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Le paysage comme espace conceptuel et fonctionnel en écologie: analyse des composantes végétales de paysages agroforestiers

par

Sylvie de Blois

Département de sciences biologiques

Faculté des arts et des sciences

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présentée par :

Sylvie de Blois

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Président-rapporteur	Luc Brouillet	Sciences biologiques
Directeur de recherche	André Bouchard	Sciences biologiques
Codirecteur	Gérald Domon	Aménagement
Membre du jury	Danielle Marceau	Géographie
Examinateur externe	Richard J. Hobbs	Professor and Chair School of Env. Sc. Murdoch University Australia

Thèse acceptée le : ....

SOMMAIRE

Cette thèse définit le concept de paysage en relation à l'écologie végétale et évalue l'influence relative des différents déterminants de la variabilité floristique pour les composantes structurales de paysages agroforestiers. Ces objectifs sont développés en trois volets. Un premier volet conceptuel pose la question de l'utilisation de la notion de paysage en écologie végétale et fait la synthèse des différents courants épistémologiques qui ont marqué son évolution. Les deuxième et troisième volets évaluent l'influence relative de différents jeux de facteurs explicatifs de la variabilité végétale pour deux composantes structurales des paysages : les îlots de végétation non-cultivés et les haies. Ces composantes sont examinées pour des paysages du sud-ouest du Québec qui contrastent par la configuration de leurs dépôts géomorphologiques et l'intensité des activités agricoles.

Pour le volet conceptuel, les rapports entre paysage et végétation sont analysés sous trois angles : 1) celui de la prédominance des conditions environnementales ; 2) celui de l'importance des perturbations, principalement celles d'origine anthropique; 3) et enfin celui de l'influence de la structure spatiale sur la végétation.

Dans le deuxième volet, un modèle de relations entre les déterminants environnemental, historique et spatial de la variabilité floristique des îlots de végétation non-cultivés est proposé et testé pour deux paysages. J'ai évalué les relations séparément pour les espèces arborescentes et les espèces arbustives et

herbacées à l'aide des tests partiels de Mantel et de l'analyse des coefficients de direction.

Le troisième volet considère une des composantes importantes de la diversité floristique en milieu agricole : les haies. Les espèces herbacées et arbustives sont échantillonnées dans ces structures linéaires afin d'évaluer l'effet des variables environnementales, de l'historique des interventions et de la nature des occupations du sol adjacentes sur la répartition des espèces. J'ai utilisé l'analyse canonique partielle des correspondances afin de départager l'influence relative de jeux de variables et de comprendre leur interrelation. L'analyse tient compte aussi des relations spatiales entre les sites échantillonnés.

Suite à l'analyse du concept de paysage en écologie végétale, je soulève trois aspects en particulier, chacun devant faire l'objet d'investigations futures afin d'améliorer les connaissances, incluant : 1) la capacité d'évaluer l'importance relative de processus multiples agissant à de grandes échelles spatiales ; 2) le besoin d'une meilleure évaluation de la réelle importance de la configuration spatiale des paysages pour les espèces végétales; 3) et enfin la reconnaissance des rapports entre nature et culture, particulièrement en ce qui a trait à la gestion de la végétation dans les paysages anthropiques.

Enfin, les résultats des analyses des paysages montrent que dans une mosaïque agricole où les activités de production ont des intensités variables, la végétation est le produit d'interactions complexes entre les contraintes imposées par les conditions

environnementales, l'historique d'occupation des sols et les pratiques d'aménagement, et le contexte spatial. De plus l'importance relative de ces facteurs et les modèles d'interaction entre ces derniers et la végétation varient à la fois en fonction des échelles d'observation, des attributs des espèces (arbres vs arbustes et herbacées), et finalement de la nature des composantes du paysage considérées (îlots vs haies).

Mots-clés : Écologie du paysage; écologie végétale; paysage agricole; paysage agroforestier; modèle de végétation; îlot; haie; Haut-Saint-Laurent.

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

REMERCIEMENTS

Il est inévitable à la fin d'une longue démarche comme celle-ci de se demander pourquoi donc avoir choisi d'étudier la végétation des paysages du sud-ouest du Québec dont les charmes sont plutôt ... comment dire ... subtils ? Au-delà des considérations scientifiques bien légitimes, risquons une interprétation psychanalytique pour expliquer un comportement qu'on peut presque considérer comme déviant dans cette ère de productivisme effréné. Il faut donc remonter à l'enfance. Je me rappelle que juste derrière la maison familiale près de Québec commençait une joyeuse exubérance végétale renfermant des trésors cachés et mille petits dangers tous plus délicieux à affronter les uns que les autres. Au centre de cet univers, un ruisseau tranquille bordé d'une haie touffue d'arbustes dont on savourait les fruits. La savoureuse amertume des cerises noires et sauvages, l'involucre pubescent des noisettes, la menace griffue des aubépines aux insipides mais comment séduisants fruits écarlates, le dard cinglant des guêpes ou la danse saccadée des « patineuses » à la surface de l'eau, tout contribuait à aiguiser les sens, à éveiller la curiosité dans cette complice anarchie végétale qui contrastait subversivement avec la pelouse familiale. Au-dessus de cet univers grouillant régnait un pin qui me paraissait géant, refuge arborescent idéal pour s'adonner à la contemplation silencieuse du monde comme seuls les enfants savent le faire. Et, oh bonheur, pas un seul nom latin pour venir troubler la joyeuse innocence de ce microcosme vivant et vibrant de sensations et d'odeurs ...

Si j'avais pu m'envoler de mon pin géant peut-être centenaire (ce n'est pas faute d'avoir essayé!) pour survoler ma « forêt » mythique, j'aurais pu voir qu'elle n'était qu'une fragile bande de végétation riveraine, dernier vestige d'une nature insoumise coincée entre la banlieue envahissante et la campagne agonisante. Avec le temps, le ruisseau a disparu pour laisser place à l'ordre sage des maisons alignées et des pelouses manicurées où le jaune mutin du moindre pissenlit devient séditieux. Dans ma quête effrénée de savoir, les noisetiers sont devenus *Corylus* et les cerisiers *Prunus*. Mais il reste encore, de ces longues heures insouciantes passées dans la contemplation heureuse de ce petit monde aussi éphémère que l'enfance, une émotion réelle qui s'attache maintenant à toute nature, si soumise soit-elle. C'est cet esprit qui m'a amenée à l'écologie…

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Enfin à toi éternellement petit Jérôme (1990-2000) pour la beauté de l'éphémère ...

Chapitre 1

INTRODUCTION GÉNÉRALE

MISE EN CONTEXTE GLOBALE

Il y a présentement en écologie et dans certaines disciplines connexes peu de concepts aussi équivoques que celui de paysage [1]. Tout effort pour le définir de façon définitive et le réduire à des dimensions étroites se bute inévitablement à la critique (Wiens 1999a ; 1999b). Certains y voient une notion purement spatiale qui met l'accent sur les patrons d'organisation dans l'espace d'entités définies par leur forme, leur composition, ou leur fonction (e.g., îlot, matrice, corridors, champs, forêt, etc.) en cherchant à les quantifier et à élucider les processus qui les ont créés (O'Neill et al. 1988; Turner 1990; Pan et al. 1999), ou encore à comprendre comment ces patrons jouent à leur tour un rôle dans la régulation des processus écologiques (Kareiva & Wennergren 1995). C'est le paysage comme mosaïque d'écosystèmes en interaction (Forman 1995 ; Pickett & Cadenasso 1995). D'un point de vue écosystémique, ce paysage peut être appréhendé comme un niveau d'organisation hiérarchique, un système écologique avec une dynamique propre, au même titre que les écosystèmes ou les populations qui le composent (O'Neill et al. 1986). Cette approche systémique est cependant remise en question par les auteurs même qui l'ont proposée (O'Neill 1999).

D'autres travaux mettent l'accent sur le paysage comme lieu d'interaction entre les processus naturels et les activités humaines. En effet, peu de systèmes écologiques n'ont pas été soumis à une quelconque influence anthropique. Les perceptions et les

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[1] Pour une revue des fondements épistémologiques voir Turner (1989), Naveh & Lieberman (1994), Forman (1995).

modes d'exploitation du territoire (Domon et al. 1993; Foster et al. 1998; Kline & Wichelns 1998 ; Macdonald & Jonhson 2000), les impératifs économiques (Turner et al. 1996), voire le rapport même des sociétés à la nature (Naveh & Lieberman 1994) doivent être pris en compte dans les modèles écologiques. À son tour, l'écologie doit éclairer les pratiques d'aménagement. Loin d'éviter les perturbations que les activités humaines engendrent et de limiter les études écologiques aux seuls territoires " naturels ", on cherche plutôt à prendre pleinement en compte la dimension humaine dans l'étude de territoires où l'antagonisme production/conservation est souvent exacerbé (Burel 1996; Bouchard & Domon 1997; Baudry et al. 2000; Hobbs & Yates 2000). C'est le cas de l'espace rural, par exemple, où le maintien de la biodiversité est souvent perçu comme une contrainte à la production. Plus qu'une simple structure, le paysage a aussi une vocation économique et sociale, et son évolution dépend d'une vision qui s'inspire du souci de réconcilier nature et culture (Hobbs 2000 ; Hobbs & Harris 2000). La volonté d'appliquer les avancées conceptuelles à la résolution de problèmes concrets à l'échelle locale demeure une préoccupation centrale (Wiens 1999a). Le paysage, ici pris dans son sens large de région ou de territoire, est alors défini par des objectifs de gestion et d'aménagement.

De quels courants se revendique cette thèse ? D'abord, malgré une tendance à les opposer, les dimensions mentionnées dans le précédent paragraphe sont loin d'être mutuellement exclusives. L'écologie du paysage est un champ de recherche au carrefour de nombreuses disciplines et c'est justement dans la multiplicité des approches qu'elle trouve tout son sens. De façon générale, la vision large inspirée des multiples courants de l'écologie du paysage dans laquelle s'inscrit cette thèse se caractérise par les traits suivants : 1) elle se nourrit de la pluralité des influences qu'elle cherche à intégrer plutôt qu'à opposer et invite une vision interdisciplinaire des phénomènes ; 2) elle reconnaît la valeur unique des particularités locales où s'expriment les relations complexes entre nature et culture ; 3) elle porte une attention particulière à l'hétérogénéité de la végétation et aux interrelations entre les multiples déterminants de cette hétérogénéité à l'échelle du paysage ; 4) elle a le souci de réconcilier théorie et pratique, chaque aspect étant perçu comme nourrissant l'autre. Voilà donc posés les grands principes qui ont inspiré cette thèse et tout le cheminement scientifique et humain qu'elle implique.

LE PAYSAGE COMME ESPACE CONCEPTUEL ET FONCTIONNEL EN ÉCOLOGIE VÉGÉTALE

Si le champ de l'écologie du paysage demeure vaste et que les approches qu'elle préconise s'inspirent de plusieurs courants, il n'en demeure pas moins qu'il a fallu en arriver à une définition plus étroite du paysage dans le cadre de cette recherche. Cette définition passe par un volet conceptuel et un volet fonctionnel. D'abord il faut souligner que le paysage est perçu avant tout dans cette thèse du point de vue de l'écologiste végétale. Or, une revue exhaustive de la littérature en préparation de cette recherche a montré que la notion de paysage demeurait encore mal définie en écologie végétale par rapport à son utilisation en écologie animale. Un premier volet théorique explore donc les rapports entre le concept de paysage et l'écologie végétale et revoit les principaux courants historiques qui contribuent à définir le paysage en relation aux problématiques végétales. C'est le paysage comme espace conceptuel en écologie végétale.

Pour ce qui est d'une définition fonctionnelle, ou encore du paysage dans l'espace réel, il se caractérise par les traits suivants. C'est avant tout une mosaïque composée d'éléments distincts : une matrice, des îlots, des structures linéaires. La matrice est l'élément prépondérant par sa superficie et par le contrôle qu'elle exerce sur la dynamique globale du paysage. Elle est, à l'échelle où nous avons défini nos paysages, parfois boisée, parfois cultivée. Les îlots ont une dynamique individuelle déterminée par les conditions abiotiques et l'histoire, mais cette dynamique peut aussi être influencée par le contexte spatial dans lequel l'îlot se retrouve. Enfin les éléments linéaires se distinguent des îlots par leur structure – ce sont des éléments dont la longueur est de loin supérieure à la largeur – mais ils sont perçus a priori comme des habitats supplémentaires, souvent négligés dans l'évaluation écologique, pouvant agir potentiellement comme des corridors facilitant la dispersion d'espèces ou contrôlant les flux écologiques. Enfin tous ces éléments structurels sont considérés du point de vue de leur composition végétale.

Le deuxième trait déterminant des paysages explorés ici est leur vocation avant tout agricole, l'exploitation forestière y étant des plus marginales et à caractère privé. Cela implique que la végétation y subit directement ou indirectement l'influence des activités reliées à cette vocation (culture, pâturage, coupe sélective, entretien des marges non cultivées, etc.). Ici il faut préciser que le fait de mettre l'accent sur le caractère agricole de ce paysage implique un changement de perspective, pour ne pas dire de paradigme, par rapport aux études antérieures de végétation dans ce territoire (voir Sites d'étude plus bas). La végétation a d'abord été analysée comme la composante d'une phase ou d'un type écologique dans une perspective de cartographie écologique permettant de quantifier le potentiel forestier des sites (Bouchard et al. 1985 ; Meilleur et al. 1994; Nolet et al. 1995). On a aussi mis l'accent sur son caractère " naturel ", i.e. son rapport à une certaine idée de la forêt climacique ancienne (Bouchard et al. 1989; Simard & Bouchard 1996) qui dominait certains dépôts géomorphologiques avant la colonisation (Brisson et al. 1988; Brisson et al. 1992). Alors que ces approches impliquent nécessairement une vision forestière du paysage, ici la végétation devient aussi une composante de l'agroécosystème. Son étude pose alors inévitablement la question des rapports entre la conservation et la gestion d'une certaine diversité végétale - et des structures qui lui sont associées (e.g., marges non cultivées) - et les pratiques agricoles dans ce territoire.

Enfin, à travers toutes ces perspectives, l'accent est mis sur un aspect central à toute la formulation des problématiques soulevées dans cette thèse : l'importance d'évaluer les interactions entre les différents facteurs explicatifs de la variabilité végétale, et ce à l'échelle du paysage, i.e. en tenant compte autant des propriétés verticales d'un site (i.e. conditions édaphiques, perturbations) que de l'influence du contexte spatial dans lequel se trouve ce site. En ce qui a trait à sa mosaïque végétale, le paysage se distingue donc non seulement par la configuration de ces éléments (i.e. sa structure), mais aussi par la nature et l'importance relative des processus déterminants de cette structure. Cela implique l'utilisation d'outils d'analyses qui permettent de prendre en compte l'effet multiple de jeux complexes de variables qui varient simultanément dans le temps et l'espace et de départager, du moins statistiquement, leur effet relatif.

