8	
	O	4.0	15.2	8.0	2.7	7.3	0.3	1.5	5.3	1.8	3.7	7.5	0.3	1.7	1.2	
DP	M	1.0	2.0	3.0	0.5	2.5	6.5	2.5	2.0	1.5	3.5	0.5	5.0	1.5	3.0	
	C	1.7	5.8	11.8	4.7	4.2	3.0	0.3	5.5	1.0	1.3	2.5	0.3	2.5	0.0	
	O	2.2	11.5	13.8	3.2	6.5	3.2	1.2	4.5	0.2	1.2	1.2	2.0	2.7	0.7	
	CP	M	0.8	3.7	5.0	4.8	3.0	6.5	4.2	4.5	0.0	1.8	5.8	1.3	3.5	2.2
	C	0.3	3.2	3.8	2.2	2.2	5.0	3.0	2.8	0.3	1.5	3.3	2.0	3.3	0.5	
	O	0.8	6.3	8.8	3.0	4.7	3.2	1.8	2.7	0.3	1.0	2.3	3.7	3.2	0.7	
ANOVA	d.f.	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	P>F	
Model	8	<0.001	<0.001	0.004	<0.001	<0.001	0.017	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.012	0.007	<0.001
Type	2	<0.001	<0.001	0.022	0.354	<0.001	0.001	<0.001	0.004	<0.001	<0.001	<0.001	<0.001	0.470	0.039	0.076
Stage	2	0.004	<0.001	0.004	0.535	0.001	<0.001	0.001	0.325	0.033	0.125	0.054	0.003	0.008	0.024	0.001
Type x Stage	4	0.008	0.002	0.018	0.001	0.152	0.350	0.025	0.114	0.149	0.837	0.150	0.014	0.080	0.198	0.047
R2 ^a	.	0.55	0.67	0.39	0.28	0.43	0.50	0.61	0.22	0.54	0.64	0.60	0.50	0.24	0.26	0.37

^a Whole model. Detailed descriptions of the groups are found in Table 4.3 and 4.4.

Understory abiotic conditions

Except for shrub leaf and herb litter, proportions of the different substrate types varied significantly among stand types and stages (Table 4.7). Substrates of coniferous plantations differed from other stand types. They were characterized by a low proportion of deciduous leaf litter and mineral soil, and a high proportion of needles. Unplanted stands had substrates with a high proportion of shrub leaf litter and rock. Among stand stages, we observed a decrease in grass litter and an increase in deciduous tree leaf litter, needle litter and downed woody debris. Only open canopy deciduous plantations had a proportion of its ground covered by mulch.

Understory light availability (% PPFD) at ground level varied significantly among stand stages, but not among stand types (Table 4.8). Light at 200 cm above the ground surface varied both among stand stages and types, with unplanted stands receiving more light than planted stands.

Tableau 4.7. Mean relative occurrence (%) of substrate types among stand types and stages. The result of a two-way ANOVA with stand types and stages are given at the bottom of the table (natural maple forests are excluded from this analysis). Nat: natural maple forest; UN: unplanted; DP: deciduous plantation; CP: coniferous plantation; M: mature; C: closed; O: open canopy.

Stand types	Stages	Grass litter	Tree leaves litter	Shrub leaves litter	Herbs litter	Needle	Mineral soil	Rock	Down woody debris	Mulch
NAT	0.0	80.1	0.6	0.2	1.9	5.3	3.1	8.7	0.0	0.0
	M	1.9	40.9	4.5	1.5	0.0	21.3	5.3	24.6	0.0
	C	35.4	3.2	8.6	1.9	1.4	35.8	3.4	10.3	0.0
	O	70.6	0.5	2.6	4.6	1.1	16.8	1.0	2.8	0.0
DP	M	1.5	68.5	0.0	0.0	0.5	17.0	0.5	12.0	0.0
	C	16.2	36.0	0.0	1.1	0.0	16.3	0.0	19.6	10.8
	O	63.3	18.4	0.0	2.7	0.0	3.7	0.0	3.7	8.2
	CP	M	1.9	10.4	0.0	2.8	77.5	0.0	0.0	7.4
CP	C	0.0	5.4	0.0	0.2	82.6	0.8	0.0	11.0	0.0
	O	82.3	0.0	1.4	2.9	5.3	5.8	0.0	2.3	0.0
	ANOVA	d.f.	P > F	P > F	P > F	P > F	P > F	P > F	P > F	P > F
	Model	8	<0.001	<0.001	0.066	0.609	<0.001	<0.001	<0.001	<0.001
Type	2	0.155	<0.001	0.008	0.601	<0.001	<0.001	<0.001	0.056	<0.001
Stage	2	<0.001	<0.001	0.619	0.148	<0.001	0.082	0.102	<0.001	0.032
Type x Stage	4	0.002	0.015	0.450	0.762	<0.001	0.103	0.087	0.007	0.032
R2 ^a	.	0.83	0.60	0.15	0.03	0.968	0.45	0.45	0.48	0.56

^a Whole model.

Tableau 4.8. Mean light availability (%) among stand types and stages. The result of a two-way ANOVA with stand types and stages are given at the bottom of the table (natural maple forests are excluded from this analysis). Nat: natural maple forest; UN: unplanted; DP: deciduous plantation; CP: coniferous plantation; M: mature; C: closed; O: open canopy.

Stand types	Stages	Light at 200 cm	Light at the soil level
		(% PPFD)	(% PPFD)
NAT		2.1	1.2
UN	M	5.6	2.2
	C	29.2	4.7
	O	93.2	31.7
DP	M	4.2	3.5
	C	5.4	3.2
	O	59.4	18.8
CP	M	11.9	6.2
	C	6.3	4.8
	O	81.5	15.9
ANOVA	d.f.	P > F	P > F
Model	8	<0.001	<0.001
Type	2	<0.001	0.307
Stage	2	<0.001	<0.001
Type x Stage	4	0.002	0.077
R ² a	.	0.92	0.52

a Whole model.

The two PCA axes of the abiotic conditions matrix illustrate light availability and substrate repartition among the different study plots ($n = 50$) and in comparison with natural maple forests ($n = 6$, Figure 4.2). The first two components extracted by PCA explained 50% of variation in the environmental data (Figure 4.2). Moreover, the stand groupings for the abiotic variables (Figure 4.2) mirrored the patterns depicted for the emergent groups in Figure 4.1. The principal component F1 represented a gradient of stand development, with open canopy stages (O) on the left and mature canopy (M) on the right. Natural maple forest (NAT) formed a homogeneous group to the right. The different stand types separated along the second principal component, with the conifer plantations (CP) being located at the top of the axis F2 and the unplanted stands (UN) mostly located near the bottom (Figure 4.2). The primary gradient (Axis 1, Figure 4.2) included light availability (L₂₀₀, L₀), and the decreasing occurrence of grass litter (G), while that of tree leaf litter (T) and downed woody debris (W) increased. The secondary gradient (Axis 2, Figure 4.2) highlighted the relative occurrence of needle substrate (N) versus mineral soil (M). Substrates in the natural maple forests (NAT) were dominated principally by tree leaf litter and downed woody debris, and by low light availability. Thus, deciduous plantations with a mature canopy (DP-M) and closed canopy (DP-C) possessed combinations of understory abiotic conditions that were most similar to natural maple forests.

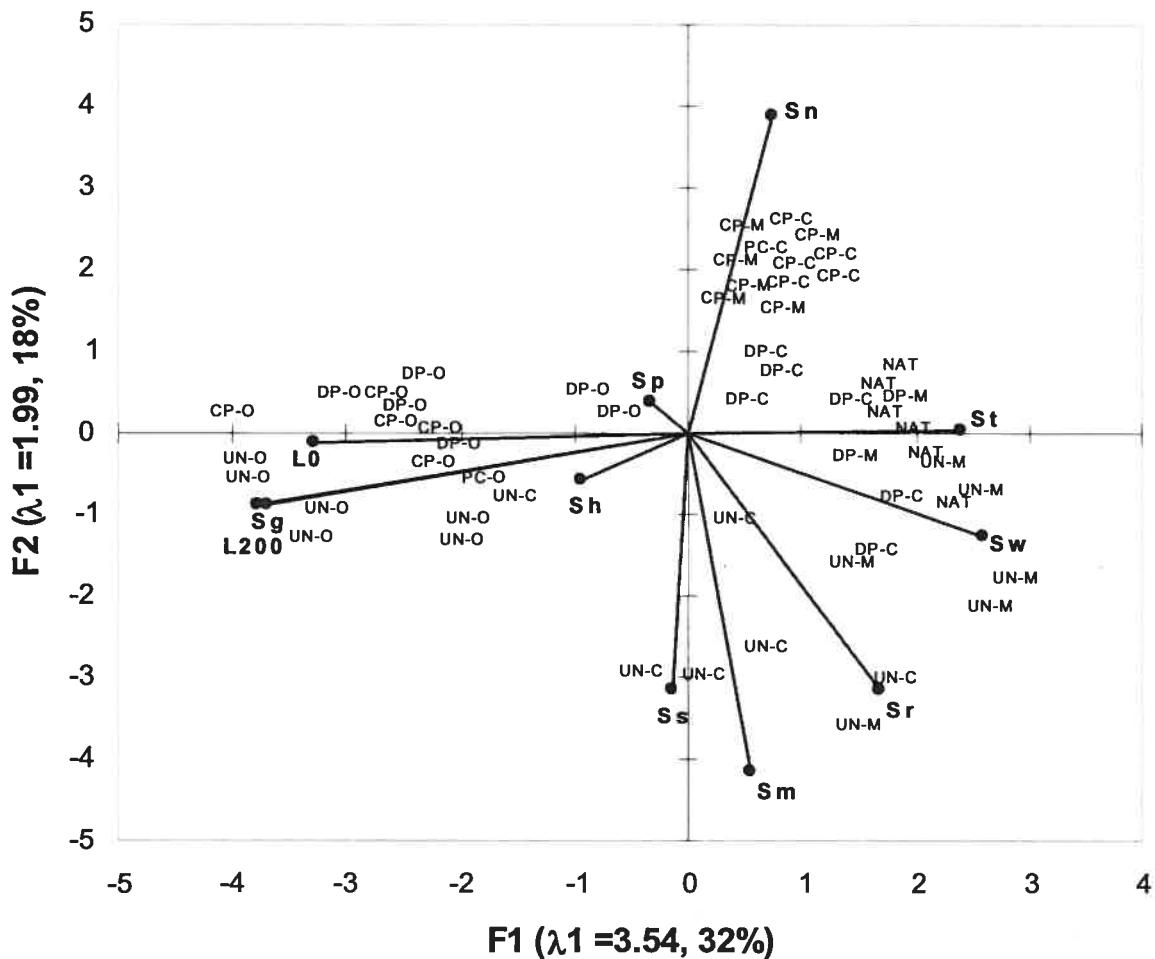


Figure 4.2. The first two axes of the PCA calculated on the environmental conditions variables. Stand types and stages: Nat: natural maple forest; UN-M: unplanted mature canopy; UN-C: unplanted closed canopy; UN-O: unplanted open canopy; DP-M: mature deciduous plantation; DP-C: closed canopy deciduous plantation; DP-O: open canopy deciduous plantation; CP-M: mature conifer plantation; CP-C: closed canopy conifer plantation, CP-O: open canopy conifer plantation. Environmental conditions: Sg: grasses; Sh: herbs; Ss: deciduous shrub leaf litter; St: deciduous tree leaf litter; Sn: needle litter; Sm: mineral soil; Sr: rock; Sw: downed woody debris; Sp: plastic mulch; L0: light (% PPFD) at forest floor; L200: light at 200 cm.