ÉNONCÉ DE LA PROBLÉMATIQUE

Cette thèse définit le concept de paysage en relation à l'écologie végétale et évalue l'influence relative des différents déterminants de la variabilité floristique pour les composantes structurelles de paysages agroforestiers. Ces objectifs sont développés en trois volets. Un premier volet conceptuel pose le problème de l'utilisation de la notion de paysage en écologie végétale et fait la synthèse des différents courants épistémologiques qui ont marqué son évolution. Les rapports entre paysage et végétation sont analysés sous trois angles : 1) celui de la prédominance des variables environnementales ; 2) celui de l'importance des perturbations, qu'elles soient naturelles ou anthropiques ; 3) et enfin celui de l'importance de la structure spatiale sur la végétation et les processus écologiques.

Le deuxième volet propose et teste un modèle de relation entre les déterminants environnemental, historique et spatial de la variabilité végétale dans deux paysages contrastant par la configuration de leurs dépôts géomorphologiques et l'intensité des activités agricoles. Des sites non-cultivés de végétation dans chacun de ces paysages sont échantillonnés afin de tester les hypothèses suivantes :

1. Les paysages se distinguent sur la base des caractéristiques environnementales, historiques et du contexte spatial des sites de végétation.

2. Les variables environnementales, l'historique de l'utilisation des sites et le contexte spatial influencent à divers degré la répartition des peuplements végétaux.
3. Ces jeux de facteurs explicatifs covarient dans le temps et l'espace.
4. L'importance relative de chacun des jeux de facteurs et la nature de leur interrelation varient en fonction de la structure spatiale des paysages.
5. L'importance relative de chacun des jeux de facteurs et la nature de leur interrelation varient en fonction de l'étendue des paysages.
6. L'importance relative de chacun des jeux de facteurs et la nature de leur interrelation varient en fonction du type de végétation considéré (i.e. les espèces arbustives et herbacées vs les espèces arborescentes).

Un troisième volet considère un des vecteurs importants de la diversité floristique en milieu agricole : les haies. Ces éléments du paysage sont étudiés sous l'angle de leur dynamique dans le temps et l'espace (Schmucki et al. en prép.) et de leur composition floristique. La végétation arbustive et herbacée des haies est échantillonnée afin de répondre aux hypothèses suivantes :

1. La composition floristique de la strate herbacée et arbustive des haies varie en fonction des caractéristiques environnementales, incluant le type de dépôt et la largeur des haies.
2. La composition floristique de la strate herbacée et arbustive des haies varie en fonction de l'historique des interventions effectuées pour contrôler la strate arborescente.

3. La composition floristique de la strate herbacée et arbustive des haies en paysage agricole varie en fonction de la nature des occupations adjacentes.
4. Ces jeux de facteurs covarient dans le temps et l'espace, la nature de l'occupation des sols, par exemple, déterminant la fréquence des activités d'entretien ou la largeur de la haie.
5. La présence dans les haies d'espèces héliophiles potentiellement envahissantes des cultures dépend, dans des proportions variables, des facteurs explicatifs déjà mentionnés.
6. La présence dans les haies d'espèces sciaphiles caractéristiques des milieux forestiers dépend, dans des proportions variables, des facteurs explicatifs déjà mentionnés.

Afin de départager l'influence relative de jeux de variables et de comprendre leur interrelation, j'ai choisi, pour tester les hypothèses des volets 2 et 3, d'utiliser deux types d'analyse appartenant à la famille des régressions partielles ou des corrélations partielles: le test de Mantel partiel (Smouse et al. 1986) et l'analyse canonique partielle des correspondances (ter Braak 1987). Le test de Mantel permet de comparer des matrices de similarité ou de distance calculées pour les mêmes objets. Le calcul de matrices d'association entre les objets repose d'abord sur le choix d'un coefficient approprié de similarité ou de distance qui tient compte des propriétés des variables choisies. L'emploi de matrices de similarité générées à l'aide d'un coefficient qui exclut les double absences, par exemple, permet généralement une évaluation vraisemblable des liens de ressemblance entre les objets. Pour évaluer les relations entre les différentes propriétés des objets (espèces, environnement, composantes historiques ou spatiales, etc.), on utilise généralement la statistique de Mantel qui met en évidence les relations linéaires entre les différentes matrices. Si des relations plus complexes entre les variables explicatives et les espèces sont présentes, comme c'est souvent le cas, elles pourraient ne pas être détectées par la statistique de Mantel. Afin de détecter les relations non-linéaires entre les espèces et les variables explicatives, Dietz (1983) a suggéré plutôt l'utilisation d'un coefficient moins contraignant basé sur la corrélation de Spearman. L'utilisation de mesures d'association appropriées qui tiennent compte des caractéristiques mathématiques des variables ainsi que l'utilisation d'une statistique non-paramétrique comme celle de Spearman pour comparer les matrices entre elles pourrait permettre une évaluation plus juste des relations espèces -environnement. Par contre, comme les analyses sont effectuées à partir de matrices qui prennent simultanément en compte l'ensemble des variables échantillonnées, il peut en résulter une perte d'information quant à l'influence unique de chacune des variables. L'interprétation des corrélations entre des mesures de similarité ou de distances peut aussi poser des problèmes d'interprétation.

L'analyse canonique des correspondances, quant à elle, a l'avantage de procéder de manière plus directe que le test de Mantel pour mettre en relation les espèces et les variables explicatives. Elle permet, dans le cas qui nous intéresse, d'évaluer l'influence de chacune des variables, et de chacun des jeux de variables, sans passer par les matrices d'association et facilite donc l'interprétation des résultats. Cependant, l'analyse canonique des correspondances a été critiquée pour sa capacité à ne dégager que les relations linéaires entre les espèces et les variables explicatives.

Enfin, que ce soit avec les tests de Mantel ou les analyses de correspondance, les variantes partielles de ces analyses permettent de contrôler statistiquement l'effet de covariables. Cette étape est essentielle quant il s'agit de comprendre les liens complexes entre des facteurs structurants dont l'effet peut se mesurer à de larges échelles temporelles ou spatiales et qu'il est souvent impossible de contrôler expérimentalement.

SITE D'ÉTUDE

La présente recherche a été conduite dans une région administrative qui a fait l'objet de plusieurs études en écologie et en aménagement: la Municipalité Régionale de Comté du Haut-Saint-Laurent (Bouchard et al. 1985; Bouchard & Domon 1997). Les projets conduits dans cette région ont eu dès le départ le souci d'acquérir une connaissance écologique approfondie du territoire afin d'éclairer les pratiques de gestion et d'aménagement. Située dans la partie la plus méridionale du Québec, le Haut-Saint-Laurent jouit, à l'échelle du Québec, d'une biodiversité et d'une productivité potentielles appréciables qui se reflètent dans la présence d'espèces végétales méridionales comme *Carya cordiformis*, *Juglans cinerea* ou *Quercus macrocarpa*. Les premiers travaux initiés dans les années 80 ont trouvé leur fondement théorique dans l'approche de la cartographie écologique du territoire (Bouchard et al. 1985; Domon et al. 1989). La cartographie des variables géomorphologiques (Delage 1988; Bariteau 1988), puis leur mise en relation avec les communautés végétales (Meilleur et al. 1992; Meilleur et al. 1994) et avec l'utilisation passée et récente des sites (Paquette & Domon 1997; Pan et al. 1999), ont montré l'importance des facteurs abiotiques dans la structuration du paysage.

L'exploitation agricole du territoire s'est d'abord effectuée en ignorant, dans une certaine mesure, les contraintes imposées par les caractéristiques géomorphologiques des sites (Paquette & Domon 1997). Cependant, la modernisation des pratiques a aujourd'hui créé une structure caractérisée par la présence de végétation naturelle principalement sur dépôt glaciaire, alors que la plaine d'argile marine est dominée en grande partie par les cultures céréalières (Pan et al. 1999). Les boisés ont des superficies variables selon qu'ils se retrouvent dans un paysage où les dépôts glaciaires sont dominants ou dispersés dans une matrice de dépôt marin. Une connaissance approfondie de la géomorphologie de la région a donc permis de comprendre l'importance de ce facteur structurant sur l'organisation spatiale des unités de paysages (forêt, friche, champs etc.).

D'autres travaux ont mis en lumière le rôle prépondérant des perturbations, puisqu'une part de variance significative dans la composition de la végétation demeurait inexpliquée par les seules variables abiotiques. Nolet et al. (1995) ont d'ailleurs démontré les limites de la cartographie écologique dans un territoire fortement perturbé comme celui du Haut-Saint-Laurent. L'intégration des aspects historiques s'avérait donc essentielle dans la compréhension des facteurs qui régissent la dynamique des communautés végétales (Bergeron et al. 1988; Brisson et al. 1988; Jean & Bouchard 1991; de Blois & Bouchard 1995). L'approche originale utilisée dans l'étude des actes notariés relatant les ventes de bois (Bouchard et al. 1989; Simard & Bouchard 1996) et la découverte d'une forêt exceptionnelle (Brisson et al. 1992) ont permis de tracer le portrait de la forêt précoloniale et par le fait même de commencer à évaluer l'impact de l'utilisation du territoire sur la structure et la composition de la végétation actuelle. Ainsi des espèces qui ont été largement exploitées au 19ième siècle (e.g., *Quercus macrocarpa, Pinus strobus, Fagus grandifolia, Tsuga canadensis*) sont maintenant relativement peu abondantes dans le territoire. Les pertes d'habitats au profit de l'agriculture et les changements dans la structure et les conditions environnementales des sites pourraient expliquer la lenteur avec laquelle certaines de ces espèces recolonisent le paysage.

Alors que le déterminisme environnemental dominait la première génération d'études dans le Haut-St-Laurent, la végétation a commencé à être perçue dans certains travaux comme la résultante de différentes influences plus complexes agissant à des échelles temporelles ou spatiales variables. Jean & Bouchard (1993) ont démontré l'importance relative de deux jeux de facteurs agissant à différentes échelles spatiales sur la dynamique des milieux humides. Leduc et al. (1992) ont souligné, au-delà de l'nfluence des variables environnementales, l'effet d'une composante purement spatiale (i.e. matrice des distances géographiques entre les sites) sur la végétation arborescente d'une forêt continue de 50 hectares. Tout en s'inspirant de la richesse des travaux précédents, la présente thèse soulève, de façon originale, la question de l'utilisation de la notion de paysage en écologie végétale, tient compte de l'importance de la structure spatiale dans l'explication de la variabilité végétale, met particulièrement en lumière les interrelations entre les différentes composantes des paysages, et inscrit le tout dans un contexte plus agricole que forestier.

Chapitre 2

LANDSCAPE ISSUES IN PLANT ECOLOGY

Ce chapitre sera soumis pour publication sous forme d'article :

de Blois, S., G. Domon, & A. Bouchard. Landscape issues in plant ecology.

SUMMARY

In the last decade, we have seen the emergence and consolidation of a conceptual framework that recognizes the landscape as an ecological unit of interest. Plant ecologists have long emphasized landscape-scale issues, but there has been no recent attempt to define how landscape concepts are now integrated in vegetation studies. To help define common research paradigms in both landscape and plant ecology, we discuss issues related to three main landscape concepts in vegetation researches, reviewing theoretical influences and emphasizing recent developments. We first focus on environmental relationships, documenting how vegetation patterns emerge from the influence of local abiotic conditions. The landscape is an environmental space. Disturbances are then considered, with a particular attention to human-driven processes that often overrule natural dynamics. The landscape is a dynamic space. As environmental and historical processes generate heterogeneous patterns, we finally move on to stress current evidence relating spatial structure and vegetation dynamics. This relates to the concept of a landscape as a patch-corridor-matrix mosaic. Future challenges involve: 1) the capacity to evaluate the relative importance of multiple controlling processes at broad spatial scales; 2) better assessment of the real importance of the spatial configuration of landscape elements for plant species; 3) and finally, the integration of natural and cultural processes and the recognition of their interdependence in relation to vegetation management issues in anthropogenic landscapes.

Keywords: Anthropogenic landscape; landscape concept; landscape dynamics; landscape ecology; landscape structure; patch-corridor-matrix mosaic; plant ecology; spatial processes; vegetation studies.

INTRODUCTION

As a scientific discipline that emerged from biogeography (Von Humboldt & Bonpland 1805), plant ecology has always been rooted in a landscape perspective. Early interest was in the broad-scale distribution patterns of plant species, or plant species assemblages, in relation to major climatic gradients. Thereafter, from the pioneering work of Clements (1916) on successional dynamics to the studies of Watt (1947), Whittaker (1956) and Curtis (1959) in North American landscapes, the effort to understand vegetation patterns at the local scale have led to the formulation of general principles. Among those, the recognition of the structuring influence of environmental gradients and of natural disturbances have been two of the most influential. Specific processes acting at the population level have been proposed to account for emergent vegetation organization. Competition for limiting resources along stress and disturbance gradients has been especially emphasized (Grime 1979; Austin 1982; Tilman 1982; Weiher & Keddy 1999).

Recently we have seen the emergence and consolidation of a formalized conceptual framework that recognizes the landscape as an ecological unit of interest (Naveh & Lieberman 1994; Forman 1995). In ecology, a landscape approach is broadly characterized by an interest in the main causes and consequences of spatial heterogeneity and a focus on horizontal processes that cross boundaries and ecosystems (O'Neill et al. 1986; Urban et al. 1987; Turner 1989; Wiens et al. 1993; Pickett & Cadenasso 1995). The scale-dependency of ecological structure and phenomena is emphasized. Human-driven processes, in particular, are investigated along with natural ones. Of course, scientists and practitioners from various fields other than ecology share a concern with landscape issues. Ecologists, geographers, land-use planners and resource managers usually stress different aspects of the landscape, creating much lively debate about the very meaning of the landscape concept as a research paradigm. Consequently, the need for a unifying conceptual structure and for formalized theories in landscape ecology has been raised (Wiens 1999a; Wiens 1999b).

Even within a more strictly biological frame of reference, however, landscape concepts tend to be integrated differently. Recent animal studies clearly stress the effect of landscape structural components and habitat configuration on population processes (e.g., Bender et al. 1998; Fahrig & Jonsen 1998; McIntyre & Wiens 1999). Predictor variables describing the spatial arrangement or spatial characteristics of surrounding habitats have been included along site factors to predict with some success animal species responses (Mazerolle & Villard 1999). The spatial concept of a landscape as a patch-corridor-matrix mosaic and its significance for species movement has been especially appealing to animal ecologists. More and more animal population models account for spatial heterogeneity and movement in a patchy environment (Kareiva & Wennergren 1995) and have been scaled up to consider metapopulations– that is populations consisting of spatially-separate subpopulations connected by the dispersal of individuals (reviewed in Hanski & Gilpin 1997). In a mosaic unsuitable for the species under study, the functional significance of corridors and the related concept of connectivity have been investigated (Andreassen et al. 1998). Island biogeography theory (MacArthur & Wilson 1967), metapopulation theory (Levins 1970; Levin 1976; Hanski 1983), source-sink model (Pulliam 1988), percolation theory (O'Neill et al. 1988a; Johnson et al. 1992), and the focal species approach (Lambeck 1997) provide theoretical foundation and guidelines against which ideas can be assessed and experiments conducted to provide some conceptual integration of animal ecological studies at the landscape scale. Recent developments seem to have significantly improved our ability to predict complex patterns of species presence and abundance for a wide variety of vertebrate and invertebrate taxa and landscape types (Mazerolle & Villard 1999).

Most animal ecologists will agree that a landscape perspective specifically involves attention to the spatial configuration of habitats as it relates to the movement and distribution of organisms. Yet, relatively few plant studies address ecological issues from this particular viewpoint. What characterizes, then, a landscape perspective in plant ecology? How does it relate to and go beyond traditional approaches? What are the theoretical underpinnings, the common themes and concepts guiding current plant and landscape researches? If attention to landscape structure is an important aspect of landscape ecology, what is the evidence relating vegetation processes and landscape structural components? These questions need to be addressed to clarify research paradigms in landscape and plant ecology and to stimulate further advances in the field.

In spite of recent attempts to narrow down its meaning (Wiens 1999a; Wiens 1999b), the landscape concept remains wide and integrative, encompassing a plurality of ecological themes. Our objective here is to present a synthesis that will help to coalesce current ideas and stimulate further thinking specifically on landscape and plant issues. To do so, we propose a conceptual framework built around three main themes that link landscape and plant dynamics. While functionally interrelated, the themes also mirror the historical progression of interests in plant ecology.

The first section focuses on environmental relationships, documenting how vegetation patterns emerge from the influence of abiotic conditions. The landscape is an environmental space. Disturbances, themselves a function of environmental conditions, are then considered in the second section, with a particular attention to human-driven processes that often override natural dynamics. The landscape is a dynamic space. As environmental and historical processes generate heterogeneous patterns, we finally move on to stress current evidences relating spatial structure and vegetation dynamics. This relates to the concept of a landscape as a patch-corridor-matrix mosaic. For each of these aspects, we review theoretical influences, emphasize recent developments, and identify issues that remain unresolved.

THE LANDSCAPE AS AN ENVIRONMENTAL SPACE

Plant ecologists have been largely involved in the description of plant populations or plant assemblages distribution at broad spatial scales. Relations to local abiotic conditions (climate, soil, topography, etc.) and modification of these relations by competitive interactions for light, water or limiting nutrients at the level of the individual plant are usually invoked as proximate ecological processes to explain the patterns observed. Environmental conditions interact with plant strategies and competition to produce spatial patterns. Although specific mechanisms of competition are still poorly understood and alternative hypotheses have been proposed to account for plant species coexistence along resource gradients (Grime 1979; Tilman 1982; Weiher & Keddy 1999), environmental relationships remain at the core of vegetation organization at the population and community levels. If disturbances play a key role in environmental models, it is because they ultimately modify resource availability and therefore the outcome of competitive interactions.

The continuum concept has provided the theoretical and methodological basis to account for vegetation variation in relation to dominant environmental gradients (reviewed in Austin 1985). Species are assumed to have different individualistic ranges of responses that may depend on the type of environmental gradient considered (Austin & Smith 1989). The nature of the response depends on the physiological tolerance of each species, but competitive interactions vary along environmental gradients and species-environment response varies with competitive context (Leathwick & Austin 2000).

Whereas the continuum can be thought of as an abstract environmental space (Austin & Smith 1989), the landscape represents a portion of that continuum in real space characterized by the nature, range and spatial distribution of environmental factors. Distribution and association patterns in a particular landscape will therefore depend not only on the nature and the level of environmental factors, but also on the spatial distribution and configuration of resources in that landscape. The length of environment gradients is determined by the extent and configuration of the landscape, and becomes a landscape characteristic. The specific relationship that exists between spatial scale and environmental gradient may be a fundamental characteristic that can help define landscapes, but this relationship has been little investigated.

Ecological cartography

In gradient analyses, the traditional emphasis is more on fundamental environmental relationships than on actual spatial distribution in the landscape. As concern with environmental planning and the need for ecological classification and land survey grew in the 1960's and 1970's, there was considerable effort to recognize and map ecological units (Christian & Stewart 1968). In this perspective, vegetation is considered a land attribute integrating the major physical characteristics of a landscape – climate, landform, soil (Austin & Cocks 1978; Rowe & Sheard 1981; Moss 1985; Domon et al. 1989). The vertical integration of these elements finds its spatial expression in the mapping of ecosystems and their associated vegetation types. As in gradient analyses, or classical vegetation classification approaches for that matter, there is no implicit notion of spatial interactions other than the cartographic juxtaposition of ecosystems and associated vegetation types when mapping is conducted. In other words, horizontal patterns emerge from the vertical integration of environmental variables and plant distribution. Nevertheless, the cartographic approach allows the specific recognition of ecological entities as spatial features of the landscape, drawing attention on the possible ecological consequences of specific configuration. Landscapes can now be differentiated not only qualitatively, on the basis of their characteristic ecosystem and vegetation types, but also quantitatively, by the proportion occupied by each landscape element and by their spatial arrangement (O'Neill et al. 1988; Turner 1990).

The ability to recognize ecological entities arises because similar environments give rise to similar vegetation types. This key assumption is at the basis of vegetation classification procedures in an ecological cartography and land survey context. The importance of these entities in the landscape is a function of the frequency of the environmental combinations and the number of occurrences of abrupt environmental discontinuities (often due to geological or geomorphological processes). Combinations may be unique to each region and will give rise, therefore, to the recognition of landscape-specific ecological entities that can become the basic management units at the regional level. However, their successful use for management may depend on the similarity between separate occurrences of the entities in the landscape. Ecological cartography and land survey programs have proven efficient at very broad spatial scale where relatively large homogeneous entities can be recognized and environmental gradients are clearly dominant (as in parts of Canada and Australia for instance). Their application in vegetation classification and management issues in anthropogenic landscapes, where environmental and cultural influences interact to produce complex spatial and compositional patterns, is more problematic (Nolet et al. 1995). In such landscapes, failure to recognize and integrate the influence of historical factors and of spatial context in relation to environmental conditions may seriously impede our ability to explain vegetation types (Foster et al. 1998; de Blois et al. in press) and devise adequate management strategies.

VEGETATION DYNAMICS: DISTURBANCES IN THE LANDSCAPE

Vegetation patterns stem not only from environmental heterogeneity but also from natural and anthropogenic disturbances, the nature, frequency and intensity of which vary in space and time. Indeed, both natural and human dynamic processes are investigated in landscape ecology. Their relationships to local environmental conditions and landscape traits are especially emphasized. In turn, the heterogeneous patterns that they produce reflect plant dynamic adaptations to changes in available resources (light, nutrients, etc.), substrate availability and physical conditions induced by disturbances.

Natural disturbances and equilibrium concept

The evidence about the diverse nature and causes of natural disturbances and their consequences for populations, communities and ecosystems has been well summarized in the literature (Pickett & White 1985), but two aspects, in particular, need to be emphasized here. First, natural disturbance regimes are closely linked to local climatic, topographic and edaphic conditions, and some community types have adapted to recurrent disturbances. This suggests that, in some systems, disturbances are an intrinsic component of vegetation organization that cannot be dissociated from environmental conditions. Secondly, if natural disturbances drive vegetation and landscape dynamics, is there a spatial and/or temporal scale at which patterns seem stable? Are equilibrium states characteristic of most natural landscapes? Following the work of Clements on successional dynamics, Watt (1947) was one of the first to emphasize space-time patterns by considering the consequences, at broad spatial scales, of local patch dynamics driven by endogenous processes. The resulting vegetation mosaic was perceived as being in a steady-state or "phasic equilibrium" providing relatively constant environmental conditions. Various concepts of equilibrium as they relate to disturbance dynamics have since been proposed (reviewed by DeAngelis & Waterhouse 1987) and nonequilibrium states have been observed (Romme 1982; Leathwick 1998; Leathwick & Austin 2000). The state of equilibrium has been defined in relation to different vegetation attributes or disturbance characteristics including biomass, species composition, distribution of seral stages, sequence of changes, rate of changes, etc. Concepts of equilibrium in natural systems, however, are being questioned for they usually imply some form of stability rarely seen in landscapes and raise the difficult question of defining "normal" conditions for the system at hand. But more importantly, by trying to define some equilibrium conditions, attention has been called to the temporal and spatial scale-dependency of these phenomena. Within this particular context, the landscape can be considered as the scale at which some of these parameters exhibit relative constancy or fluctuate within acceptable ranges. Different landscape dynamics will result from differences in disturbance frequency, rate of recovery from disturbance, and spatial extent of disturbance in relation to the spatial extent of the landscape (Turner et al. 1993).

Anthropogenic landscapes

For many, if not most landscapes, the dominant dynamic influence has been that of human activities. To borrow the vocabulary of disturbance dynamics, human actions have generally resulted in a modification of both the nature, the intensity and the scale of disturbances. Most importantly, human activities have been generally highly selective, impacting some landscape and vegetation types more than others. As a result, they have produced spatial patterns that are often quite disruptive of natural processes. Although the recognition of human influences in shaping landscapes is not new (Dansereau 1957), one of the original contribution of a landscape approach is precisely to integrate, instead of avoiding, human processes in the study of ecological systems. As with natural disturbances, there are complex interactions between environmental conditions, human activities, and vegetation distribution. Climate, soil, and topography, for example, will determine opportunities or constraints for specific activities (agriculture, forestry, etc.), but these relationships will also change with time, either because practices change or because the environment has been modified in a way that excludes previous exploitation activities (Pan et al. 1999). In turn, vegetation patterns reflect plant dynamic adaptations to changes in available resources (light, nutrients, etc.), substrate availability, and physical conditions induced by human activities. These points are illustrated by studies conducted in different landscapes throughout the world. Perspectives vary, though, depending on local environmental conditions and the duration and intensity of human impacts.

North-American ecological studies have traditionally emphasized natural processes in landscapes. Vegetation is perceived to be the result of the interaction between environmental factors and natural disturbances. However, recent studies in several American landscapes highlight the ecological consequences of human processes on long-term vegetation dynamics. In the United-States, changes in temperate forest composition since European settlement was assessed using current and historical data (Foster 1992; Foster et al. 1992; White & Mladenoff 1994; Abrams & Ruffner 1995; Foster et al. 1998; Fuller et al. 1998). Formerly widespread tree species seem to have difficulties recolonizing current forest sites. Evidence suggests that shade-tolerant, long-lived taxa are especially vulnerable to changes in structure. Land-use activities are seen as disrupting vegetation-environment relationships that were previously considered as the main structuring force in the landscape (Foster et al. 1998). As a consequence, relatively homogeneous vegetation patterns emerge where distinct patchy distributions, driven by heterogeneous environmental conditions, were seen before.

Similar patterns are observed in agroforested landscapes of eastern Canada. Rapid forest clearing and agricultural activities at the time of settlement took place regardless of environmental constraints (Paquette & Domon 1997), but current broad land-use patterns (cultivated fields, woodlands, etc.) are strongly related to the underlying geomorphic conditions (Pan et al. 1999). As agricultural practices changed, natural revegetation occurred mainly on sites less amenable to agriculture. Historical evidence, however, suggests that current forest composition on these soils has become quite differentiated from presettlement patterns (Bouchard et al. 1989;

Brisson et al. 1994; Simard & Bouchard 1996). Current plant species assemblages are best predicted by land-use history (de Blois & Bouchard 1995; de Blois et al. in press). The relationships vary among growth forms, herbaceous and shrub species retaining more strongly than tree species the influence of environmental conditions and showing differential responses depending on the nature of the surrounding landscape.

As in North American landscapes, European settlement is relatively recent in Australia, but the continent being largely under arid conditions, European agricultural and pastoral practices have led to a rapid deterioration of local ecosystems. Temperate Eucalypt woodlands, once covering large areas, have been essentially cleared from the better soils to give place to crops and pastures. Tree dieback, lack of tree recruitment, soil deterioration and exotic species invasion have been identified as major consequences of anthropogenic influences in the remnant fragments (Hobbs & Yates 2000). Some of these effects may be mediated by the modification of natural fire regime after European settlement (Yates et al. 1994). In effect, little is known of the floristic composition of some presettlement vegetation types, although vegetation models have been used to fill the gap (Austin 1998). Because current practices are clearly unsustainable, the emphasis is now on acquiring knowledge and initiating actions to restore the productivity and diversity of degraded landscapes (Hobbs & Norton 1996; Yates & Hobbs 1997). This requires knowledge of previous patterns and individual species niche definitions (Austin et al. 1990; Austin et al. 1994; Austin & Meyers 1996).

European landscapes, on the other hand, have been long shaped by cultural processes, but changes in the spatial distribution, nature and intensity of human activities in the 20th century are especially emphasized. The intensification of practices in some areas, while others are being abandoned, raises issues of vegetation and landscape management. Interestingly, natural successional processes following abandonment of traditional management (e.g., tree cutting, grazing) are sometimes perceived as posing a threat to the diversity of cultural or semi-natural landscapes (Partel et al. 1999a; 1999b). This reflects a different attitude toward human disturbances that are often seen as being an integral part of land systems. If a certain equilibrium is to be achieved, it is more between cultural values and ecological processes rather than a return to some "natural" state. The ecological value of ancient forests is nonetheless recognized. Ancient forests show structural and compositional differences with younger ones, suggesting differences in habitat quality, persistence of historical influence and/or recruitment limitation (Brunet & Vonoheimb 1998; Bossuyt et al. 1999; Hermy et al. 1999; Honnay et al. 1999).

The influence of human practices on plant diversity and distribution is clearly emphasized in current landscape studies. Some important insights emerge from this recognition. First of all, the lasting influence of human impacts raises the question of the resilience, or lack thereof, of some vegetation types to human disturbances. This is especially true if human practices do not mimic or strongly contrast with natural disturbance regimes. Some of the strong patterns that emerge, at least in temperate forest landscapes, are a decrease in late successional species and an increase in early-successional and exotic species. However, these patterns may not be transitional as in succession dynamics but rather persistent in human landscapes. But to assess thoroughly the long-term consequences of human changes, we still have to understand how changes in structure and composition affect ecological functions. For example, in arid landscapes of Australia (Ludwig et al. 1997), disturbances from cattle ranching and overgrazing have modified structural landscape patterns that are seen to maintain important ecological functions. Vegetation patches in a matrix of bare, poor soil function as sinks that intercept scarce resources from the surrounding area and so maintain biotic diversity in the patches (Ludwig & Tongway 1995). When these functions are altered, structural and compositional shifts ensue. These observations lead to questions about the degree of resilience of different landscapes to changes.