Understory vertical stratification

Understory vertical stratification differed markedly among stand types and stages (Table 4.9, Figure 4.3). Unplanted stands possessed a higher vegetation occurrence for all strata than planted stands. Deciduous plantations possessed the lowest vegetation occurrence for all strata, except for 250 cm and greater. Vegetation occurrence in strata under 150 cm decreased with stand stage, while strata over 150 cm were generally denser in closed canopy stages.

Vertical stratification of the vegetation was pronounced for all stand types (Figure 4.3). The recurring pattern of vertical stratification of the understory vegetation that was observed for natural maple forest was the presence of a well-developed low stratum (0-50 cm), strata between 50-200 cm that had little vegetation, and a high stratum (≥ 250 cm) that was moderately developed (Figure 4.3). Vertical patterning of the vegetation differed significantly among stand types and stages (Friedman's test, blocking on strata: $\chi^2_r = 34.63$, $P < 0.0001$, d.f. = 9), but most strongly between UN-C and a group consisting of DP-M, CP-C and DP-C. The treatments were ordered as: UN-C \geq CP-O = UN-O = UN-M = NAT = DP-O \geq DP-M = CP-C = DP-C. Consequently, closed canopy stands were least like natural maple forests (NAT). Unplanted mature canopy stands (UN-M) were most similar to natural maple forests in terms of the vertical patterning of their understories (Figure 4.3).

Tableau 4.9. Two-way ANOVA on the mean occurrence (%) for each vertical stratum among stand types and stages. See Figure 4.3 for a representation.

ANOVA	d.f.	0-50	50-100	100-150	150-200	200-250	250 +
Model	8	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Type	2	<0.001	0.033	<0.001	<0.001	<0.001	<0.001
Stage	2	<0.001	<0.001	0.001	0.277	0.012	0.004
Type x Stage	4	<0.001	0.006	<0.001	<0.001	<0.001	<0.001
R ² a	.	0.82	0.56	0.59	0.73	0.78	0.76

^a Whole model.

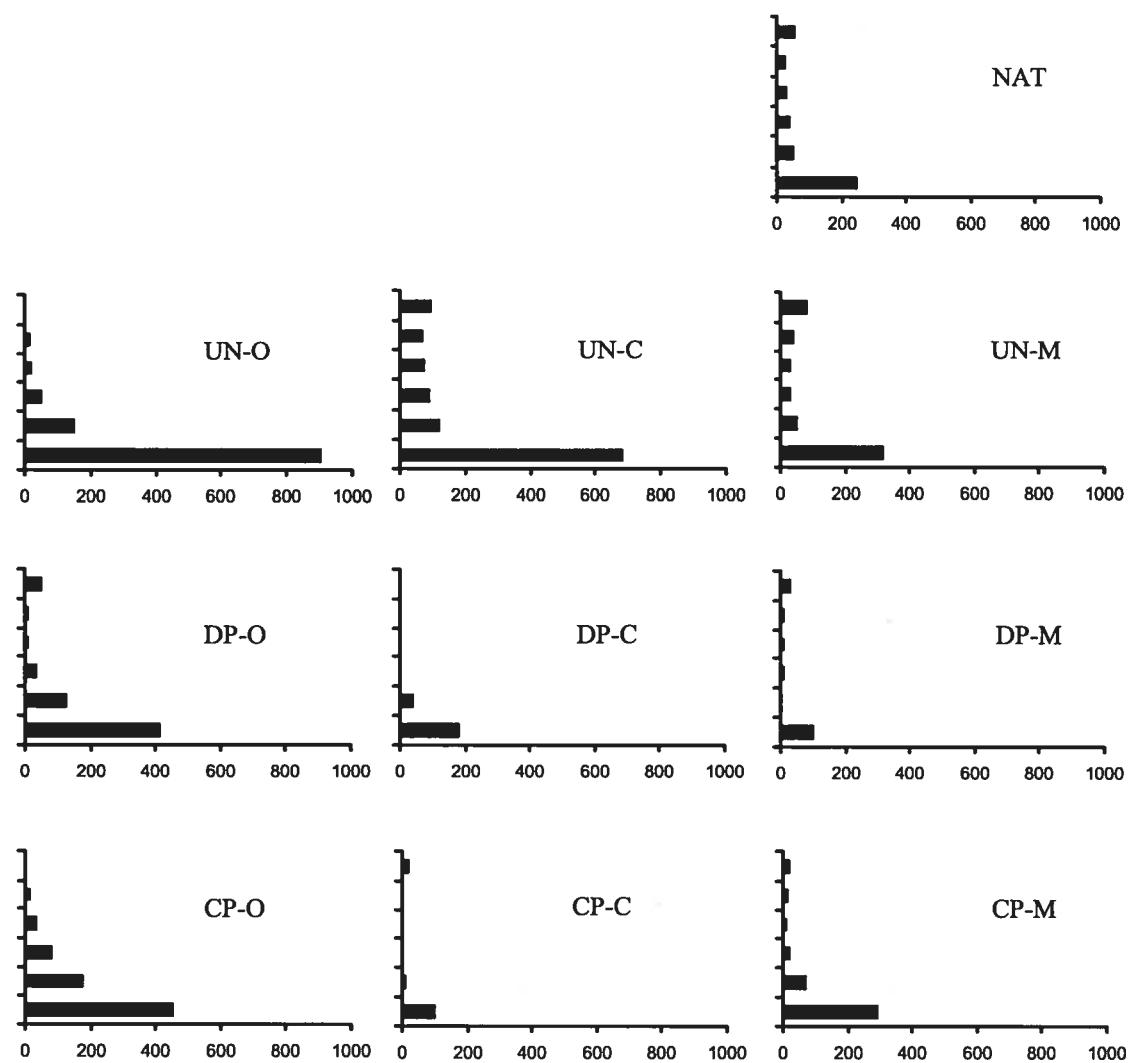


Figure 4.3. Cumulative occurrence of vegetation by vertical stratum for each stand type and stage. X axes: % of occurrence; Y axes: 6 vertical strata from 0 cm to 250 cm +. Nat: natural maple forest; UN-M: unplanted mature canopy; UN-C: unplanted closed canopy; UN-O: unplanted open canopy; DP-M: mature deciduous plantation; DP-C: close canopy deciduous plantation; DP-O: open canopy deciduous plantation; CP-M: mature conifer plantation; CP-C: close canopy conifer plantation, CP-O: open canopy conifer plantation.

Discussion

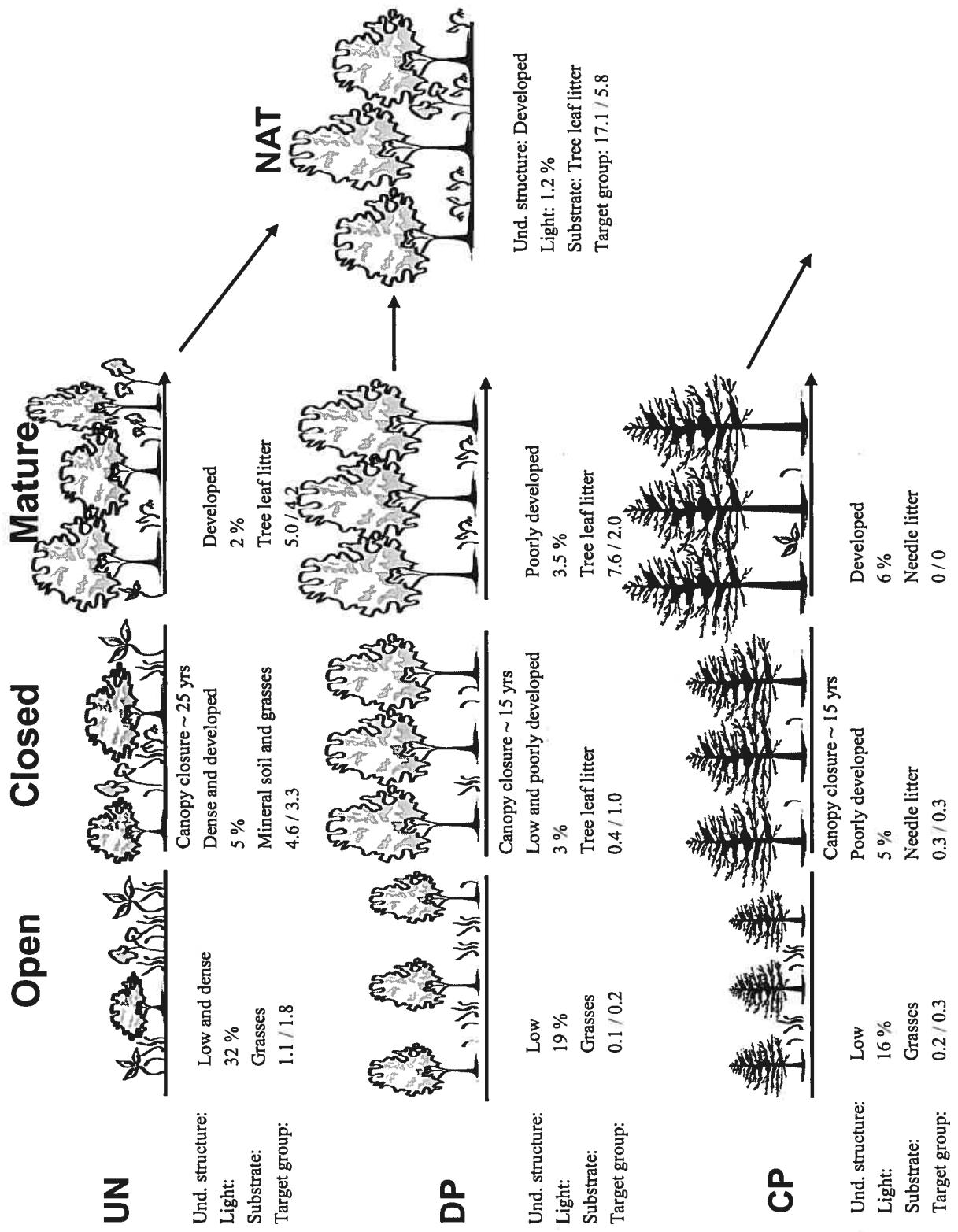
Based on the results, we synthesised in a schematic illustration the understory development in the stand types under study (Figure 4.4). Major differences were found in species traits responses among the two plantation types and in comparison with natural maple forests and unplanted stands. In order to assess if plantations can develop the understory attributes of a natural forest ecosystem, these differences in trait responses have to be discussed with the view of the temporal dynamic along stand developmental stages, and of the differential understory development among stand types.