Secondly, land-uses are often constrained by environmental conditions, and historical gradients can therefore be confounded with environmental gradients. Statistical tools and experimental design become important in evaluating the relative influence of both sets of factors, although true replication is often hard to achieve at the landscape-scale. But complex interactions are precisely what characterize landscapes, so it becomes a matter of finding the tools to deal with this complexity rather than trying to avoid it. Also, like natural disturbances, human activities modify resource availability (light, nutrient, etc.) and possibly competitive interactions. Identifying plant traits that confer competitive ability in modified systems becomes important to predict the effect of changes on vegetation dynamics. Efforts to summarize patterns of human processes in different landscapes should be enhanced by plant functional classification schemes aiming to identify such traits (see Lavorel et al. 1997).

Finally, one of the most original contributions of a broad landscape approach is that it calls attention to the factors that ultimately trigger land-use changes in human landscapes. From an ecologist perspective, these factors, often of cultural, political, and socio-economic origin, become predictors to integrate in models of vegetation dynamics (Crow et al. 1999). From a management point of view, cultural and ecological insights can be combined to anticipate and/or direct future landscape transformations (Domon et al. 1993; Bouchard & Domon 1997). Within this context, the attention is shifting toward restoration efforts, raising questions as to which processes should actually be restored, which species should be reintroduced, or, more fundamentally, to what purposes (e.g., maintain animal habitats, reintroduce threatened plant species, increase forest productivity, etc.) should we restore vegetation in the landscape (Hobbs 1993).

To summarize, a focus on the ecology of natural disturbances has led to a better understanding of spatial vegetation patterns and patch dynamics (Pickett & White 1985). The emphasis on anthropogenic processes characteristic of most landscape ecological studies should bring significant insights into the ecology of anthropogenic disturbances and lead to broad generalizations that will help us to interpret complex patterns over broad spatial scales.

SPATIAL INTERACTIONS: THE LANDSCAPE AS A PATCH-CORRIDOR-MATRIX MOSAIC

Environmental heterogeneity and disturbances produce mosaics of ecosystems and land-uses which differ by the nature, size and spatial arrangement of their constituent elements. In several landscapes, these factors have often combined to reduce original forest cover and isolate remnant vegetation fragments amidst other land-uses. Understanding how the structure of the mosaic in turn influences population and community processes is at the core of a landscape approach. Although the spatial concept of a landscape as a patch-corridor-matrix mosaic has been largely integrated in animal studies, its significance has been less clearly defined for plant species. The following section focuses on the evidence relating landscape structure - including patch size and relationship to other adjacent or similar patches in the mosaic – and vegetation processes.

Hypotheses about the influence on biotic components of landscape structural characteristics clearly stem from island biogeography theory, which initially provided concepts to be tested in land mosaic (Burgess & Sharpe 1981). Size and degree of isolation of habitat "islands", the latter characteristic relating to the spatial arrangement of patches in the landscapes, were thought to influence species richness through colonization and extinction patterns. This implied that the surrounding matrix offered some resistance to species dispersal. Although, theoretical aspects of island biogeography still influence landscape ecological studies, the recognition of the influence of patch size and spatial arrangement on biological processes now goes well beyond the initial hypotheses about species richness. For plant species, discussions about the effect of patch size and fragmentation inevitably call attention to the environmental parameters that correlate with size. Edge-mediated effects, in particular, are paramount in explaining changes in species composition and dynamics in fragmented landscapes. As for the concept of patch isolation, it usually implies dispersal limitations that are seldom assessed for plant species. Yet current evidence suggests that dispersal limitation may play a significant role in reinforcing patchy distribution patterns at the landscape scale. If isolation is a significant factor, do corridors function to facilitate plant species dispersal?

Patch size and edge-mediated effect

Indeed, species composition varies with patch size, and plant diversity has been shown to decline with patch size in land systems. These patterns, however, appears to depend less on size itself than on some other natural or anthropogenic processes that correlate with size. Large forest remnants, for instance are more likely to show greater environmental heterogeneity and greater interior to edge ratio. The alteration of within-patch characteristics, including changes in microclimate, light, wind or water fluxes as patch size decreases, is likely to influence regeneration patterns for interior specialists, while facilitating the invasion of other, including nonnative, species. Ownership patterns and exploitation pressure may differ across remnants of different sizes with consequences for species persistence. Large patches, even if they show relatively homogeneous abiotic conditions, may be under several management regimes, and therefore may show heterogeneous vegetation patterns. Small fragments of forests, on the other hand, can have surprisingly high proportions of forest specialists compared to large fragments, if they are under less intensive management regime (Lawesson et al. 1998) or if populations established in pre-fragmentation habitats survive well in the new conditions.

Because of the diverse environmental and historical influences at broad spatial scales, controlling for other factors while determining the unique effect of size is problematic. Experimental tests can go a long way in clarifying hypotheses and disclosing mechanisms, but the problem is that they have to be conducted at spatial and temporal scales meaningful for plant species and the processes at hand. In fact, few landscape-scale, long-term experiments have been conducted to evaluate the effect of reduced patch size through fragmentation of previously continuous habitats on plant species dynamics. Biomass reduction, increased mortality of interior tree species and marked edge effects were especially noticeable in forest fragments of the Brazilian Amazon (Laurance and Bierregaard 1997). In a tall-grass prairie oak-hickory woodland landscape in Kansas, patch size did not markedly affect the rate or pattern of early secondary succession after six years in abandoned agricultural fields (Robinson et al. 1992; Holt et al. 1995). Patterns of plant diversity and functional group abundance seemed to be little influenced at the spatial and temporal scale of the experiment. The strongest effect observed was that the population persistence of clonal species was lower in the smaller patches. In an experimentally fragmented regrowth eucalypt forests of South-East Australia (Margules 1992), preliminary results highlight the importance of distinguishing between the effects of environmental heterogeneity, temporal fluctuations in available resources from infrequent or episodic climatic events, and landscape configuration on plant species dynamics when experiments are conducted at such broad spatial and temporal scale (M.P. Austin, pers. comm.).

Altogether, responses to fragmentation may vary depending on species traits and natural adaptations of the local taxa to disturbance regimes. Therefore, more information is needed across a wider variety of landscapes to draw general conclusions about the effects of fragmentation. Broad community measures must be coupled with detailed examination of population dynamics to obtain a more accurate evaluation of plant species responses to landscape changes. However, true replication is often hard to achieve in experimental tests at broad spatial scales. On the other hand, untangling the relative contribution of various confounding variables may be difficult for observational tests whose conclusions are also often limited by a lack of knowledge about previous history and initial conditions.

Sharp transition between patch interior conditions and the surrounding matrix are common in landscapes and effects related to patch size and geometry are often the consequences of a modified interior to edge ratio. Edge effects are therefore critical to explain changes in species composition or dynamics. Edge-mediated effects include gradients of light intensity, air temperature, soil moisture or litter moisture that can affect species performance and recruitment on both sides of the edge (Matlack 1993; Matlack 1994b; Jules & Rathcke 1999; Meiners & Pickett 1999). There is, however, little agreement on the spatial extent of edge effects or, for that matter, on the biological patterns at edges which can be both site and species-specific (Murcia

1995). Edge effects seem to vary depending on edge orientation, physiognomy, and age, but other landscape variables such as the nature of the surrounding matrix (i.e. landscape context) and the transition in cover types (e.g., forest/crop, forest/pasture, old/young forest, i.e. the degree to which the patches differ) modulate the intensity of edge gradients. Fagan et al. (1999) propose to consider not only biotic patterns, but also edge functions in the landscape. Edges may act as dispersal barriers or filters, influence mortality rates of organisms, and generate novel species interactions.

Several vegetation management and conservation issues require that edge effects and the proximate landscape context be taken into account in the search of ecological solutions. In agricultural landscapes, management practices in adjacent fields often contribute to maintain or enhance edge effects in forest fragments. Constant edge fluctuations at the woodland/crop interface as agricultural practices intensify, have been observed in agricultural landscapes of eastern Canada (Pan et al. 1999), with the possible consequences of facilitating herbaceous species invasion and maintaining the system in a successional state (de Blois et al. in press). These effects may be enhanced by fertilizer and herbicide drifts which have been shown to affect plant species performance in patches adjacent to intensively managed fields (Kleijn & Snoeijing 1997; Boutin & Jobin 1998). In forest landscapes, forest recovery and species richness in harvested patches seem to be enhanced by adjacent species-rich forests, whereas neighboring single-species plantations will have opposite effects (Liu & Ashton 1999). Knowledge about the influence of the landscape context can be used to orient future management strategies, either to enhance species richness for conservation or revegetation purposes, or, conversely, to direct successional processes if vegetation control is the objective. Vegetation management in utility corridors, for example, may integrate knowledge about landscape context and edge effects in the search for long-term ecological solutions (Brisson et al. 1997).

Dispersal limitation and patch dynamics

Plants are sessile organisms showing strong spatial structure and restricted dispersal capabilities. These characteristics should facilitate meta-population and meta-community studies where colonization limitation is a significant factor. Yet the notion of patch isolation and its consequences on patch dynamics seem to be more easily addressed for animal species than for plant species, although there is still much to learn about the complexity of animal movement and habitat selection (Lima & Zollner 1996). For plant species, determining whether dispersal limitation is actually a critical factor depends on our ability to link knowledge about dispersal capacity, dispersal vectors, competitive ability, and longevity with data on landscape configuration and patch dynamics (Johnson et al. 1981; Johnson 1988; Perry & Gonzalez-Andujar 1993; Chambers & MacMahon 1994; Lavorel et al. 1995). Features specific to plant populations, such as buried seed pools, diversity of dispersal modes, temporal heterogeneity, and persistence through vegetative propagations further complicate our assessment of dispersal limitation as a significant factor in isolated vegetation patches. Rare long-distance dispersal events, for example, can increase significantly spread-rate predictions (Cain et al. 1998; Higgins & Richardson 1999).

Given plant species traits, it is not surprising that relatively few empirical studies have addressed plant species "movement" in the landscape in relation to landscape patterns or adopted a metapopulation approach (Husband & Barret 1996). The results of observational studies testing the effect of recruitment limitation for some temperate forest species have shown species number, rate of recovery, and subsequent species dynamics in isolated patches to be affected by the low recruitment of slow dispersers as distances from a propagule source increases (Peterken & Game 1984; Dzwonko & Loster 1992; Dzwonko 1993; Matlack 1994a; Brunet & Vonoheimb 1998; Grashof-Bokdam & Geertsema 1998). Theoretical metapopulation models, however, assume that, given time and if habitat patches are relatively stable in a landscape, all patches will eventually be colonized regardless of the dispersal capacity of the species involved. This suggests that, ultimately, biotic and abiotic conditions at the time of dispersal will be determinant in facilitating or limiting species establishment and subsequent patch dynamics. Transplant experiments may be used to test the alternative hypotheses of recruitment limitation and environmental constraints for some plant species (Primack & Miao 1992).

For plant communities, some of the processes likely to be affected by recruitment limitation include successional dynamics and competition as determinants of plant diversity. Successional theory first recognized the importance of the differential availability of species as a determinant of long-term community dynamics (Egler 1954; Pickett et al. 1987). Particular sequences of species replacement may ultimately depend on the competitive ability and life history of the species involved. More recently, specific processes involving recruitment limitation have been proposed to account for species coexistence and patchy distribution in the landscape. If spatial dispersal limitation and neighborhood interactions are taken into account, relatively poor competitors may be allowed to persist at sites where there is little recruitment of superior competitors (Tilman 1994). Neighborhood effects will therefore tend to increase patchiness of plant species distribution (Frelich et al. 1998). Interspecific trade-offs among colonization ability, competitive ability and persistence ability seem to facilitate species coexistence and increase diversity at the landscape scale (Tilman 1994; Holt 1997). Habitat generalists, often assumed to be better dispersers, may be favored as patchiness increases. That remains to be tested whether these phenomena and their ecological consequences are likely to be more important in landscapes where habitat patches are few and far apart in a matrix of agricultural, urban or other land-uses and where dispersal limitations could be very significant.

In patchy compared to continuous habitats, metacommunity models predict higher total species richness because of high differentiation among patches (Caswell & Cohen 1991; Tilman 1994; Holt 1997). Predictions from metacommunity models about the relationship between habitat patchiness at the landscape scale and the components of species richness have been tested for woody and herbaceous species on serpentine soils (Harrison 1998; Harrison 1999)]. Both woody and herbaceous species showed higher total diversity in a patchy landscape compared to sites within continuous habitat, although patterns of average local diversity differed among the two life-forms. However the authors suggest that edge effects may be more important in explaining the observed patterns than other processes related to patchy coexistence.

These findings emphasize the difficulties of distinguishing among the confounding effects of patch attributes such as size and shape on one side, and isolation on the other. Whereas other patch attributes can be easily measured, patch isolation remains largely a species-specific concept.

Corridors and species movement

If patch isolation is a critical factor, linear features of the landscape such as hedgerows, fencerows, field margins, riverine strips, rights-of-way, road verges, etc., may function as corridors that facilitate species movement and connect available habitats (Forman & Baudry 1984; Fahrig & Merriam 1985; Taylor et al. 1993; Burel 1996). Such elements, therefore, would provide a unique opportunity to test structural and functional links in the landscape. Although it is still arguable whether these structures actually have an impact on animal metapopulation dynamics (Rosenberg et al. 1997; Beier & Noss 1998), they undoubtedly serve as supplementary habitats in landscapes that are highly transformed by human activities. This can be said also of plant species whose distribution along linear features of the landscape has been related to environmental and structural attributes (e.g., width, height, cover, etc.), adjacent management practices, and landscape position (Le Coeur et al. 1997; de Blois et al. submitted).

Are forest plant species able to disperse using linear features of the landscape? Unlike animal species that may only transit through corridors, perennial plants must find suitable environmental conditions that will sustain their life-cycle. Some forest plant species are indeed able to colonize and survive in narrow habitats in the landscape (Fritz & Merriam 1994; Jobin et al. 1997; de Blois et al. submitted), and there is evidence that proximity and a physical connection to a propagule source facilitate species dispersal (Baudry & Forman 1983; Corbit et al. 1999). But how this relates to the demography of forest species in fragmented habitats is not known. There is yet no evidence that relates corridor function and plant metapopulation dynamics. The question also remains as to whether only a subset of forest species could be able to take advantage of such structures (McCollin et al. 2000), species that could precisely be the ones less in need of corridors at the landscape level. The fact that species most sensitive to fragmentation and edge effects cannot establish persistent populations in narrow linear features makes ecological sense but needs to be tested. Again, this raises the problem of trade-off between dispersal capacity, competitive ability, and shade tolerance. Other challenging research questions to be resolved involve relationships between biological dispersal vectors such as small mammals and birds that use linear structures in the landscape, and distribution patterns of plant species.

CONCLUSION

Landscape ecology has been described as the study of the reciprocal effects of spatial patterns on ecological processes (Pickett & Cadenasso 1995). From early on, plant ecology had a broad spatial perspective in the sense that its main concern was to explain the distribution of organisms, populations, or communities, especially in relation to the physical characteristics of the land. The current landscape paradigm builds on and goes beyond this initial view. We are gaining a better knowledge of the variety of processes that create spatial organization and are starting to focus on the complex interrelationships between natural and cultural influences. Environmental conditions indeed constrain species distribution but also influence disturbance dynamics. Natural and cultural processes interact to produce structural landscape patterns that can in turn act upon ecological processes. A landscape, therefore, is characterized by a specific combination and configuration of environmental variables and disturbances that interact to produce patchy vegetation and land-use patterns.

One of the challenges of landscape ecological analyses rests in the capacity to evaluate the relative importance of controlling processes at broad spatial scale and to integrate knowledge about their complex interactions into our vegetation models. Whereas environmental, historical and spatial processes operate in all landscapes, their relative influence on vegetation dynamics will vary across spatial and temporal scales. In some landscapes, for instance, human processes may alter ecological function to the point of modifying natural dynamics, whereas in other environmental gradients remain strong and determinant. The relative influence of a particular factor may change significantly through time, especially in relation to changes in management regime. Therefore specific models of functional relationships between controlling processes and vegetation are likely to be landscape-dependent. Landscape will remain a locational concept, however, if we do not move beyond the locally-specific to extract broad patterns. Comparing models or relationships across landscapes can lead to valuable generalizations and new insights in landscape and plant ecology. Common patterns of plant species adaptations or population and community responses may emerge.

If we have gained a better knowledge of the different processes producing structure, we still have little evidence, however, of the real importance of the spatial configuration of landscape elements for plant species. How does landscape structure influence disturbance dynamics, successional patterns, competition processes or vegetation organizational rules? Are all ecological levels equally affected and what are the parameters that change most at the landscape scale in response to changes in landscape structure? Metapopulation and metacommunity concepts have been little investigated for plant species, so are there conditions (interaction of specific landscape structure and particular life-history traits, etc.) for which these concepts will prove useful? Some concepts successfully applied to animal population studies may not be appropriate for plant species given their life-history traits, dispersal strategies, and requirements for microsites suitable for germination and establishment. Current evidence regarding landscape structural changes mostly points at edge and patch effects and the deleterious consequences of fragmentation and habitat loss. Fine scale processes at boundaries between patches seem critical to maintain or alter ecological functions with consequences for diversity, but there is little knowledge on the importance of topological patterns (i.e. the spatial arrangement of patches and their connectivity) at broader spatial scales.

The ability to predict the effect on vegetation patterns of changes in disturbance or management regimes is an important aspect of plant ecological research. Natural landscapes have an essential role to play in acquiring knowledge about natural processes, but in several areas of the world, the remnant vegetation has been transformed in ways that are not always well assessed since natural vegetation types are often poorly known. In such landscapes, political and economic decisions may have far greater impacts on future changes than any other factors. Human impacts, instead of being ignored or avoided, should be fully taken into account into ecological models. Whether they should be considered as exogenous "disturbances" or as an integral part of landscape dynamics is an open question. After all, landscape boundaries in ecological studies often coincide with political ones and are frequently being defined according to management imperatives. Vegetation management practices may have several objectives, ranging from the will to mimic as much as possible natural dynamics to the desire to maintain structure that have cultural values. Again the integration of natural and cultural aspects and the recognition of their interdependence is one of the challenging areas of investigation in landscape and plant studies.

Finally, the continuum concept, gradient analyses, disturbance and patch dynamics, island biogeography, metapopulation and metacommunity theory have to be explicitly acknowledged as part of a core of concepts, principles, and theories guiding investigations of plant ecologists that adopt a landscape perspective. The unique value of such a perspective precisely lies in its capacity to borrow from all these influences in order to integrate knowledge about natural and human processes that operate at several ecological and spatial scales. Because vegetation is such an important structural component of landscapes, indicating environmental conditions, regulating carbon exchanges, providing habitats and resources for other organisms and humans, and reflecting how humans interact with nature, plant ecologists are especially well positioned to contribute to these synthesis efforts.

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Chapitre 3

ENVIRONMENTAL, HISTORICAL AND CONTEXTUAL DETERMINANTS OF VEGETATION COVER: A LANDSCAPE PERSPECTIVE

Ce chapitre a fait l'objet d'une communication à l'échelle internationale et d'une publication dans Landscape Ecology :

de Blois S., R. Schmucki, G. Domon, and A. Bouchard. 1998. Vegetation and hedgerows dynamics in contrasting landscape units of Southern Quebec. New tasks for ecologists after RIO 1992. International Association for Ecology. Proceedings of the VII International Congress of Ecology, Florence, Italy. Abstract p. 106.

de Blois, S., G. Domon, & A. Bouchard. Environmental, historical and contextual determinants of vegetation cover : a landscape perspective. Landscape Ecology. Sous presse.

SUMMARY

We formulated and tested models of relationships between determinants of vegetation cover in two agroforested landscapes of eastern North-America that differ by the spatial arrangement of their geomorphic features and intensity of agricultural activities. Our landscape model compares the woody plots of each landscape in terms of the relative influence of environmental attributes, land-use history (1958 – 1997), and spatial context (i.e proximity of similar or contrasting land-cover). Our vegetation model evaluates the relative contribution of the same sets of variables to tree distribution and herbaceous and shrub species distribution. Relationships are assessed using partial Mantel tests and path analyses. Significant environmental and contextual differences were found between the vegetation plots of the two landscapes, but disturbance history was similar. Our vegetation model confirms the dominant effect of historical factors on vegetation patterns. Whereas land-use history overrides environmental and contextual control for trees, herbaceous and shrub species retain an environmental component. Context becomes determinant only for understory species in older, less-disturbed plots. Results are discussed in relevance to vegetation dynamics in a landscape perspective that integrates interactions between environmental and human influences.

Keywords : agricultural landscape; agroforested landscape; human disturbance; landscape model; land-use history; Mantel test; path analysis; Quebec; spatial context; vegetation model.

INTRODUCTION

Vegetation patterns are constrained by various processes linked by a complex network of relationships. The nature as well as the relative importance of these processes will likely vary across landscapes and through time. For example, forest composition of the presettlement landscape of New England has been found to correlate with climate and soil conditions, whereas the current vegetation patterns mostly reflect human disturbances that seem to have obscured environmental control (Foster et al. 1998; Fuller et al. 1998). In boreal forests, vegetation patterns reflect the intricate interactions between site conditions, natural disturbance regime and landscape configuration (Bergeron et al. 1997; Flannigan et al. 1998). In deciduous agroforested landscapes of southern Quebec, human activities have overridden natural disturbances in frequency and intensity. Current tree composition seems to bear little resemblance to the original forest cover (Brisson et al. 1988; Bouchard et al. 1989; de Blois and Bouchard 1995; Simard and Bouchard 1996) and shows complex responses to environmental gradients (Leduc et al. 1992; Meilleur et al. 1994).

In a physically heterogeneous landscape, environmental factors are generally assumed to be the prime determinant of vegetation patterns, the influence of a particular factor varying with the scale of observation (e.g., climate gradient at small geographical scale) (Austin and Smith 1989). In an agroforested landscape, however, land clearance is often a selective process that depends on the suitability of the underlying physical characteristics to sustain agricultural activity. In this case, uncultivated patches are likely to correlate with particular fine-scale soil conditions indicating their unsuitability for agriculture (e.g., steep slope, rocky soil, etc.), while some original vegetation types associated with more favorable edaphic characteristics may be underrepresented in the remnant fragments (Hobbs and Saunders 1993). In southern Quebec, an area of high agricultural productivity, this translates into non-crop vegetation patches being primarily left on glacial soil deposits, whereas agricultural activities have concentrated, over time, on rich marine soil deposits (Paquette and Domon 1997; Pan et al. 1999).

Environmental factors and historical processes are important in our understanding of vegetation patterns and both are closely interrelated. Natural disturbances such as wind, fire, or insect outbreaks, have been shown to interact with environmental constraints at the site or landscape scale. For example, xeric conditions enhance fire frequency (Barton 1993), and climate changes alter the cycle of insect outbreaks (Bergeron and Leduc 1998). When the landscape is intensively managed, however, land-use history can override natural disturbance as the most important driving force altering both vegetation and landscape patterns. Just as with natural disturbances, different land-use regimes will be related to the spatial heterogeneity of environmental conditions (Iverson 1988; Simpson et al. 1994; Pan et al. 1999).

Constrained by the environment, human activities in intensively managed landscapes often produce a mosaic showing sharp (e.g., woodland/crop) or more diffuse (e.g., woodland/brushland) boundaries between the different land-covers. As a consequence, interactions between patches and surrounding areas, as described by the influence of spatial context or variables describing landscape structure, are receiving more and more attention in vegetation models (Rescia et al. 1994; Brosofske et al. 1999; Harrison 1999; Liu and Ashton 1999). Context, used here to describe the surrounding land-cover, is a complex variable that can integrate different ecological processes. When measured at a fine-spatial scale around the patch of interest, context acts as a surrogate for edge-driven effects (Murcia 1995; Meiners and Pickett 1999), allows to evaluate the influence of adjacent management practices (Boutin and Jobin 1998) or of the proximity of propagule sources for revegetation (Dzwonko 1993; Matlack 1994a).

We expect, therefore, the vegetation mosaic of an agroforested landscape to reflect, at different intensities, the complex interactions between environmental, historical, and contextual processes. Unraveling the relative contribution of each set of variables and testing models of relationships across landscapes is a crucial step in our understanding of vegetation and landscape dynamics. At the local scale, it may help us to formulate and test hypotheses on the influence of a particular variable, or set of variables, that has proved critical. From a management point of view, such models become essential to address conservation issues in mosaics integrating elements under intensive exploitation pressure (Hobbs et al. 1993; Bouchard and Domon 1997; Hobbs 1997). As well, models of relationships are likely to be scale- or landscape dependent. Applying such models to landscapes under similar or different management regimes will lead to some useful generalization in landscape ecology (Wiens 1999).

The objective of this study is to assess the relative importance of environmental, historical, and contextual processes on vegetation distribution within two agroforested landscapes that differ in the spatial arrangement of their geomorphic features and in the intensity of agricultural activities. Our approach emphasizes broad controlling processes of vegetation distribution rather than specific species responses to these processes. We believe, as well, that the approach used here can be widely applied to other landscapes and taxa. The main questions asked in our analyses were the following:

- Can we differentiate the two landscapes on the basis of the environmental, historical and contextual characteristics of their vegetation plots? What are the interrelationships between these sets of variables ?
- What are the main determinants of tree species distribution ?
- What are the main determinants of herbaceous and shrub species distribution? Do herbaceous and shrub species show a response different from that of tree species ?
- What are the main determinants of tree species distribution and of herbaceous and shrub species distribution when each landscape is analyzed separately? How do local responses differ from the overall response?

METHODS

Study area

The study area is located in Godmanchester, a rural municipality of 139 km^2 within the Haut-Saint-Laurent region in the southernmost part of the Province of

Quebec, Canada (figure 1). The area is part of the humid mid-cool temperate ecoclimatic region of Canada. Average seasonal temperature ranges from -10°C in January to 20.8°C in July (Environment Canada 1982). The region is part of the deciduous forest of the Great Lakes and St-Lawrence River system (Rowe 1972). Mesic forests are generally dominated by *Acer saccharum*, with *Carya cordiformis*, *Ostrya virginiana*, *Tilia americana*, *Fagus grandifolia*, and *Tsuga canadensis*. Following European settlement in the 19th century, the area has been under intensive exploitation, first for timber and then for agriculture. Today uncultivated vegetation patches are often confined to the numerous moraine islets and ridges of glacial origin generally considered unsuitable for agriculture. Agricultural activities, mostly dairy farming and grain and cereal production, are concentrated in the rich lowlands covered with marine clay deposit left by the ancient Champlain sea. Privately owned, woodlands are often used as a source of firewood and/or as pasture for cattle. Land-use dynamics in this area is typical of many other agricultural or agroforested landscapes in eastern North America.

Sampling and data collection

Using SPANS GIS (INTERA TYDAC 1991), we first developed an extensive spatial database as a tool to conduct integrated ecological and landscape management studies in Godmanchester. The main geomorphic surface deposits (glacial, marine, peat) (Bariteau 1988), elevation, and land-cover types (forest, abandoned land or brush, permanent pasture, crop, urban land, road) interpreted from aerial photographs for 1958, 1965, 1973, 1983, and 1993, and validated by land surveys, were digitized.

Using the resulting geomorphic and land-cover maps, we delineated two characteristic landscape units that differ by the spatial arrangement of glacial surface deposits (figure 2). The first unit, referred hereafter as the glacial landscape, is dominated by continuous glacial deposits (96.6% of the surface area) with a few pockets of peat (3.4%). It is characterized by low agricultural intensity and shows a relatively continuous vegetation cover with embedded fields generally used for fodder crops. Non-crop vegetation patches, including forest, brush and pasture, cover 68% of the landscape, whereas fields account for 31% of the landscape (figure 2). From 1958 on, following changes in agricultural practices, most pastures were abandoned and successional processes were allowed to go on in these parcels as well as in land that had been abandoned prior to 1958. As a result, the percentage of forest increased considerably in this landscape (figure 2).

The second unit, referred to as the mixed landscape, is dominated by marine clay deposits (73% of the surface area) with interspersed glacial islets (23%). Agricultural activity is more intensive, with the clay plain being cultivated mostly for corn, whereas the glacial islets are left uncultivated. Uncultivated vegetation patches and crops cover respectively 26% and 73% of the landscape (figure 2). Since 1958, abandoned land decreased by 5% and forest increased by 3%. Pastures stayed relatively stable within this landscape.

Both landscapes were sampled for vegetation cover in the summer of 1996 and 1997. A grid consisting of sampling points placed at 200-m intervals along staggered rows separated by 200 m was superimposed on each unit. This interval is small enough to sample isolated forest patches in the mixed landscape, without over-sampling the larger vegetation patches in the glacial landscape. It is also the average width of agricultural fields in this area and often marks current or ancient property lines. Only grid points for which canopy coverage on aerial photographs was ≥ 5% were sampled in the field, using 50 m x 4 m plots (total number of sampling plots = 176; glacial landscape = 89 plots; mixed landscape = 87 plots). Plots were generally centered on the grid point, always using the same compass direction, and were occasionally relocated to avoid sampling dissimilar cover types. For tree species, individuals were identified and diameter at breast-height was measured for all individuals with DBH > 1 cm. Percent cover of herbaceous and shrub species was evaluated (<1; 1-5; 5-10; 10-25; 25-50; 50-75; ≥ 75) in the first and last 5 m x 4 m of the 50 m line. From two to four trees were cored in each plot in order to estimate the minimal age of the stand. A soil sample was taken in the first mineral horizon and textural analyses were performed (% of sand, silt and clay). Soil drainage (4 semi-quantitative classes: poor, imperfect, moderate, rapid), evidence of a high water table at less than 50 cm from the surface, and stoniness of the soil surface (6 semi-quantitative classes of % cover: < 1; 1-3; 3-15; 15-50; 50-90; ≥90) were evaluated in the field. Signs of current or past management regime (stumps, fences, large trees left for cover, animal paths, cattle dung, etc.), as well as the spatial context of the sampling plot (proximity to a field or other land-cover) were noted. Aerial photographs and the digitized database were used to complete environmental and historical records from field sampling as well as to quantify the spatial context for each sampling plot (see below).