Species traits responses to stand developmental stages

Clear patterns in species trait responses do exist along stand developmental stages. These differences were used to compare the understory developmental status between the different stand types and with natural forests. Light-demanding species and wind-dispersed species groups, such as grasses, exotics and summer- or late summer-flowering herbs, were predominant in young stands. An understory possessing a high proportion of these groups can be described as being at an early successional stage. Conversely, woody groups, together with ferns and ant-dispersed spring flowering herbs were associated with mature canopy stands and natural maple forest. Many studies have associated ant-dispersed spring flowering herbs with natural unmanaged forests or ancient forests (Froborg & Eriksson, 1997; Bossuyt, Hermy & Deckers, 1999; Scheller & Mladenoff, 2002; Aubin et al., 2007). Their slow growth and low colonisation capacity make them particularly sensitive to human disturbance (Bierzychudek, 1982; Meier, Bratton & Duffy, 1995; Whigham, 2004). The species in other herb groups that were found in mature canopy stands or natural maple forests (H4, H6, H7 and H8; Figure 4.1) are normally encountered in a range of forest types or are associated with forest edges (e.g. *Aralia nudicaulis*). These generalist species are found in many different stand types and are generally less sensitive to disturbance (Ramos & Roberts, 2005). The spring flowering herbs that are dispersed by ants have been considered as having high conservation value and are used as an indicator of natural forests

for the deciduous temperate biome (Keddy & Drummond, 1996; Hermy et al., 1999; McLachlan & Bazely, 2001; Aubin et al., 2007). An occurrence and a redundancy of this target group comparable to those of natural maple forest are thus used in this study as an indicator of the development of a mature understory.

(on next page) Figure 4.4. Schematic illustration of understory development in the two plantation types: DP: deciduous plantation and CP: coniferous plantation, in comparison with UN: unplanted and NAT: natural maple forest. Understory structure: description from Figure 4.3. Light: % PPFD at the forest floor. Substrate: main substrate type. Target group: Mean relative occurrence / mean richness of the spring flowering herbs dispersed by ants group (H9).



Differential understory development between deciduous and coniferous plantation

We noted contrasting differences in understory development between coniferous and deciduous plantations. At young stages, the understory assemblage and understory environmental conditions were quite similar between the two plantation types. However, they were radically different in mature canopy stands. Understory attributes were much more similar to natural maple forests for deciduous plantations than coniferous. In deciduous plantations, the proportions of the different emergent groups were similar to those of natural maple stands. The group consisting of ant-dispersed spring flowering herbs, which was our main indicator group, also occurred in deciduous plantations with frequencies comparable to natural forests. However, the richness of this group was low and its understory structure was poorly developed in deciduous plantations compared to natural maple forests. Understory development in conifer plantations followed a trajectory that was greatly different from the deciduous plantations. Their understory vegetation assemblage was compositionally, structurally and functionally different from that of natural or planted deciduous stands. Our main indicator group (spring geophytes dispersed by ants) decreased in its frequency of occurrence along stand stages in conifer plantations, and was totally absent from the mature canopy stage. Herault, Honnay and Thoen (2005) have also observed a low frequency of occurrence of spring geophytes in mature conifer plantations and contrasting floral assemblages between Norway spruce plantations and natural deciduous forests in Europe. In our study, the understory environmental conditions in coniferous plantations were also radically different than in deciduous stands and may have constrained the establishment of forest herbs associated with deciduous stands. For example, the acidic and nutrient-limited needle litter layer (Hunter, 1990; Augusto et al., 2002), together with cool and dark spring conditions found under conifer canopy comparative to that of a deciduous canopy, may have inhibited the establishment of many spring flowering herbs, which are known to be nutrient- and light-demanding species during their short spring time, vegetative cycle (Lapointe, 2001; Whigham, 2004). At the

species level, we did not find any high conservation species, such as orchids, associated with acidic litter.

Differential understory development between planted and unplanted stands

For a similar stand stage, the understory of plantation was generally less developed than unplanted old field stands, suggesting that traditional tree plantation does not effectively promote the development of a mature and functional forest understory. Although they possessed a younger and smaller canopy stratum than plantations, the understory vegetation assemblage of unplanted stands was species-rich, with well-developed structure, and much closer to that of a natural forest. Unplanted stands on former pasture have been found to possess a good potential for natural understory recovery (Chapter 3). This potential is likely based on biological legacies (*sensu* Franklin et al., 2000) not found in plantations such as soil micro-topography favourable for forest herb establishment (Beatty, 2003; Flinn & Marks, 2007) and heterogeneous vegetation structures that promote seed dispersal by birds and mammals (McDonnell & Stiles, 1983).

The differences between planted and unplanted stands may also be attributed to the site preparation in planted stands which may have profoundly altered some important features of the stand biological legacy. Site preparation in plantations, such as plowing or soil scarification, destroyed the established flora, as well as the pit-and-mound microtopography characteristic of natural forests (Beatty, 2003). The resulting uniformity of the soil surface can reduce habitat diversity and may impede forest herb establishment via environmental limitations and competition (Beatty, 2003; Flinn & Vellend, 2005; Flinn & Marks, 2007). The established flora in former pastures may also contain forest species that have persisted as relict populations of the original forests (Chapter 3; Stover & Marks, 1998). If the land has been plowed, species such as ant-dispersed spring flowering herbs may take century to get reestablished via seed dispersal (Scheller & Mladenoff, 2002; Beatty, 2003; Flinn & Vellend, 2005; Flinn & Marks, 2007).

Finally, silvicultural treatments in plantations such as thinning, pruning and weed control may also have contributed to the divergence between unplanted and planted stands. Site preparation and maintenance activities in plantations are generally focused exclusively on promoting tree growth, while paying little attention to the ground flora except as an undesirable source of competition. Thinning has been known to disturb extant vegetation and the forest floor, to increase light availability, and to modify the microclimate (Hunter, 1990; Hansen et al., 1991). Pruning likely had a similar, but less pronounced impact than thinning. Thinning has generally favoured the development of the shrub and herb strata, and thus, has generally been perceived as a positive step for understory development (Hunter, 1990; Parker et al., 2001; Thysell & Carey, 2001). However, it has been reported to principally favour generalist (Herault, Honnay & Thoen, 2005) and exotic (Parker et al., 2001; Newmaster et al., 2006) species. Many forest herbs are sensitive to competition with pioneer species, which is likely to occur following such disturbance (Meier, Bratton & Duffy, 1995), as well as being sensitive to desiccation following forest floor disturbance (Metzger & Schultz, 1981). For its part, the impact of weed control on understory development will vary according to the technique used (chemical, mechanical or plastic mulch). Globally, weed control are also likely to favour species adapted to disturbance. This suggests that silvicultural treatments favour pioneer species, to the competitive disadvantage of forest herb specialists. Accordingly, we observed a high relative occurrence for groups that were associated with pioneer stages in deciduous plantations; this stand type received the most frequent and intensive silvicultural treatments. However, our study did not specifically address this question and consequently, more research on the impact of these treatments on understory development is needed.

Can plantations develop the understory attributes of a natural forest ecosystem?

A dichotomy was observed in plantations between the tree cover development and those of the understory stratum. Planting a tree cover resulted in the rapid development of a forest structure which will be attractive for wildlife species and which may indeed favour

the development of forest herbs by creating understory environmental conditions comparable to a natural forest. The rapid creation of a tree cover has been shown to facilitate tree seedling growth and survival in many biomes (Paquette, Bouchard & Cogliastro, 2006b). However, the impact of planting trees on understory development will vary according to the species planted and the intensity of site preparation and silvicultural treatments. These activities are recurrent disturbances that can slow down the development of the understory stratum and favour the persistence of those species better adapted to regular disturbances. We speculate that these disturbances also affect other components of the ecosystem closely associated with the understory vegetation (e.g., fungi, insects and herbivores) and slow down the development of the whole ecosystem.

The understory development in conifer plantations was very different from that found in natural habitats dominated by temperate deciduous species in the region. These plantations might, however, be comparable to white pine (*Pinus strobus*) stands that were more frequent in northern hardwood regions prior to intense harvesting in the 19th century (Simard & Bouchard, 1996; O'Keefe & Foster, 1998). However, in pre-colonial forests, white pine was mainly found scattered throughout the hardwood forest. Pure stands of pine were rare and confined to dry and poor sites (Brisson & Bouchard, 2006). The structure, composition and function of the understory found in monospecific conifer plantations are not representative of the conditions found in natural forests of the temperate deciduous biome. They should then be avoided, minimized and/ or confined to localised poor soil conditions to preserve the ecological integrity of the biome. Conversion of such plantations into deciduous woodlands has become a major objective for forest management in Europe (Herault, Honnay & Thoen, 2005) and might become a preoccupation in North America with the continuing decline of natural forests.