Data analyses

All plots were grouped to perform a series of analyses that considered the two landscapes simultaneously. As well, plots were analyzed separately for the glacial and for the mixed landscape. Moreover, given their different life histories and traits, trees were analyzed separately from the herbaceous and shrub species. Previous studies in the area had shown a distinct response to environmental factors for trees and for herbaceous and shrub species (Meilleur et al 1992; 1994).

Computation of data matrices

Several matrices were compiled in order to perform multivariate analyses to assess relationships between our sets of explanatory variables and response variables. For the response variables, the matrices are:

- Landscape identification matrix (LAND)

  A similarity matrix was constructed by coding pairs of plots with zero (samples are from different landscape units) or one (samples are from the same landscape) (Sokal and Rohlf 1995; Legendre and Legendre 1998). The resulting matrix was used to test the hypothesis of environmental, historical and contextual control of landscape differentiation in a goodness-of fit Mantel test (for theory see Sokal and Rohlf 1995; Legendre and Legendre 1998; for other applications see Legendre and Fortin 1989; Somers and Green 1993). In this test, the response matrix is constructed to represent the model to be tested. Because the plots are classified into groups, the Mantel test is equivalent to a nonparametric mutivariate analysis of variance (Legendre and Legendre 1998).

- Vegetation matrices (TREE, HERB&SHRUB, OLDTREE, OLDHERB&SHRUB)

  TREE : Total basal area calculated for each tree species (30 species) in each plot. Three matrices were produced, one grouping all plots, and one for each landscape separately.

  HERB&SHRUB : Herbaceous and shrub species cover (139 species) for each plot. Three HERB&SHRUB matrices were produced, one grouping all plots, and one for each landscape.

  OLDTREE and OLDHERB&SHRUB: After initial analyses, we restricted our vegetation set to plots in both landscapes in age classes 3 and 4 (> 60 years), that have been forested since 1958, and that showed no sign of grazing activity during the reference period. The two matrices include only the 47 plots retained for this analysis (24 plots in the glacial landscape and 23 plots in the mixed landscape). This was done to evaluate the relative influence of the environment and the context within older plots that have been apparently less disturbed.

For the explanatory variables, the matrices are:

- Environmental matrices (ENVI)

  Environmental attributes include % cover of geomorphic surface deposit in each plot (glacial, marine or peat), % of sand, loam and clay in the soil sample, soil drainage, evidence of a high water table, soil stoniness, elevation (m), and slope (0 – 30°; 30 – 60; 60 – 90). Given its poor predictive performance in preliminary analyses, slope aspect was left out in the final environmental matrix that included all other attributes.

- Historical matrices (HIST)

  Historical descriptors were compiled from field observations, aerial photographs, and the spatial database to reflect as much as possible past and present disturbances and practices that may have influenced vegetation distribution (land-use and land-cover change). They include:

  1. Land-cover trajectory from 1958 to 1996 (5 qualitative classes coded as binary dummy variables: field to brush; brush to brush; brush to forest; forest to brush; forest to forest). Brush are shrubby woodland or open forests dominated by small trees and/or shrubs with a canopy cover ≤ 25%.
  2. We used 2 indices to reflect as much as possible the impact of grazing activity on vegetation. First, the index of grazing frequency, F_g, records the number of times evidences of use as pasture was noted in the six reference periods 1958 – 1965 – 1973 – 1983 – 1993 – 1996. It is indicative of the duration of grazing activity in the plot and thus indirectly of grazing pressure. Second, we computed an index of recent grazing activity, $I_g = 1/t_{last}$, where t_{last} refers to the number of years spent since evidence of grazing was last recorded. It reflects the fact that grazing impact on plant species will decrease with time. Evidence of grazing only in 1996 as opposed to grazing only in 1958 should have a greater impact on species present today, especially on understory species.

3.Minimal age of the tree community from sample cores. Ages were grouped into 4 classes to minimize estimation errors, i.e. < 30 years old, 30 to 60, 60 to 90 and > 90 years old.

- Spatial context matrices (SPCO)

  Using SPANS GIS and the 1993 land-use layer, a circular buffer (r = 50 m) was drawn around the center of each sampling plot. Although spatial context has been measured for scales up to 1000 m (Rescia et al. 1994; Grashof-Bokdam 1997), we chose to consider processes at a finer scale reflecting proximate edge or dispersal effects relevant to plant species distribution. Edge effect up to 50 m having been reported for forest fragments of eastern North America (Matlack 1993; Matlack 1994b), the percentage of forest, brush, pasture and/or crop was recorded at this scale, excluding the cover in the sampling plot itself. The spatial context matrix takes into account the nature, proximity and the heterogeneity of adjacent land-covers. For instance, a forested plot can be embedded within a forest matrix, or within a combination of forest, field and/or brush.

Mantel tests among similarity matrices and path analyses

Prior to analyses, quantitative variables in the environmental and contextual matrices were log-transformed to approximate a normal distribution. All data matrices were converted into similarity matrices for further multivariate analyses. The Steinhaus coefficient, an asymmetrical coefficient which lessens the effect of the largest difference (Legendre and Legendre 1998), was used for species matrices. For the environmental matrices, we used the Easterbrook and Rogers coefficient adapted to mixtures of quantitative, semi-quantitative and qualitative descriptors, whereas the Gower's coefficient (Gower 1971) was used for the context matrices (for equations and rationale, see Legendre and Legendre 1998).

To evaluate the relations between the vegetation and landscape identification similarity matrices, and our three sets of explanatory variables, we computed a series of Mantel (Mantel 1967) and partial association tests. Mantel tests compare resemblance matrices computed about the same objects. Instead of using the standard Mantel statistic that brings out only the linear component of the relationship between our matrices, the actual similarity values were transformed into ranks. This is the equivalent of using the Spearman's nonparametric correlation coefficient between the similarity matrices (Dietz 1983) and allows the detection of non-linear relationships between the matrices. As for partial tests, they allow the computation of partial correlations between two similarity matrices, controlling for the effect of a third one (Smouse et al. 1986). They are used here to evaluate the unique effect of each set of explanatory variables on the dependent variables, a step which is essential given the possible covariation among our sets of descriptors. Significance is assessed by repeated permutations. We ran 1000 permutations in general and up to 10 000 permutations for tests that showed borderline results according to the recommendation of Jackson and Somers (1989) on the instability of Mantel tests. Levels of significance were corrected to take multiple testing into account (Holm's procedure, Holm 1979). Corrections were done according to the level at which simultaneous tests were conducted, i.e. 32 simultaneous tests at the grouped level, 23 tests for each landscape, and 9 tests for the set restricted to older plots. The resulting simple correlation coefficients from the Mantel tests were then used as input into path analyses, an extension of multiple linear regression (Sokal and Rohlf 1995) which allowed us to evaluate and test models of relationships among our sets of descriptors. Because they were computed from resemblance matrices, path coefficients in our models were tested for significance through the partial Mantel tests.

Our general model is schematically represented in a path diagram, where arrows depict the network of relationships (figure 3). The overall influence of environmental, historical, and contextual variables on species distribution was first tested for all plots, and then for each landscape taken separately, in order to assess the relative importance of controlling factors. When the response variable is the similarity matrix of the landscape identification, our model compares the two landscapes based on the environmental, historical, and contextual characteristics of their vegetation plots.

In our model, environmental conditions are assumed to have a direct influence on species distribution, but will also affect land-use history and the spatial context, which can both in turn directly influence species distribution (figure 3). For instance, steep slopes may prevent agricultural activities on sites that will consequently remain forested, whereas sites with mixed marine and glacial deposits often border crops. Moreover, covariation between the context and the historical matrices is also likely to be significant, the magnitude of this relationship depending on the configuration of the landscape. If sampling plots are found within large, relatively homogeneous patches in terms of land-use history, the correlation between these two matrices is likely to be high. Finally, to refine our understanding of the significant relationships between sets of explanatory variables uncovered by the Mantel tests and path analyses, we computed a series of Spearman correlations between pairs of individual variables of the explanatory variables sets. Computation of similarity coefficients, Mantel tests, and path analyses were performed using the R package (Casgrain and Legendre 1999), whereas SAS (SAS Institute 1988) was used to calculate correlation coefficients among variables of the explanatory variable sets. Spatial analyses were performed using SPANS GIS (INTERA TYDAC 1991).

RESULTS

Landscape model

The landscape model assumes that spatial differentiation of vegetation sites (LAND) reflects environmental, historical and/or contextual differences between the uncultivated vegetation patches of the two landscapes (table I; figure 4). We found a significant relationship between landscape identification and the environment when controlling for history and context. Despite the fact that both environment and history influence the context, there is also a unique contribution of the context to our landscape identification. Historical factors, however, were not significantly related to the landscape identification at our conservative probability level.

Regarding the relationship between sets of explanatory variables, the environment shows an influence on context when controlling for historical variation (table I; figure 4). Examination of the correlations among the environmental and contextual variables (table II) reveals that their common structure is mostly due to the positive relationship between marine geomorphic deposits and the proximity of a field (field context), whereas glacial deposit and elevation are inversely correlated to a field context.

Land-use history and context are also significantly related, even when we control for environmental variation (table I; figure 4). In this case, a significant part of the relationship can be attributed to the positive association between a brush context and plots that have remained brush since 1958, and/or where frequency of grazing activity is high, and a negative relationship between a brush context and plots that remained forested, and a brush context and age (table II).

Vegetation model

Our general vegetation model assumes environmental, historical and contextual control of vegetation patterns in the landscape. Results show that this control differs according to the type of vegetation considered i.e. trees vs herbaceous and shrub species as well as in relation to the level of analyses considered, i.e. all plots vs individual landscape (table I, figure 5).

When all plots are considered, history explains a significant proportion of tree distribution when controlling for other sets of variables (table I, figure 5). Although the context also has a weak but significant relation to tree distribution, this relationship is mostly due to the common variation shared by the context and history. The context has no unique contribution when we partial out the effect of history. Interestingly, there is no overall significant contribution of our selected environmental variables to tree distribution. Land-use history remains the most determinant factor.

For herbaceous and shrub species, land-use history has again a unique contribution to the observed variation. In this case, there is also a significant influence that can be uniquely attributed to the environment, whereas the context is not significant.

For plots in the glacial landscape only, tree distribution is chiefly under historical control, although the environment is nearly significant (corrected p = 0.072) (table I, figure 5). Both history and the environment have an influence on herbaceous and shrub species distribution. Again, there is no significant variation that can be explained by the context alone, although the relation between tree distribution and the context is nearly significant (corrected p = 0.056). Moreover, historical variables are significantly related to the context but, contrary to our previous findings for all plots, there is no relationship between the environment and the context or between the environment and history (table I; figure 5). Analyses of the variables within the historical and contextual sets reveal a positive association between a brush context and the index of grazing activity, and a negative relationship between a pasture context and age in this landscape (table III).

Unlike what we observed in the glacial landscape, there is no significant relationship among the sets of explanatory variables in the mixed landscape (table I, figure 5). Again historical control has a unique and significant contribution to tree species distribution and a nearly significant contribution to herbs and shrubs distribution (corrected $p = 0.056$). The other sets of variables have no unique influence.

Overall, the most constant significant relationship was found between all vegetation types and land-use history. Environmental control appears to be more determinant for herbaceous and shrub species composition than it is for tree composition. The two landscapes show environmental and contextual differences, but this is not reflected in the history of their vegetation patches.

Given the importance of historical effects on vegetation in our landscapes, we conducted further analyses to evaluate the influence of the context and the environment within older plots that were apparently less disturbed (table IV; figure 6). Although the context has still no unique influence on tree species distribution, herbaceous and shrub communities maintained a significant partial association with the context when controlling for environmental variables (figure 6). In this case, environmental control is non significant for both vegetation types but is nearly significantly related to the spatial context ($p = 0.056$).

Table I. Spearman correlation coefficients from Mantel and partial Mantel tests between the environmental (ENVI), historical (HIST) and spatial context matrices (SPCO) and, for the dependent variables, the landscape identification matrices (LAND), the tree communities (TREE) and the herbaceous and shrub communities (HERB&SHRUB). The matrix following the slash bar has been partialled out in partial association tests. Analyses for the vegetation model were performed grouping all plots, for plots in the glacial landscape only, and for plots in the mixed landscape only. *significant relationship at the Holm-corrected probability level for an overall probability level of 0.05 (32 simultaneous tests for the landscape and vegetation model at the grouped level; 23 simultaneous tests for the glacial landscape and 23 simultaneous tests for the mixed landscape).

LANDSCAPE and VEGETATION MODEL (all plots)

	ENVI	HIST	SPCO	ENVI/HIST	ENVI/SPCO	HIST/ENVI	HIST/SPCO	SPCO/ENVI	SPCO/HIST
ENVI		-0,024	0,174*						0,184*
HIST			0,226*					0,234*	
<u>LAND</u>	0,263*	0,014	0,209*	0,263*	0,235*	0,021	0,035*	0,172*	0,211*
<u>TREE</u>	0,070	0,222*	0,091*	0,077	0,055	0,224*	0,208*	0,081	0,043
<u>HERB& SHRUB</u>	0,175*	0,135*	0,062	0,180*	0,167*	0,142*	0,125*	0,032	0,032

Table I. (Continued)

VEGETATION MODEL (glacial landscape)

	ENVI	HIST	SPCO	ENVI/HIST	ENVI/SPCO	HIST/ENVI	HIST/SPCO	SPCO/ENVI	SPCO/HIST
ENVI		-0,01	-0,072						-0,074
HIST			0,412*					0,370*	
TREE	0,127	0,253*	0,146	0,134	0,140*	0,256*	0,217*	0,157*	0,058
HERB& SHRUB	0,291*	0,136*	0,020	0,295*	0,293*	0,145*	0,138*	0,020	-0,033

VEGETATION MODEL (mixed landscape)

	ENVI	HIST	SPCO	ENVI/HIST	ENVI/SPCO	HIST/ENVI	HIST/SPCO	SPCO/ENVI	SPCO/HIST
ENVI		0,033	0,068						0,064
HIST			0,147					0,145	
TREE	0,052	0,191*	-0,033	0,047	0,054	0,189*	0,198*	-0,037	-0,063
HERB& SHRUB	0,064	0,158	0,045	0,060	0,062	0,156	0,153	0,041	0,022

Table II : Spearman correlation coefficients between the contextual, the environmental, and the historical variables (all plots). Only the significant relationships ($p < 0.05$) are shown. *Ns = non-significant

	Field context	Brush context	Pasture context	Forest context	Road context
Glacial	-0,515	0,189	ns*	0,382	ns
Marine	0,605	-0,221	0,170	-0,445	
Peat	ns	ns	ns	ns	ns
Sand	-0,219	ns	0,22	ns	-0,273
Clay	0,172	ns	-0,273	ns	0,252
Silt	0,1809	ns	ns	ns	0,207
Drainage	0,237	ns	ns	ns	ns
Stoniness	0,229	-0,186	ns	ns	ns
Water table	-0,238	ns	ns	ns	ns
Slope	0,225	-0,176	ns	ns	ns
Elevation	-0,562	0,365	ns	0,297	-0,291
Field-Brush	ns	0,231	ns	-0,175	ns
Brush-Brush	ns	0,536	ns	-0,294	ns
Brush-Forest	ns	ns	ns	ns	ns
Forest-Brush	ns	ns	0,246	-0,159	ns
Forest-Forest	ns	-0,382	-0,162	0,222	ns
Last grazing	ns	0,261	0,219	-0,251	ns
Frequency grazing	ns	0,313	0,257	-0,287	-0,149
Age	ns	-0,331	ns	0,215	ns

Table III: Spearman correlation coefficients between the contextual and historical variables (glacial landscape only). Only the significant relationships ($p < 0.05$) are shown. *Ns = non-significant.

	Field context	Brush context	Pasture context	Forest context	Road context
Field-Brush	ns	0,255	ns	- 0,264	ns
Brush-Brush	ns	ns	ns	ns	0,245
Brush-Forest	ns	ns	ns	ns	ns
Forest-Brush	ns	ns	ns	ns	ns
Forest-Forest	-0,213	ns	ns	ns	ns
Last grazing	ns	0,390	0,263	ns	ns
Frequency grazing	ns	ns	0,265	ns	ns
Age	ns	ns	-0,279	ns	ns

Table IV: Spearman correlation coefficients from Mantel and partial Mantel tests between the environmental (ENVI) and the spatial context matrices (SPCO) and, for the dependent variables, the tree communities (OLDTREE) and the herbaceous and shrub communities (OLDHERB&SHRUB) (less-disturbed older plots only); *significant relationship at the Holm-corrected probability level (9 simultaneous tests) for an overall probability level of 0.05.

VEGETATION MODEL (less disturbed plots only)

	ENVI	SPCO	ENVI/SPCO	SPCO/ENVI
ENVI		0198		
<u>OLDTREE</u>	0,132	0,089	0,117	0,065
<u>OLDHERB &SHRUB</u>	0,151	0,211*	0,114	0,187*

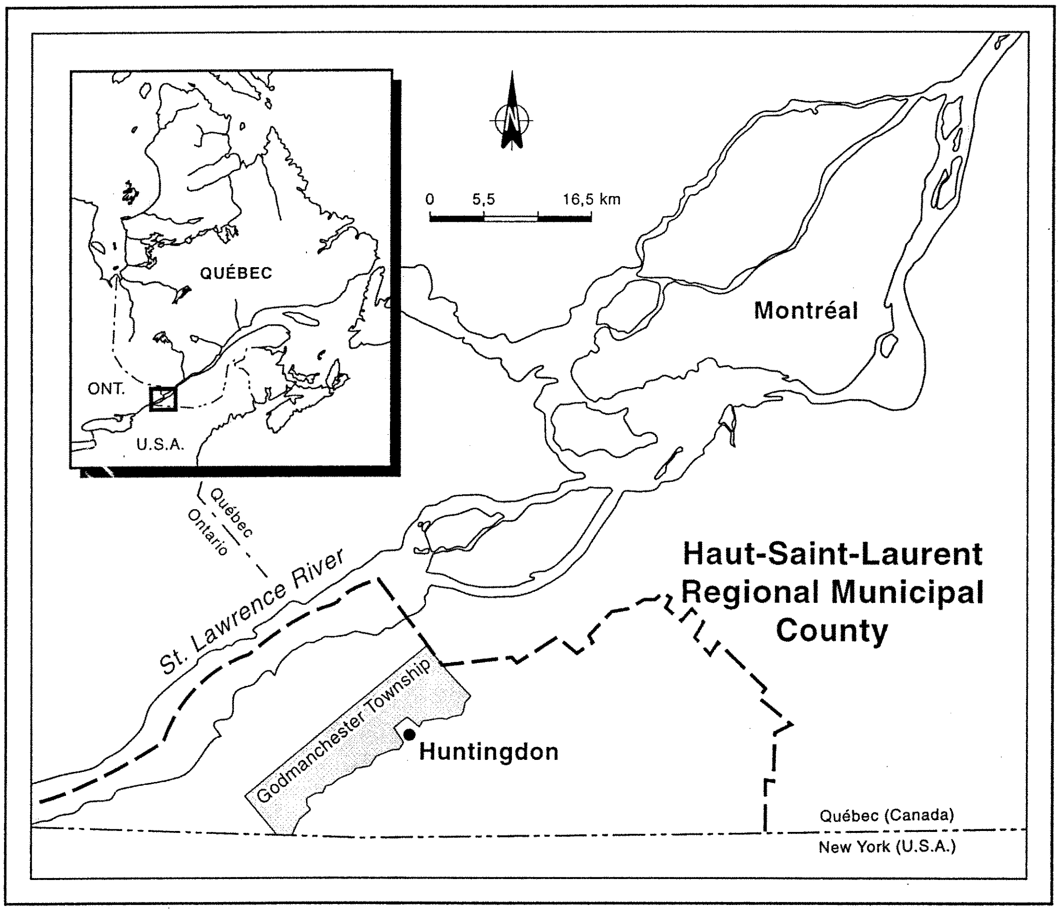
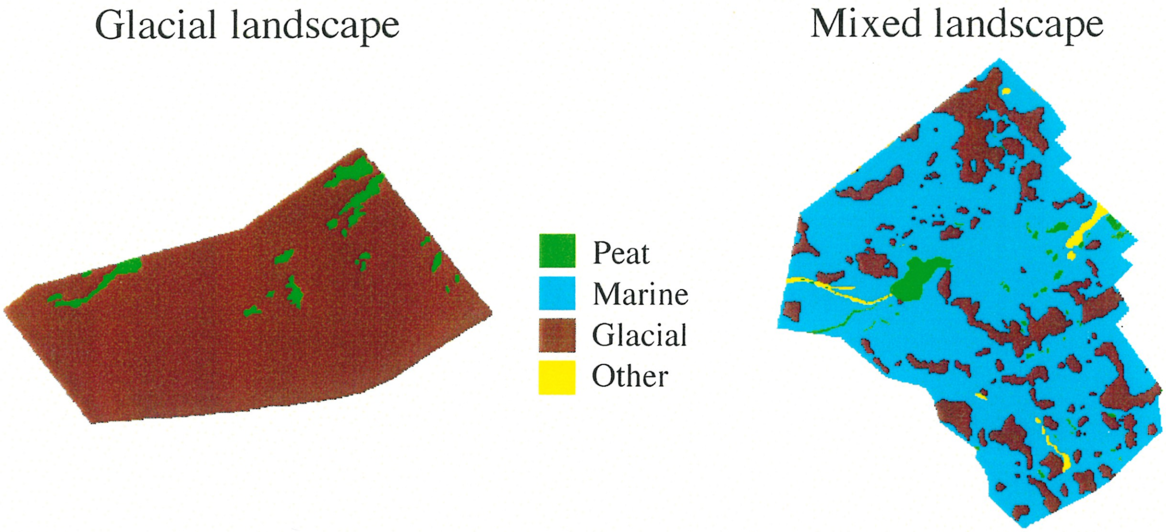


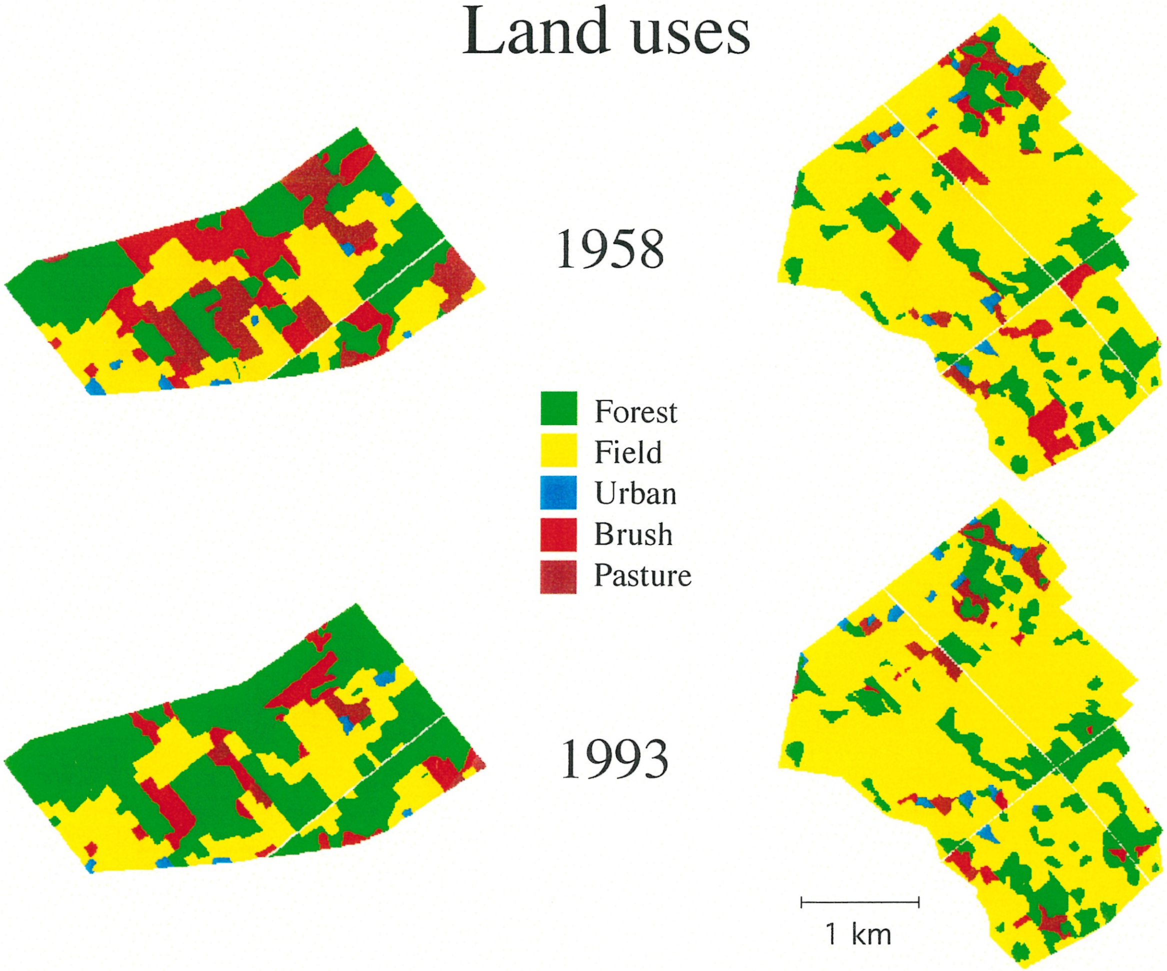
Figure 1: Location of study area.

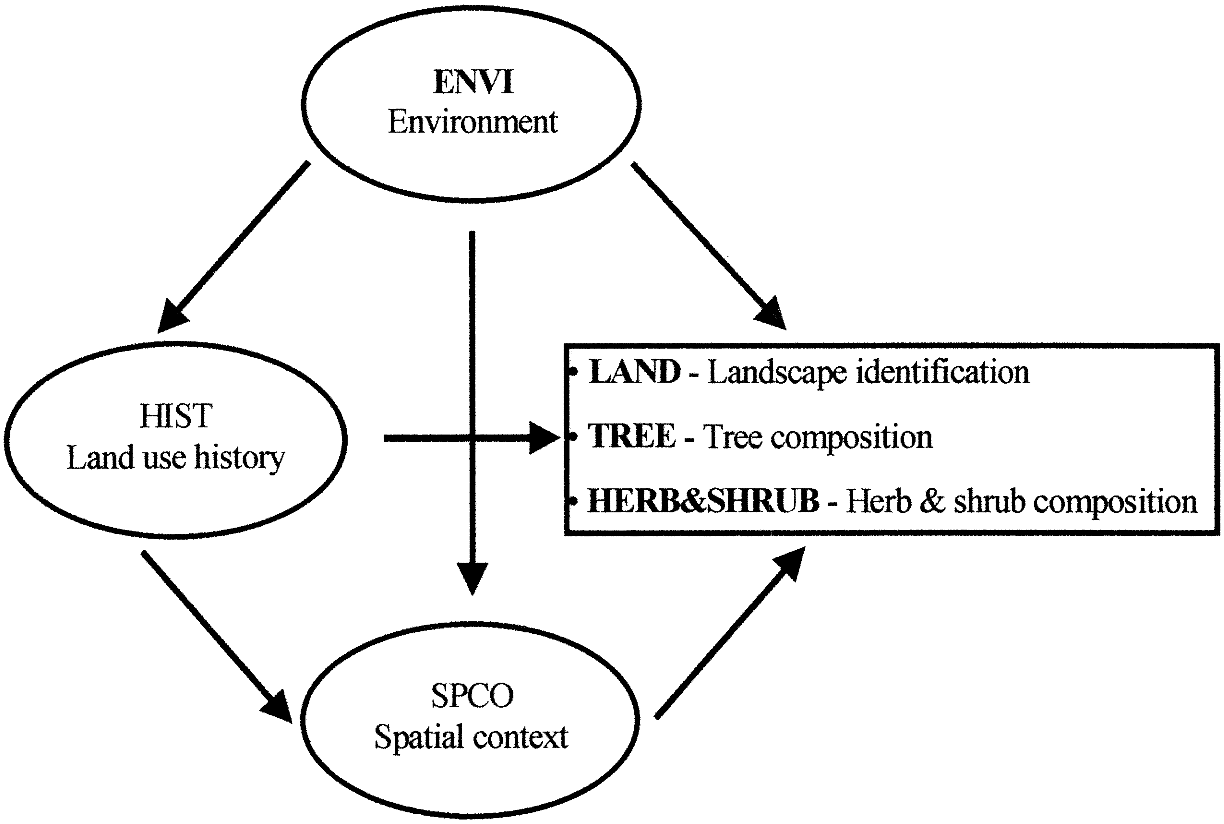
Figure 2: Geomorphic deposits and land-cover types (1958 and 1993) in the glacial and in the mixed landscapes

Geomorphic Deposits



Land uses




ENVI
Environment
HIST
Land use history
SPCO
Spatial context
• LAND - Landscape identification
• TREE - Tree composition
• HERB&SHRUB - Herb & shrub composition