Deciduous plantations developed understories that were compositionally, functionally and structurally similar to those of natural forests. However, they remained impoverished in terms of high conservation value species even after 50 years. Post-agricultural forests have been known to take upwards of a century to recover their original

understory composition (Peterken & Game, 1984; Matlack, 1994b; Bossuyt, Hermy & Deckers, 1999; Flinn & Marks, 2007). The native forest flora face both dispersal and environmental constraints on their establishment in post-agricultural lands (Ehrlen & Eriksson, 2000; Nordén & Appelqvist, 2001; Flinn & Marks, 2007). Dispersal is known to limit the establishment of many forest herbs, especially those with short distance dispersal such as spring flowering herbs that are dispersed by ants (Ehrlen & Eriksson, 2000; Flinn & Vellend, 2005). Environmental limitations have been less frequently documented, but may be just as important as dispersal capacity in determining the establishment success of forest herbs (Nordén & Appelqvist, 2001; Flinn & Marks, 2007). For many forest herbs, colonisation cannot take place in a stand if suitable microhabitats, such as coarse woody debris or a particular microtopographic feature, are not present (Scheller & Mladenoff, 2002; Beatty, 2003; Flinn & Marks, 2007). Similarly, some species are confined to a low light environment where they have a competitive advantage (Collins, Dunne & Pickett, 1985).

A first step in the establishment, development and persistence of high conservation value forest herbs in plantations required that understory environmental conditions similar to those of their natural habitat be attained. In our study, understory environmental conditions in mature canopy deciduous plantations corresponded to those of natural forests. Consequently, we suspect that dispersal limitation may have been the major factor impeding the establishment of high conservation value species in these stands. Restoration activities such as plantation or seeding of these species may be the prescribed treatments in this case.

How can development of a mature understory be promoted in plantations?

How different would be plantations established with the goal of creating high quality forests in ecological terms rather than being allocated primarily for wood production? Based on our results and our understanding of the ecology of natural temperate

deciduous forests of eastern North America, one should: (1) favor deciduous species instead of conifers; (2) preserve the natural stand microtopography, soil properties and other structural legacies by minimizing site preparation; (3) favor silvicultural activities that preserve or recreate the prevailing environmental conditions and stand structural heterogeneity encountered in natural forest; (4) favor longer rotation to allow sufficient time for the development of a mature understory community; and (5) when understory environmental conditions are favourable, reintroduce forest herbs that have high conservation value and low seed dispersal capacity, for example, ant-dispersed spring flowering herbs. Clearly, enrichment planting is a good alternative to conventional planting techniques since it would tend to preserve understory community and stand legacy while ensuring good tree growth (Paquette, Bouchard & Cogliastro, 2006a, b).

Conclusion

Although some limitations inherent to coarse synthesis have to be considered in the interpretation of this study, the approach used here gives a comprehensive and broadly applicable portrait of the ecological integrity of plantations. This study has shown that plantation can be a viable habitat for native flora. However, the success of the natural restoration of the understory will be function of the type of planted trees and presumably to its associated activities. Important population attributes not studied here such as fine scale species distribution patterns or genetic variability might be different in plantation than in natural unmanaged forest. These modifications might have a profound impact both at the level of population stability and ecosystem processes.

Further research is needed to refine our understanding of understory development in plantations. A lack of knowledge of the ecological traits of many species has impeded our understanding of their responses to the different environmental filters. In this study, the use of other important but insufficiently documented ecological traits such as seed longevity, soil chemistry requirements and interactions with mycorrhizae, herbivores and pollinators would have substantially improved our understanding of understory development

mechanisms. It is important to note that distance to a seed source (forest) was relatively small in our study, facilitating understory recovery. The surrounding landscape and the neighbouring forests have to be taken into account in determining the potential of a plantation to develop as a forest.

The marked decline of natural unmanaged forest has prompted us to develop tools that quantify the ecological integrity of these human-created ecosystems, which could help us in managing them in such a way as to increase their naturalness. Therefore, in regions where the proportion of natural forest is low or declining, the goal of tree plantation should include a restoration objective as well.

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Chapitre 5

Conclusion

Conclusion

Le Québec d'aujourd'hui n'est plus une contrée aux inépuisables forêts sauvages. Avec l'augmentation de la demande en fibre et la pression grandissante sur nos forêts qui en découle, les forêts aménagées et les plantations occupent une part grandissante de notre paysage forestier. Dans le sud du Québec, là où nos forêts sont les plus riches et diversifiées, s'ajoutent les besoins de l'agriculture et de la construction résidentielle qui morcellent et transforment les îlots forestiers résiduels.

Devant la raréfaction des forêts naturelles et l'omniprésence de l'homme sur le domaine forestier, il devient nécessaire de développer des outils permettant de quantifier notre impact sur les écosystèmes forestiers. Ces outils doivent permettre d'évaluer des écosystèmes variés, que ce soit des forêts subissant diverses interventions humaines se conjuguant dans le temps et l'espace, de tout nouveaux agencements d'espèces lors d'une revégétalisation naturelle ou encore des plantations. Ces outils doivent être basés sur les caractéristiques intrinsèques des écosystèmes forestiers naturels et prendre en compte leur complexité et leur variabilité.

L'intégrité écologique est généralement pressentie comme base conceptuelle d'une telle évaluation. Ce concept demeure cependant difficilement applicable sur le terrain. Théoriquement, pour parvenir à évaluer l'intégrité écologique, il faudrait pouvoir quantifier les structures écologiques et les processus qui définissent le fonctionnement d'une forêt, et ce, à différentes échelles spatiales et temporelles. Également, la comparaison à un état de référence, point central de ce concept, est difficile dans plusieurs régions où les habitats naturels représentatifs se font rares. Dans la pratique, des espèces ou des éléments structuraux clés sont utilisés comme indicateur. Cependant, les disparités régionales dans la distribution des espèces limitent bien souvent l'utilisation de ces indicateurs à une large échelle.

Dans le cadre de cette thèse, j'ai développé une approche novatrice permettant l'évaluation de l'impact des interventions humaines sur l'intégrité écologique des écosystèmes forestiers. Les écosystèmes forestiers sont bien souvent caractérisés uniquement en termes de leur strate arborescente, avec peu d'attention pour les autres composantes de l'écosystème. Tel que présenté au premier chapitre, les difficultés inhérentes à la caractérisation de la végétation de sous-bois, les limites des méthodes statistiques traditionnelles et notre pensée cartésienne simplificatrice, ont longtemps freiné l'intégration de la diversité végétale du sous-bois dans notre compréhension de la dynamique forestière. Dans les travaux présentés ici, la perspective est différente. La végétation de sous-bois est vue comme une force structurante de la dynamique forestière. À l'aide de nouvelles méthodes statistiques, la réponse de la végétation de sous-bois aux interventions humaines est synthétisée et ensuite utilisée comme indicateur global de l'intégrité écologique de l'ensemble de l'écosystème.

Une des particularités de cette thèse est l'utilisation d'une approche basée sur les traits fonctionnels des espèces plutôt que l'approche traditionnelle basée sur la taxonomie. L'utilisation d'une telle approche était une première pour le Québec. En permettant de comparer des écosystèmes similaires de différentes régions, cette approche offre une méthodologie novatrice pouvant s'appliquer à une vaste échelle. Cette approche m'a ainsi permis de dépasser les disparités régionales dans la distribution des espèces et d'apporter une évaluation représentative de l'ensemble des forêts du Québec méridional.

J'ai également développé plusieurs nouvelles applications possibles de cette approche pour une meilleure compréhension de l'impact des interventions humaines sur les grands processus régissant le fonctionnement des écosystèmes. Je suggère également plusieurs applications possibles de cette approche à l'aménagement de nos forêts. Par exemple, cette approche permet d'effectuer le suivi de l'impact des activités humaines même là où il est difficile de trouver des forêts naturelles servant de témoin.

Cette thèse apporte non seulement de nouvelles applications de l'approche par groupes fonctionnels, mais également une meilleure compréhension des différents types de

classification fonctionnelle. Ils existent en effet plusieurs types de classification, basés sur différents jeux de données et méthodologies, et apportant des résultats très différents. Ainsi, les écologistes utilisent généralement des groupes émergents, soit des groupements d'espèces basés sur la co-occurrence de traits. Cependant, la question qui intéresse les écologistes est la réponse de la végétation à un gradient environnemental, soit des groupes réponses. Cette thèse a souligné certaines faiblesses des classifications par groupes émergents et a démontré les avantages qu'offrent les nouvelles approches directes de classification fonctionnelle, tel que le 4^e coin utilisé au chapitre 2.

Forte de cette nouvelle approche, cette thèse apporte une vision globale et inédite de la réponse de la végétation de sous-bois aux principales perturbations humaines de la forêt feuillue du Québec méridional. Plus spécifiquement, cette thèse offre de nouvelles perspectives dans la compréhension : de l'impact des interventions humaines sur les érablières, des processus de revégétalisation dans les friches agricoles, et des processus de naturalisation des plantations.

Les érablières possèdent un sous-bois résilient qui fait face à des possibles modifications dans le futur

La dégradation de la strate arborescente de la forêt feuillue du Québec méridional est bien connue et documentée (Coulombe et al., 2004). Cependant, nous n'avions qu'une connaissance parcellaire de l'état des autres composantes de l'écosystème. En dépassant les disparités régionales des études traditionnelles basées sur la taxonomie, cette étude apporte une connaissance globale de notre domaine forestier nécessaire à l'orientation de nos activités d'aménagement.

Un des résultats les plus marquants de cette thèse est la remarquable stabilité de la végétation de sous-bois des érablières. Après 200 ans de perturbations humaines et malgré la dégradation de la strate arborescente, la structure du sous-bois et la répartition des groupes fonctionnels de sa flore demeurent semblables à celles de forêts non aménagées.

Posséder un sous-bois intègre est un facteur déterminant assurant notamment l'établissement et la survie des semis d'arbres qui formeront la canopée de demain. Ainsi, l'ensemble des forêts que nous avons échantillonnées semblait avoir conservé leur potentiel de restauration naturelle de leur strate arborescente à long terme. Certains facteurs tels le manque de semenciers peuvent cependant considérablement appauvrir ce processus de restauration naturelle (D'Orangeville, accepté). Ces résultats suggèrent que les forêts perturbées peuvent jouer un rôle dans la préservation de la biodiversité et de l'intégrité écologique de notre domaine forestier. Il est donc possible d'envisager d'inclure une certaine proportion de forêts dégradées dans notre stratégie de conservation et ainsi répondre au besoin urgent de consolider notre réseau d'aires protégées dans le sud du Québec.

Cependant, les résultats du chapitre 2 laissent entrevoir certains risques de modification de l'assemblage du sous-bois dans le futur, particulièrement avec une intensification des interventions humaines. Les modifications suivantes pourraient affecter l'intégrité écologique des érablières :

- Augmentation de l'occurrence des groupes associés aux milieux ouverts, incluant les espèces exogènes
- Diminution de la diversité et de l'occurrence des géophytes printanières
- Diminution de l'occurrence de certaines espèces forestières adaptées aux conditions sombres de sous-bois dont les espèces saprophytes
- Modification de la structure du sous-bois par une occurrence plus importante des arbustes et semis d'arbres.

Les friches possèdent un potentiel de restauration naturelle non négligeable

Ce chapitre a démontré que la revégétalisation naturelle suite à une déprise agricole est globalement efficace du point de vue du fonctionnement de l'écosystème même lorsque la strate arborescente est dégradée. Une flore de sous-bois se développe dès la fermeture de

la canopée, soit environ 30 ans après abandon dans les sites échantillonnés. Cette restauration peut cependant prendre des siècles avant d'être complétée. En fait, nos résultats suggèrent qu'elle ne l'était pas encore dans les forêts matures issues d'ancien pâturage que nous avons échantillonnées. Certaines espèces forestières possédant une capacité de colonisation limitée telles les géophytes printanières pourraient ne jamais se rétablir par elles-mêmes. Le succès de rétablissement variait grandement entre les espèces de ce groupe, certaines espèces étant retrouvées dans de jeunes friches tandis que d'autres étaient exclusivement retrouvées dans les forêts matures. Cette étude souligne le rôle crucial mais méconnu de legs biologiques tels les individus survivant dans un environnement non forestier pour le potentiel de restauration naturelle des anciennes terres agricoles.

Traditionnellement, l'évaluation du potentiel de restauration d'un écosystème était basée sur le développement de la strate arborescente. Dans les travaux présentés ici, la perspective est totalement différente. Le potentiel de restauration est basé sur les traits fonctionnels des espèces du sous-bois. Ce changement de perspective a permis de constater un potentiel de restauration de la strate de sous-bois différent de celui de la strate arborescente. Ce constat est crucial pour le domaine de la restauration écologique et pourrait modifier notre vision des friches et autres forêts dégradées.

Suite à cette étude, il est possible d'affirmer que les friches peuvent jouer un rôle non négligeable dans notre stratégie de conservation. Leur transformation à des fins d'agriculture ou par une rapide afforestation via de la plantation traditionnelle n'est pas souhaitable du point de vue de leur valeur écologique. Afin d'évaluer le potentiel de ces friches à se restaurer naturellement et de ce fait leur valeur écologique, il est important de prendre en compte leur nature dynamique et d'inclure une échelle de temps réaliste dans notre objectif de restauration. Même lorsqu'il est impératif de développer un écosystème forestier dans un court laps de temps, une connaissance approfondie du développement naturel de la végétation est nécessaire afin de choisir une activité de restauration convenant au stade de développement du site. Des activités ne respectant pas ces processus naturels peuvent mener à un tout nouveau patron de développement de la végétation et ainsi

appauvrir irrémédiablement la communauté végétale déjà établie. Ce chapitre a permis de définir certains points clés pour la restauration naturelle de friches agricoles :

- Les activités de restauration doivent être judicieusement choisies selon le stade de développement du site et en préservant le legs biologique.
- Avant la fermeture de la canopée, les activités de restauration devraient prioriser le développement d'une strate arbustive et arborescente, tout en conservant l'hétérogénéité structurelle, les propriétés du sol et la végétation établie.
- Après la fermeture de la canopée, lorsque les conditions environnementales en sous-bois sont favorables, les activités de restauration devraient inclure l'ensemencement ou la plantation d'espèces à haute valeur de conservation possédant une faible dispersion, telles que les herbacées printanières dispersées par les fourmis.

La capacité de naturalisation d'une plantation est fonction de nos choix sylvicoles

Cette thèse a démontré que les plantations de feuillues peuvent se naturaliser et devenir un habitat viable pour la flore de sous-bois. Pour sa part, le sous-bois des plantations de conifères suit un patron de développement différent que celui des forêts naturelles du Québec méridional. À 50 ans, les plantations de feuillues ont développé un sous-bois similaire à celui de forêts naturelles de la région au point de vue de la répartition des traits biologiques des espèces et des conditions environnementales. Cependant, les plantations de feuillues demeurent pauvres en espèces forestières à haute valeur écologique, plus pauvres que des sites d'âge similaire n'ayant pas été plantés. Puisque les conditions environnementales retrouvées dans le sous-bois des plantations de feuillues sont similaires à celles de forêts naturelles, la faible représentativité de ces espèces serait principalement liée à leur élimination lors des activités associées aux plantations, ainsi qu'à leur capacité de dispersion limitée.

Nos résultats suggèrent que la capacité de naturalisation d'une plantation est fonction des espèces plantées mais également grandement influencée par le mode de

plantation et de traitements sylvicoles. Plus spécifiquement, nous avons défini des critères essentiels pour l'établissement de plantations ayant comme premier objectif la création d'écosystèmes forestiers de qualité en terme écologique :

- Choisir des espèces feuillues croissant naturellement ou historiquement dans la région
- Préserver la micro topographie, les propriétés du sol et les autres legs structurels en minimisant la préparation du sol
- Prioriser les travaux sylvicoles qui préservent ou recréent les conditions environnementales et l'hétérogénéité structurelle retrouvées dans un peuplement naturel d'âge similaire
- Prévoir des rotations suffisamment longues pour permettre le développement d'une flore de sous-bois mature
- Lorsque les conditions environnementales en sous-bois le permettent, réintroduire des espèces forestières cibles possédant une forte valeur écologique ainsi qu'une faible capacité d'établissement (par exemple les géophytes printanières dispersées par les fourmis).

Traditionnellement, la dynamique de la flore de sous-bois des plantations n'a reçu que peu d'attention, si ce n'est que comme source de compétition. Avec la raréfaction des forêts naturelles, les informations fournies dans ce chapitre sont cruciales afin de d'évaluer le potentiel des plantations à servir d'habitats à la flore indigène. Ces informations sont également déterminantes pour l'orientation de nos choix sylvicoles, pour la compréhension des grands processus régissant les écosystèmes, de même que pour assurer la résilience de ces écosystèmes.

La résilience du sous-bois

Un résultat marquant de cette recherche est la remarquable résilience que semble démontrer la végétation de sous-bois face aux perturbations humaines. Que ce soit suite à une perturbation en forêt mature (chapitre 2), lors de processus de restauration naturelle

(chapitre 3) ou en plantation (chapitre 4), l'assemblage de la végétation de sous-bois tend globalement vers un retour à un assemblage comparable à celui d'un habitat naturel.

La résilience présentement observée n'est cependant pas gage d'une résilience à long terme. Tel que souligné par Drever et al. (2006), la forte tendance vers l'augmentation des stress de nature anthropique sur la forêt pourrait modifier la capacité des forêts à se réorganiser suite à une perturbation et ainsi faire basculer un système jusque-là résilient vers un état alternatif.

Avec l'augmentation des pressions humaines et la diminution des surfaces forestières, je crois que la résilience du sous-bois est menacée. Tel que présenté au chapitre 2, les forêts naturelles devront faire face à des modifications de leurs assemblages dont notamment la diminution des herbacées forestières sensibles, l'envahissement par des espèces exotiques et la modification de la structure du sous-bois par une densification de la strate arbustive et de gaulis. Nous pouvons également prévoir dans le futur un retour plus difficile à un assemblage naturel pour les stations avec discontinuités forestières comme les friches et les plantations dans un paysage de plus en plus anthropisé.

Puisque la strate de sous-bois réagit dans une échelle de temps plus court que celle de la strate arborescente (Strykstra, Bekker & Andel, 2002), une perte de résilience du sous-bois pourrait s'observer dans un premier temps par une strate de sous-bois dominée par quelques espèces exotiques sous une strate arborescente naturelle. Il est fréquent d'observer un tel phénomène dans les îlots forestiers en zone urbaine. Meiners et al. (2002) ont également décrit une dichotomie de ce genre pour de jeunes forêts secondaires sur d'anciennes terres agricoles. On peut présumer que cette modification profonde et potentiellement irréversible de l'assemblage du sous-bois aurait des conséquences sur l'avenir de la strate arborescente puisque c'est dans le sous-bois que se développent les semis qui formeront la canopée de demain.

L’assemblage de sous-bois est-il un indicateur adéquat de l’intégrité écologique de l’ensemble de l’écosystème ?

La nature intégrative de l’approche ainsi que la possibilité de comparaisons dépassant les disparités régionales sont les principales forces de l’approche utilisée dans cette thèse. Ainsi, l’utilisation de cette approche nous a permis de comparer le sous-bois d’un vaste ensemble de forêts, réparties dans deux régions différentes. Cette étude n’aurait pas été possible avec une méthode classique basée sur la taxonomie. De plus, le fait de conjuguer des attributs structuraux et fonctionnels a permis une caractérisation globale et dynamique d’une partie de l’écosystème. Je crois que l’approche proposée ici aborde un élément clé de la dynamique forestière, notamment puisque l’état biophysique du sous-bois est déterminant pour assurer l’établissement et la survie des arbres qui vont dominer le système dans le futur.

Mais l’assemblage de sous-bois analysé à l’aide d’une approche par groupes fonctionnels peut-il être un indicateur fiable et pratique de l’intégrité écologique de l’ensemble de l’écosystème? Il est, je crois, bien improbable de trouver un indicateur qui saurait rendre compte de toutes les composantes et processus clés de l’écosystème. Pour parvenir à évaluer adéquatement l’intégrité écologique d’un écosystème, le principe de précaution nous dicte de combiner l’assemblage du sous-bois à d’autres indicateurs, dont notamment des indicateurs structuraux (p. ex., bois mort) et des indicateurs basés sur d’autres composantes de l’écosystème (e.g. entomofaune ou les prédateurs).

Il est également nécessaire d’apporter quelques limitations quant à la portée de cette étude. Comme toutes les synthèses, l’approche par groupes fonctionnels donne peu de poids aux espèces rares ou à faible occurrence qui sont les plus susceptibles d’être affectées par les activités humaines (Jolls 2003). Les groupes fonctionnels sont en fait une simplification, une modélisation, permettant une meilleure compréhension du système et non une préconisation de gestion. De plus, tel que souligné par Gitay, Wilson et Lee (1996), il peut être dangereux d’appliquer le concept de redondance écologique au domaine de la

conservation. Cette approche doit donc être utilisée en complément à une approche taxonomique traditionnelle.

La remarquable résilience observée chez l'assemblage de la végétation de sous-bois dans cette étude pose également un problème pour son utilisation à titre d'indicateur. Étant globalement résiliente, la végétation de sous-bois est un moins bon indicateur puisque l'un des premiers attributs d'un indicateur est sa sensibilité à la perturbation visée. Un bon indicateur doit en effet être le premier à réagir.

Cependant, de cet indicateur global, et au-delà de cette résilience globale, il est possible de définir des groupes d'espèces sensibles aux perturbations humaines à savoir les espèces saprophytes et les géophytes printanières dispersées par les fourmis. De même, il est possible de déterminer des groupes d'espèces favorisées par les perturbations comme les phanérophytes et les espèces exotiques. Sur un aspect pratique, il serait possible d'utiliser ces groupes d'espèces à titre d'indicateur. Cependant, ici encore, il faudrait les combiner à d'autres indicateurs.

En résumé, je crois que l'assemblage de la végétation de sous-bois est un bon indicateur possédant les forces et les faiblesses d'un indicateur holistique. Comme tout autre indicateur, il doit être combiné à d'autres afin de rendre compte de l'ensemble de l'écosystème. Ce n'est seulement lorsque d'autres études semblables seront menées sur d'autres composantes clés de l'écosystème (par exemple l'entomofaune), que l'on pourra valider l'approche et ainsi confirmer ou infirmer de la fiabilité de cet indicateur. D'autres études seront éventuellement nécessaires afin de statuer du potentiel opérationnel de cette approche.

Après l'avoir ignorée, il nous reste à découvrir la végétation de sous-bois

Beaucoup reste à découvrir, tant au niveau de la dynamique des populations de la végétation de sous-bois que de la compréhension de ses multiples interactions et de son rôle

dans le fonctionnement de l'écosystème. Malgré la vitalité de ce domaine de recherche durant la dernière décennie, la végétation de sous-bois demeure encore méconnue. Des recherches sont nécessaires afin de raffiner notre compréhension du développement du sous-bois dans les écosystèmes forestiers. Des traits tels que la longévité des semences, les besoins en éléments nutritifs, ainsi que les interactions avec les mycorhizes, les herbivores et les polliniseurs sont déterminants pour le fonctionnement de l'écosystème mais insuffisamment documentés pour de nombreuses espèces de sous-bois. L'utilisation de ces traits dans une étude comme la notre améliorerait de façon substantielle notre compréhension des processus régissant l'établissement, le développement et le maintien de la flore de sous-bois de même que sa réponse aux perturbations humaines.

Après avoir perturbé, nous devons maintenant restaurer

De tout temps, la complexité des écosystèmes forestiers nous a effrayés. Cette complexité freine notre compréhension. Nous avons cherché à simplifier pour mieux domestiquer. Maintenant, c'est l'omniprésence de l'homme qui nous effraie. Comme le soulignent Holling et Meffe (1996), ce besoin de maîtriser la nature est une maladie qui menace maintenant la survie même de l'humanité. Apprivoiser la complexité et apprendre à l'intégrer à la gestion du territoire forestier est le défi qui nous attend. Pour ce faire, nous devons développer une nouvelle façon de penser l'utilisation de notre territoire forestier préservant sa naturalité, sa complexité et sa variabilité et ainsi conserver son potentiel à nous offrir de nombreux services écologiques. Nous devrons faire des choix : transformer nos forêts en de vastes monocultures afin de satisfaire nos besoins sans cesse grandissant en bois ou bien préserver une portion substantielle de forêts naturelles pour les générations futures par une utilisation responsable de ce patrimoine.

Avant toute chose, il faudra bien définir ce que nous considérons être une forêt ainsi que les objectifs de nos interventions sylvicoles. Soyons clair, l'aménagement forestier vise prioritairement l'augmentation de la productivité en bois et très rarement une véritable amélioration de la fonctionnalité ou de l'intégrité de l'écosystème. Dans la majeure partie

des cas, la forêt se porte très bien sans nous. Il faudra de même clarifier nos intentions en ce qui concerne les plantations et faire la distinction entre des plantations pour la production de bois de celles ayant comme objectif de recréer un écosystème forestier. Ces deux objectifs sont constamment mélangés, tant par la population que par les instances gouvernementales. L'augmentation des surfaces allouées aux plantations occulte trop souvent la perte de forêts naturelles. En ce qui concerne la fonctionnalité de l'écosystème, cette thèse a bien démontré qu'une friche possède un potentiel équivalent sinon plus grand que celui des plantations. La valeur des friches et autres forêts dégradées doit être reconnue puisqu'elles font face à de fortes pressions de conversion à d'autres usages « plus productifs ».

Plusieurs petits propriétaires terriens du Québec méridional acceptent une plantation de conifères sur leur terre en pensant ainsi recréer une forêt. Les alternatives qui s'offrent à eux sont peu nombreuses et demandent une vision à long terme pour accepter les interventions récurrentes nécessaires à leur bon développement. Il faudrait développer des méthodes de plantation spécifiques à leur besoin, ainsi que répondant au besoin croissant de restauration écologique.

Nous avons colonisé les moindres recoins de notre planète. Il n'est plus possible de partir au large pour découvrir de nouvelles ressources à exploiter. Après avoir perturbé, le défi qui nous attend est celui d'apprendre à restaurer...

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Annexe 1

Liste des sources utilisées dans le développement de la base de données TOPIQ (Traits Of Plants In Québec)

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Annexe 2

Liste des stations

Liste des stations

Code terrain	Chapitre 2	Chapitre 3	Chapitre 4	Longitude	Latitude
<i>Haut St-Laurent</i>					
AF001	UND1	.	.	W74°17'44.2"	N45°04'52.3"
AF004	PAS1	MA04	NAT04	W74°16'55.1"	N45°03'56.3"
AF005	PAS2	MA05	NAT05	W74°16'45.0"	N45°03'50.6"
AF009	UND2	.	.	W74°21'33.4"	N45°05'03.5"
AF014	.	MA14	NAT14	W74°19'39.6"	N45°08'23.2"
AF018	PAS3	MA18	NAT18	W74°17'11.8"	N45°04'12.9"
AF022	ACE1	.	.	W74°14'37.1"	N45°02'11.1"
AF023	.	MA23	NAT23	W74°14'30.8"	N45°02'19.3"
AH104	PAS4	MA104	NAT104	W74°06'12.1"	N45°05'42.4"
AH107	UND4	.	.	W74°06'30.9"	N45°05'33.1"
AH123	ACE2	.	.	W73°58'57.1"	N45°01'42.9"
AH124	ACE3	.	.	W73°59'10.1"	N45°01'43.1"
AH125	ACE4	.	.	W73°57'24.2"	N45°02'05.9"
AH126	UND3
FACON05	.	YT1	UN-M1	W74°14'37.0"	N45°02'06.5"
FACOO01	.	YT2	UN-M2	W73°57'59.1"	N45°03'33.0"
FAERS02	.	YT3	UN-M3	W73°59'39.2"	N45°02'23.0"
FAFRA04	.	YT4	UN-M4	W74°15'36.0"	N45°06'03.6"
FAFRA06	.	YT5	UN-M5	W74°15'37.8"	N45°06'00.4"
FAGOY02	.	YT6	UN-M6	W74°15'03.5"	N45°06'12.0"
FFCAZ01	.	TS01	UN-C1	W74°16'47.3"	N45°05'48.4"
FFCAZ02	.	TS02	UN-C2	W74°17'02.7"	N45°06'01.0"
FFCOT01	.	TS03	UN-C3	W74°18'50.7"	N45°04'40.2"
FFGOY01	.	TS04	UN-C4	W74°15'03.4"	N45°06'11.4"

(suite)	Chapitre 2	Chapitre 3	Chapitre 4	Longitude	Latitude
FFLUK02	.	TS05	UN-C5	W74°16'09.0"	N45°04'19.7"
FFRID01	.	TS06	UN-C6	W74°09'41.9"	N45°02'17.1"
FOARP01	.	LS01	UN-O1	W74°20'35.9"	N45°03'25.5"
FODRO01	.	LS02	UN-O2	W74°18'43.3"	N45°04'39.9"
FODUH01	.	LS03	UN-O3	W74°13'10.0"	N45°06'03.9"
FOFAU01	.	LS04	UN-O4	.	.
FOHIG01	.	LS05	UN-O5	W74°17'03.4"	N45°05'50.1"
FOLUK01	.	LS06	UN-O6	W74°16'08.1"	N45°04'20.5"
PABUE01	.	PA01	.	W74°14'32.2"	N45°04'02.2"
PACOF01	.	PA02	.	.	.
PADRO02	.	PA03	.	W74°18'36.0"	N45°05'00.1"
PADUH01	.	PA04	.	W74°18'40.1"	N45°05'42.6"
PAMCG01	.	PA05	.	W74°17'57.3"	N45°03'54.4"
PAREC01	.	PA06	.	W74°14'58.4"	N45°04'27.4"
<i>Drummondville</i>					
PFE-50-01	.	.	DP-M1	W72°00'17.4"	N45°55'32.0"
PFE-50-02	.	.	DP-M2	W72°00'14.2"	N45°55'33.7"
PFE-F-01	.	.	DP-C1	W72°30'21.3"	N45°56'31.6"
PFE-F-02	.	.	DP-C2	W72°30'25.6"	N45°56'27.7"
PFE-F-03	.	.	DP-C3	W72°30'31.7"	N45°56'30.1"
PFE-F-04	.	.	DP-C4	W72°30'18.4"	N45°56'27.4"
PFE-F-05	.	.	DP-C5	W72°30'52.0"	N45°56'35.8"
PFE-F-06	.	.	DP-C6	W72°30'47.0"	N45°56'33.5"
PFE-O-01	.	.	DP-O1	W72°30'24.3"	N45°56'30.1"
PFE-O-02	.	.	DP-O2	W72°30'21.8"	N45°56'27.9"
PFE-O-03	.	.	DP-O3	W72°30'14.9"	N45°56'27.8"
PFE-O-04	.	.	DP-O4	.	.
PFE-O-06	.	.	DP-O5	W72°34'58.1"	N45°52'33.7"

(suite)	Chapitre 2	Chapitre 3	Chapitre 4	Longitude	Latitude
PFE-O-07	.	.	DP-O6	W72°35'00.4"	N45°52'35.1"
PPIR-15-01	.	.	CP-O1	W72°34'11.5"	N45°57'31.9"
PPIR-15-02	.	.	CP-O2	W72°34'04.0"	N45°57'36.0"
PPIR-15-03	.	.	CP-O3	W72°33'32.5"	N45°53'22.7"
PPIR-15-04	.	.	CP-O4	W72°35'02.6"	N45°52'43.0"
PPIR-15-05	.	.	CP-O5	W72°17'33.8"	N45°39'33.0"
PPIR-15-06	.	.	CP-O6	W72°17'11.7"	N45°52'31.6"
PPIR-25-01	.	.	CP-C1	W72°34'06.0"	N45°58'22.2"
PPIR-25-06	.	.	CP-C2	W72°34'35.9"	N46°01'25.4"
PPIR-25-07	.	.	CP-C3	W72°13'33.7"	N45°52'18.7"
PPIR-25-08	.	.	CP-C4	W72°30'52.4"	N45°46'03.5"
PPIR-25-09	.	.	CP-C5	W72°09'15.1"	N46°00'13.6"
PPIR-25-10	.	.	CP-C6	W72°13'10.9"	N45°59'39.2"
PPIR-50-01	.	.	PC-M1	W72°30'56.2"	N45°56'46.8"
PPIR-50-02	.	.	PC-M2	W72°31'11.6"	N45°57'28.9"
PPIR-50-03	.	.	PC-M3	W72°32'14.6"	N45°56'57.8"
PPIR-50-04	.	.	PC-M4	W72°31'35.2"	N45°56'44.7"
PPIR-50-05	.	.	PC-M5	W72°31'27.6"	N45°56'33.6"
PPIR-50-06	.	.	PC-M6	W72°32'05.6	N45°57'35.1"
<i>Outaouais</i>					
A-LBLANC01	OGF1	.	.	W75°17'46.3"	N45°42'52.4"
A-LECL01	OGF2	.	.	W75°24'02.8"	N45°52'48.6"
A-MLEF01	OGF3	.	.	W74°59'55.2"	N46°06'53.9"
A-MLEF02	OGF4	.	.	W75°00'56.0"	N46°06'54.7"
A-PPB01	OGF5	.	.	W75°43'04.6"	N46°06'06.0"
A-TUCKER01	OGF6	.	.	W75°47'54.6"	N45°56'46.9"
CJ2-A01	RSH1	.	.	W75°24'07.5"	N45°46'40.0"
CJ2-A02	RSH2	.	.	W75°24'05.8"	N45°46'27.8"

(suite)	Chapitre 2	Chapitre 3	Chapitre 4	Longitude	Latitude
CJ2-G01	RSH3	.	.	W75°31'29.4"	N45°56'56.1"
CJ2-L02	RSH4	.	.	W75°07'53.9"	N45°56'23.4"
CJ2-L03	RSH5	.	.	W75°47'43.0"	N45°52'37.8"
CJ2-S01	RSH6	.	.	W74°58'44.5"	N46°07'16.5"
CJ90-LCL01	OSH1	.	.	W75°15'00.4"	N45°52'49.3"
CJ90-LPR01	OSH2	.	.	W75°03'25.3"	N46°02'32.2"
CJ90-LVE01	OSH3	.	.	W75°14'48.8"	N45°51'33.2"
CJ90-MLEF01	OSH4	.	.	W75°00'38.0"	N46°05'12.1"
CJ90-MLEF02	OSH5	.	.	W75°00'24.8"	N46°05'54.3"
CJ90-STC01	OSH6	.	.	W75°50'38.3"	N45°48'13.8"

Voir les chapitres respectifs pour la définition des codes.

Annexe 3

Spectre biologique des stations du chapitre 2

Spectre biologique* des stations du chapitre 2

Haut Saint-Laurent

Station	UND1	PAS1	PAS2	UND2	PAS3	ACE1	UND3	PAS4	UND4	ACE2	ACE3	ACE4
RA_ch	0.0	0.0	0.0	0.3	0.0	0.0	0.0	1.0	0.0	0.4	0.4	0.4
RA_h	5.7	1.4	11.1	37.7	7.3	10.4	15.3	6.9	11.2	16.5	14.8	8.8
RA_g	38.7	20.7	18.1	28.2	32.0	13.5	46.0	19.1	39.9	38.4	21.9	45.4
RA_mc	4.1	17.8	8.2	4.3	7.6	2.7	2.0	9.7	2.4	1.7	5.3	1.7
RA_mg	51.4	60.1	62.6	29.5	52.9	73.4	36.7	62.5	46.6	42.2	57.2	43.7
RA_t	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.8	0.4	0.0
PER_1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	4.2	1.1	0.0
PER_2	0.0	0.0	0.2	0.0	0.3	0.4	0.6	0.3	0.0	0.8	0.0	0.0
PER_3	99.7	100.0	99.8	100.0	99.7	99.6	99.4	99.0	100.0	94.9	98.9	100.0
PFO	2.2	1.0	3.2	11.8	3.5	3.1	4.3	2.1	0.5	1.7	1.1	1.9
SFO_el	3.8	1.9	4.0	7.5	8.8	3.5	13.3	10.1	10.7	16.5	12.7	23.7
SFO_de	0.6	0.0	0.2	7.2	1.5	1.2	1.7	2.1	4.5	3.8	4.6	4.6
SFO_e	6.0	0.5	4.2	18.7	1.3	8.1	16.5	2.4	1.0	7.2	3.5	2.5
SFO_um	8.3	9.6	5.0	4.6	22.9	3.5	12.7	1.0	24.2	19.4	9.9	1.3
SFO_vi	2.9	0.5	0.2	0.0	0.5	0.8	0.3	2.1	1.7	4.2	2.1	0.0

(suite)	UND1	PAS1	PAS2	UND2	PAS3	ACE1	UND3	PAS4	UND4	ACE2	ACE3	ACE4
SFO_g	25.1	9.1	13.9	25.6	1.5	5.8	14.7	10.1	4.8	2.1	1.8	21.4
SFO_me	0.6	1.9	1.0	0.7	5.3	0.4	0.6	1.4	0.2	0.0	0.0	0.2
SFO_ms	49.8	74.0	64.9	29.5	52.4	73.0	36.7	61.5	45.4	41.8	58.7	44.5
SFO_nl	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2
SFO_mu	2.5	1.4	4.7	3.6	2.3	1.9	1.2	7.3	1.7	1.3	2.8	0.6
SFO_r	0.3	1.0	2.0	2.6	3.5	1.9	2.3	2.1	5.7	3.8	3.9	0.8
DEF	1.3	2.4	2.0	7.5	6.3	2.3	1.4	4.2	3.8	3.8	6.0	4.2
FPH_su	10.6	5.8	11.9	33.4	10.5	18.5	11.4	14.1	17.3	23.8	19.1	10.7
FPH_sp	86.2	93.8	86.9	64.9	88.3	78.8	84.8	82.5	78.4	74.1	77.4	87.4
FPH_sf	3.2	0.5	1.2	1.6	1.3	2.7	3.8	3.5	4.3	2.1	3.5	1.9
POL_a	48.6	56.7	64.4	40.3	51.6	66.4	39.0	61.1	44.7	41.4	51.6	42.2
POL_b	54.6	82.7	54.5	66.6	67.5	59.1	55.8	62.5	69.1	78.5	70.3	46.2
POL_n	2.9	9.6	5.7	1.3	8.6	1.5	9.2	3.5	2.6	19.8	9.9	0.0
POL_na	4.8	0.0	0.2	13.8	0.5	6.9	5.8	1.7	0.5	4.2	1.8	2.1
DI_w	58.4	69.2	66.3	53.4	62.2	82.2	51.4	64.6	69.6	64.1	69.3	35.7
DI_ez	9.2	24.5	20.5	26.2	17.1	16.6	7.2	11.5	11.9	35.4	26.5	22.3
DI_zz	1.9	0.5	1.7	0.3	3.5	1.9	1.4	5.2	8.3	8.0	4.6	0.2
DI_an	30.2	10.1	19.3	27.5	20.4	8.1	41.6	10.4	7.8	6.8	5.7	43.1

DI.bi	8.3	20.2	17.3	19.7	10.8	7.3	5.5	19.1	12.8	9.3	13.1	20.4
DI.ex	4.8	0.0	0.2	14.1	3.0	8.1	15.6	2.1	2.6	6.8	4.6	23.1
DI.hd	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.4	0.0	0.0
SE_1	34.3	12.5	19.8	31.5	26.4	9.3	32.4	14.6	9.7	13.9	8.1	21.2
SE_m	7.3	2.9	7.4	20.3	11.3	7.3	20.5	13.5	38.2	17.3	17.3	29.6
SE_s	0.3	0.5	0.5	3.3	1.0	2.7	2.9	2.8	3.3	2.5	3.9	1.7
SE_vs	4.8	0.5	0.5	13.8	0.5	7.3	6.4	3.1	1.7	4.6	1.8	2.1
SE_xl	53.0	83.7	69.3	30.5	60.5	73.4	37.6	65.6	46.6	61.2	68.9	45.0
DO_nd	0.6	0.5	1.0	1.0	0.0	3.1	0.6	0.3	1.7	3.8	7.8	0.4
DO_sc	2.5	2.9	3.7	2.6	3.0	8.1	1.2	1.4	3.6	5.9	8.1	2.1
DO_dp	93.0	88.0	91.6	74.1	96.7	86.5	89.0	91.7	95.2	84.8	85.2	94.3
LUM_i	25.2	11.1	11.4	26.6	6.7	9.7	23.8	14.4	30.6	7.0	7.6	45.8
LUM_m	31.3	16.8	41.3	16.2	35.6	20.3	29.0	16.3	19.5	14.6	15.7	6.5
LUM_s	43.2	72.1	47.3	56.6	57.4	69.7	46.8	68.9	46.6	77.6	75.3	46.8
STA	0.0	0.5	1.0	1.6	1.3	0.8	1.2	2.4	1.7	3.8	1.1	0.2
REP_gr	0.3	1.9	1.7	1.0	3.0	1.5	2.0	3.1	1.4	5.9	1.8	0.4
REP_ms	39.7	36.5	27.0	56.1	26.2	20.8	43.4	29.5	45.6	50.2	39.9	66.0
REP_ve	54.9	59.1	65.6	31.1	66.8	73.7	49.4	60.8	46.1	38.8	49.5	30.9

* Occurrence relative des traits pour chacune des stations (Division par l'abondance totale des espèces d'une même station, puis multiplié par 100). Voir le chapitre 2 pour les codes des stations (Table 2.2) et des traits (Table 2.3).

Outaouais

Station	OGF1	OGF2	OGF3	OGF4	OGF5	OGF6	RSH1	RSH2	RSH3	RSH4	RSH5	RSH6	OSH1	OSH2	OSH3	OSH4	OSH5	OSH6
RA_ch	0.0	14.6	0.3	3.9	0.7	0.0	0.3	0.8	0.6	0.3	0.0	1.0	0.2	0.8	0.9	1.9	3.0	0.6
RA_h	8.1	5.0	9.1	12.6	2.3	9.3	23.3	31.0	43.2	28.9	9.4	15.2	41.6	5.8	9.2	0.7	5.5	7.9
RA_g	43.6	22.5	30.0	27.0	27.2	37.7	20.7	25.0	19.4	25.6	24.9	7.6	19.8	20.7	18.4	6.7	13.1	31.1
RA_mc	2.6	7.6	3.4	9.0	8.7	1.9	5.3	3.8	7.0	8.1	0.9	7.1	3.3	3.7	9.8	1.5	4.2	6.7
RA_mg	45.6	50.3	57.1	46.9	61.1	51.1	48.8	38.4	29.1	37.2	64.5	68.2	33.6	69.1	61.7	89.1	74.3	53.3
RA_t	0.0	0.0	0.0	0.6	0.0	0.0	1.6	1.0	0.8	0.0	0.3	1.0	1.6	0.0	0.0	0.0	0.0	0.3
PER_1	0.0	0.0	0.0	0.6	0.0	0.0	1.6	1.0	0.8	0.0	0.3	1.0	1.6	0.0	0.0	0.0	0.0	0.3
PER_2	0.0	0.0	0.0	0.0	0.0	0.0	0.8	2.2	1.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PER_3	100.0	100.0	100.0	99.4	100.0	100.0	97.6	96.8	98.1	99.7	99.7	99.0	98.4	100.0	100.0	100.0	100.0	99.7
PFO	0.3	18.7	3.7	11.8	1.7	3.8	4.2	6.2	5.1	3.8	0.6	5.6	7.5	4.2	5.0	4.9	5.1	4.8
SFO_el	8.8	1.5	0.9	3.7	3.4	3.8	4.2	6.0	9.1	8.4	3.8	6.1	9.8	2.4	3.9	3.4	5.9	9.8
SFO_de	6.5	15.5	3.1	6.2	2.3	2.2	7.4	15.3	23.6	15.7	4.7	11.1	13.7	2.1	4.2	2.6	4.6	3.2
SFO_e	2.3	5.0	4.6	12.6	3.4	16.0	10.3	12.9	11.4	6.6	2.1	3.5	18.3	4.2	5.6	0.4	3.8	7.9
SFO_um	6.5	0.6	4.3	0.6	1.7	1.0	1.9	4.2	0.2	0.3	0.6	1.5	1.0	1.3	1.5	1.9	3.0	3.2
SFO_vi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SFO_g	25.7	19.0	26.3	20.2	18.1	22.4	19.1	14.1	22.3	22.3	1.5	13.4	17.0	13.1	0.7	3.8	14.9	
SFO_me	1.3	0.3	0.0	0.3	0.0	0.0	1.3	0.6	1.0	1.0	0.3	10.6	0.3	2.1	0.3	2.6	0.8	0.3
SFO_ms	45.3	57.0	59.4	53.7	68.8	51.4	49.6	38.0	28.3	36.7	64.2	57.6	34.9	69.6	68.2	86.9	76.8	57.1
SFO_nl	0.0	0.3	0.3	0.3	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.2	0.3	0.0	0.4	0.4	0.0	0.0
SFO_mu	1.6	0.6	1.1	2.0	1.0	1.6	3.2	3.6	6.8	7.6	0.9	7.1	1.6	1.0	3.0	1.1	0.8	2.5

(suite)	OGF1	OGF2	OGF3	OGF4	OGF5	OGF6	RSH1	RSH2	RSH3	RSH4	RSH5	RSH6	OSH1	OSH2	OSH3	OSH4	OSH5	OSH6
SFO_r	2.0	0.3	0.0	0.6	0.7	1.3	2.9	5.2	5.5	1.5	1.2	1.0	6.7	0.0	0.3	0.0	0.0	1.0
DEF	0.3	0.0	1.7	0.8	0.7	1.3	6.6	8.0	14.8	16.2	3.2	8.1	6.5	0.8	1.5	0.4	0.4	1.9
FPH_su	5.0	5.0	8.6	13.5	3.0	7.8	19.1	30.6	34.6	27.6	8.5	14.9	33.6	7.2	7.6	1.5	6.5	9.7
FPH_sp	92.0	94.7	91.1	86.2	96.6	90.9	78.8	67.4	63.1	70.6	90.3	84.1	63.7	91.5	91.2	98.1	92.6	89.4
FPH_sf	2.9	0.3	0.3	0.3	1.3	2.1	2.0	2.3	1.8	1.2	1.0	2.8	1.3	1.2	0.4	0.8	1.0	0.0
POL_a	48.2	51.2	59.4	47.8	62.1	51.8	51.2	42.5	32.7	41.3	64.8	62.1	36.7	68.6	63.8	89.5	75.5	53.3
POL_b	68.1	52.9	70.3	66.0	59.1	55.6	63.4	65.4	71.5	56.7	56.6	62.1	61.5	58.4	65.0	62.5	49.4	62.9
POL_n	1.0	0.0	0.3	0.8	0.0	1.0	2.1	2.8	1.1	0.5	0.9	2.5	0.7	0.5	1.2	0.7	0.4	1.3
POL_na	0.3	17.8	4.6	13.5	2.3	5.4	4.5	4.6	5.7	6.3	0.6	4.0	11.1	5.0	5.3	1.9	3.4	5.7
DI_w	37.8	43.9	55.7	48.0	32.9	28.1	39.0	49.7	37.5	34.7	41.1	41.4	50.7	58.9	50.1	63.7	38.0	49.8
DI_ez	21.2	27.8	14.0	19.4	35.2	37.1	36.6	24.1	32.5	29.1	35.5	52.0	27.0	19.9	30.6	35.6	51.9	21.0
DI_zz	0.7	0.0	0.0	0.8	0.3	0.6	0.3	0.6	3.2	0.3	0.3	0.0	3.8	0.0	0.3	0.0	0.4	0.6
DI_an	35.5	21.1	24.6	22.2	32.9	23.6	21.5	22.4	27.3	24.6	3.0	20.1	18.3	14.8	1.5	4.6	23.2	22.5
DI_hi	18.6	33.9	14.9	23.3	41.9	34.2	35.8	21.3	34.2	39.7	33.7	50.0	23.6	22.3	30.6	30.3	49.4	20.3
DI_ex	2.6	5.8	4.3	13.2	6.0	6.7	8.5	8.0	13.3	12.7	2.1	4.5	17.7	5.5	5.0	0.4	3.4	12.1
DI_hd	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0
SE_l	38.8	20.8	26.3	22.8	19.5	26.5	22.5	19.3	13.5	25.3	23.5	5.1	17.3	25.7	17.8	3.0	7.2	20.3
SE_m	11.1	3.8	4.0	5.6	6.4	14.7	13.8	21.5	38.4	25.6	9.4	20.2	24.5	5.0	6.8	4.5	9.3	15.9
SE_s	2.9	0.3	4.0	2.2	1.0	0.6	7.7	14.7	10.1	2.8	1.2	2.5	12.6	2.1	1.5	0.4	2.1	1.0
SE_vs	0.7	18.1	4.9	14.3	3.4	5.8	4.8	4.8	6.1	6.6	0.9	4.5	11.5	5.5	5.3	2.6	4.2	6.3
SE_xl	46.3	57.0	59.1	55.1	69.8	52.1	50.7	39.0	30.8	38.2	64.5	67.2	33.4	61.5	68.2	89.5	76.8	56.2
DO_nd	2.0	0.0	4.0	0.0	0.3	1.3	2.6	2.3	0.8	0.0	1.5	0.2	1.6	0.3	0.7	0.8	0.0	0.0
DO_sc	1.3	0.6	2.0	1.7	0.3	1.3	9.0	9.3	16.2	2.5	2.6	0.5	9.8	0.5	1.8	0.4	0.8	1.6

(suite)	OGF1	OGF2	OGF3	OGF4	OGF5	OGF6	RSH1	RSH2	RSH3	RSH4	RSH5	RSH6	OSH1	OSH2	OSH3	OSH4	OSH5	OSH6
DO_dp	94.1	80.7	89.7	81.7	95.3	81.8	86.7	73.4	77.0	76.7	93.8	83.8	77.1	90.8	95.1	91.6	88.3	
LUM_i	27.5	19.9	26.6	20.2	20.8	23.2	27.3	24.3	32.7	38.7	26.4	18.4	18.3	20.5	15.3	0.0	3.6	24.3
LUM_m	15.1	1.2	5.1	3.7	2.2	12.3	12.5	16.3	16.2	14.2	4.5	10.4	16.4	15.6	5.5	7.5	5.3	5.7
LUM_s	57.3	78.9	68.3	76.1	76.7	64.5	59.4	53.7	50.2	41.0	68.8	71.2	65.0	63.9	79.2	92.5	91.1	69.7
STA	0.3	0.0	0.0	0.3	0.0	0.6	1.1	5.4	2.5	1.3	0.9	1.5	0.7	0.3	0.0	0.4	0.4	0.6
REP_gr	0.3	0.3	0.0	0.8	0.0	0.6	2.7	3.8	2.5	0.5	0.9	2.0	2.0	0.5	1.2	0.4	0.8	1.0
REP_ms	58.0	73.7	49.7	63.5	67.8	74.1	63.4	54.3	66.2	72.7	58.9	54.0	62.4	43.7	55.5	36.0	64.1	54.0
REP_ve	37.8	24.9	49.1	34.3	30.2	22.7	30.0	34.8	24.0	23.0	37.8	42.4	28.3	53.9	42.4	62.5	32.9	41.3

* Occurrence relative des traits pour chacune des stations (Division par l'abondance totale des espèces d'une même station, puis multiplié par 100). Voir le chapitre 2 pour les codes des stations (Table 2.2) et des traits (Table 2.3).