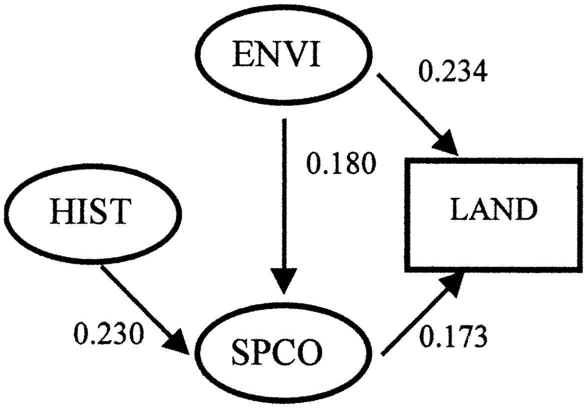
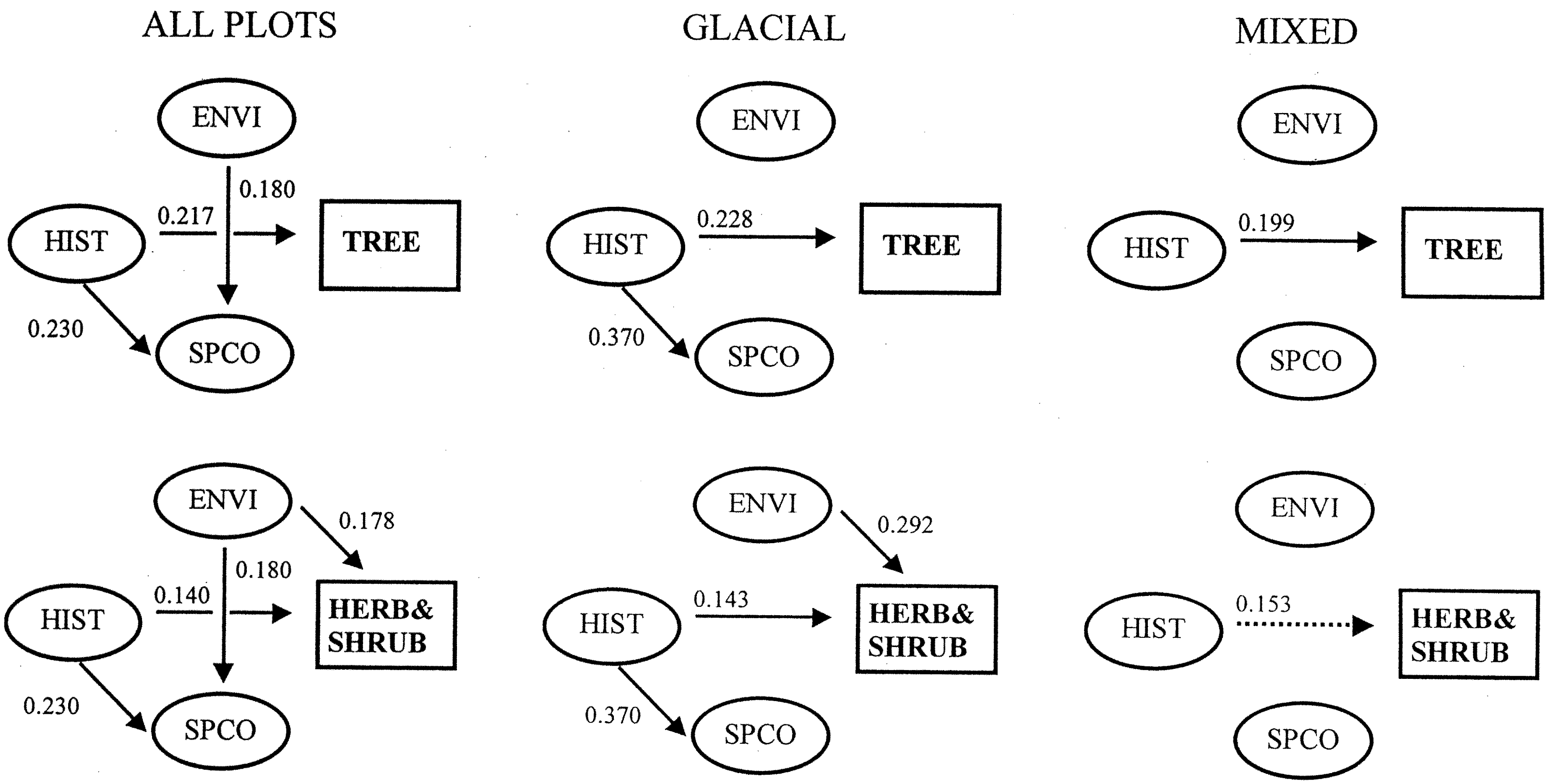


Figure 4: Landscape model showing relationships (path diagrams) linking sets of variables for all plots. Significant relations at the Holm's corrected probability level for an overall significant level of 0.05 are shown with solid arrows. Numbers are path coefficients ranking from 0 to 1 computed from Mantel tests. Higher values denote stronger relationship.

Figure 5: Vegetation models showing relationships (path diagrams) linking sets of variables for all plots and for each landscape separately. Significant relations at the Holm's corrected propability level for an overall significant level of 0.05 are shown with solid arrows. Marginally significant relationships (p between 0.05 and 0.06) are shown with broken arrows. Numbers are path coefficients computed from Mantel tests.



ALL PLOTS

GLACIAL

MIXED

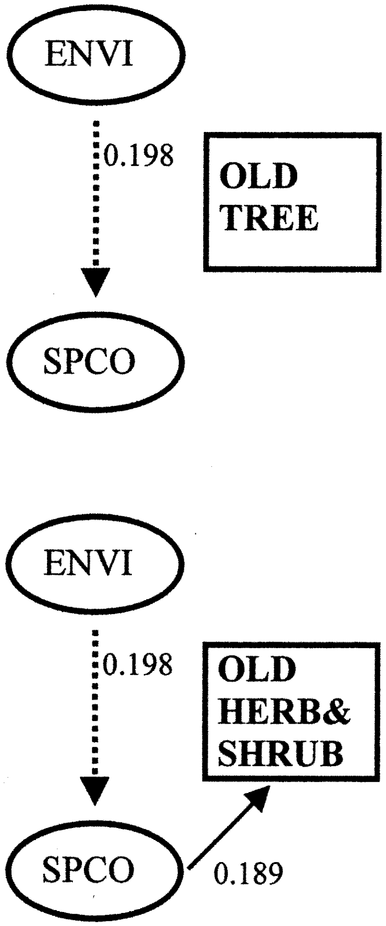
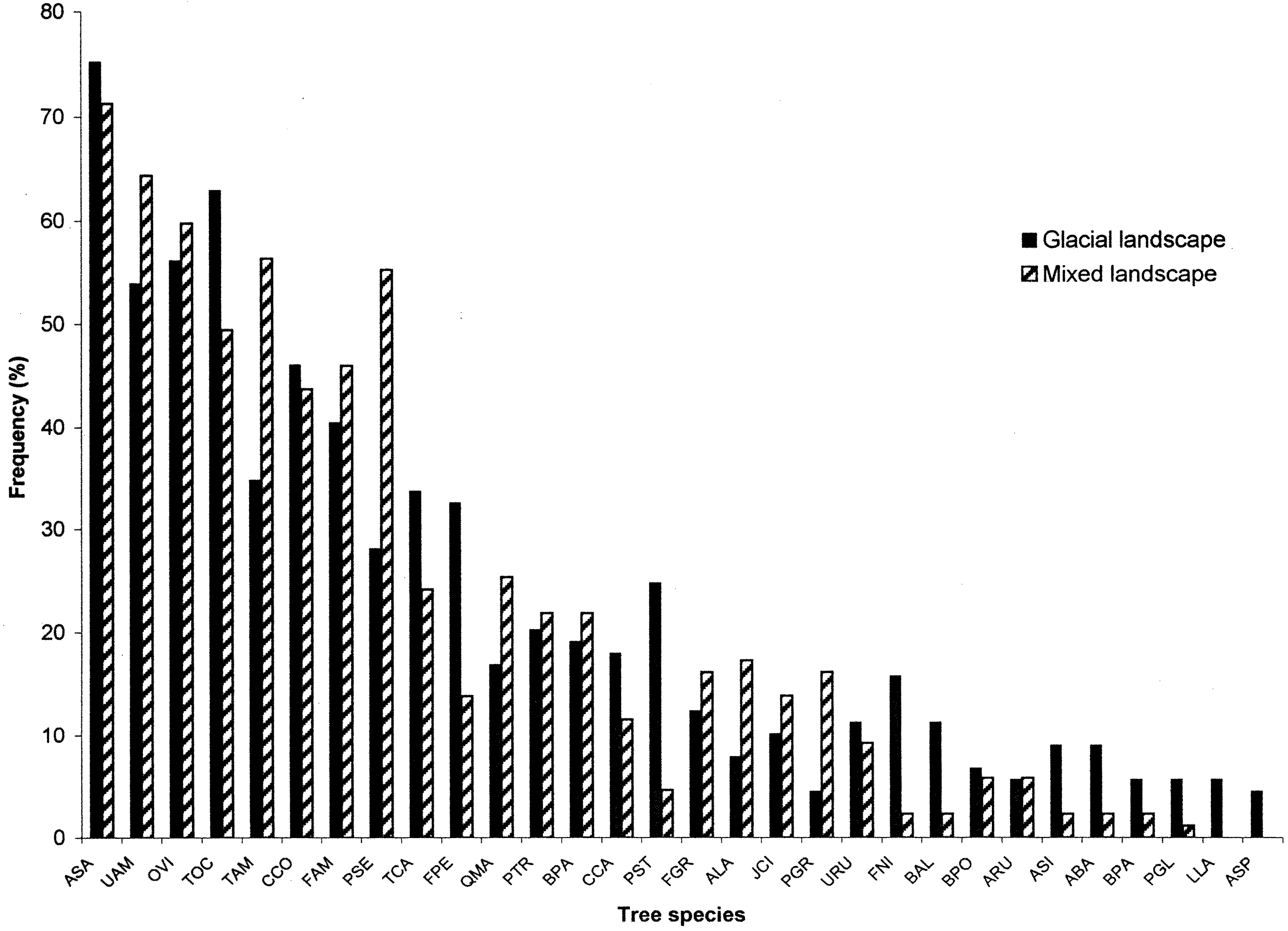


Figure 6: Vegetation model showing relationships (path diagrams) linking sets of variables for the older and less disturbed plots in both landscapes. Significant relations at the Holm's corrected probability level for an overall significant level of 0.05 are shown with solid arrows. Marginally significant relationships (p between 0.05 and 0.06) are shown with broken arrows. Numbers are path coefficients computed from Mantel tests.

Figure 7: Tree species frequency distribution in the glacial and mixed landscapes. Abbreviations stand for:ABA: *Abies balsamea*; ALA: *Amelanchier laevis*; ARU: *Acer rubrum*; ASA: *Acer saccharum*; ASI: *Acer saccharinum*; ASP: *Acer spicatum*; BAL: *Betula alleghaniensis*; BPA: *Betula populifolia*; BPA: *Betula papyrifera*; BPO: *Betula populifolia*; CCA: *Carpinus caroliniana*; CCO: *Carya cordiformis*; FAM: *Fraxinus americana*; FGR: *Fagus grandifolia*; FNI: *Fraxinus nigra;* FPE: *Fraxinus pennsylvanica*; JCI: *Juglans cinerea*; LLA: *Larix laricina*; OVI: *Ostrya virginiana*; PGL: *Picea glauca*; PGR: *Populus grandidentata*; PSE: *Prunus serotina*; PST: *Pinus strobus*; PTR: *Populus tremuloides*; QMA: *Quercus macrocarpa*; TAM: *Tilia americana*; TCA: *Tsuga canadensis*; TOC: *Thuya occidentalis*; UAM: *Ulmus americana*; URU: *Ulmus rubra.*


Frequency (%)
0
10
20
30
40
50
60
70
80
Tree species
ASA
UAM
OVI
TOC
TAM
CCO
FAM
PSE
TCA
FPE
QMA
PTR
BPA
CCA
PST
FGR
ALA
JCI
PGR
URU
FNI
BAL
BPO
ARU
ASI
ABA
BPA
PGL
LLA
ASP
■ Glacial landscape
▨ Mixed landscape

DISCUSSION

Landscape model

As the two landscapes were selected on the basis of the spatial configuration of glacial deposits, we were anticipating some environmental and contextual differences to show up and indeed the findings validate our model. What is unexpected, however, is that we did not detect any significant differences between the two landscapes in terms of history of their vegetation plots. This suggests that human activities in the woodlots were, at some time, little constrained by environmental or contextual differences.

During the reference period (1958 – 1996), changes in vegetation cover were mostly due to successional processes that were allowed to go on when grazing activities declined. Historically, plots seem to have been used for pasture or to provide fuel, or otherwise were left little disturbed regardless of their context. Indeed, some small, isolated islands of vegetation in the mixed landscape have remained forested, whereas others were intensively exploited. Although they experience relatively homogeneous environmental conditions, large patches in the glacial landscape showed a variety of land-cover types, often corresponding with ownership boundaries. These patterns suggest that exploitation activities in the plots appear to have been influenced less by the configuration or environmental characteristics of the sites than by other unmeasured factors that may rest on the individual behavior of owners. Broad ownership patterns (e.g., private, corporate, or public) do influence landscape dynamics (Turner et al. 1996; Crow et al. 1997), but within the same ownership regime, as in private woodlands in rural areas, individual perceptions, needs, or preferences are likely to be determinant (Domon et al. 1993; Kline and Wichelns 1998). This is especially true when the woodlots do not provide the main source of income and are rather perceived as marginal agricultural land (Domon et al. 1993), as it is often the case in prime agricultural area. Although other spatial constraints, such as proximity to farm buildings, cannot be ruled out, the management or conservation of these vegetation patches is likely to rest mainly on individual decisions that are often hard to determine.

Vegetation model

The importance of land-use history

At the scale of our study and for the environmental variables considered, vegetation distribution is best explained by historical factors in both landscapes. Land-use history seems to overrule environmental control for trees. Across our study area, geomorphic deposits are considered stable environmental features determining edaphic conditions. They have been used in ecological classification studies to predict both regional vegetation types (Meilleur et al. 1994; Nolet et al. 1995) and land-use patterns (Paquette and Domon 1997; Pan et al. 1999). However, predictability remains poor for tree communities, especially on mesic sites. A previous study on tree species distribution in relation to soil conditions using spatial coordinates as covariables showed that there remained a significant spatial component when environmental conditions were statistically controlled for (Leduc et al. 1992). This suggests that other factors possessing spatial structure, such as those measured in our study, play a significant role.

Our findings are consistent with patterns observed in other agroforested landscapes of eastern North America, where the intensity and frequency of human activities have led to significant changes in forest type distribution (Foster 1992; Palik and Pregitzer 1992; White and Mladenoff 1994; Abrams and Ruffner 1995; Foster et al. 1998; Fuller et al. 1998). In our area, widespread removal of the original vegetation cover in the 19th and 20th century was followed by spontaneous reforestation, mainly on glacial deposit, after agricultural abandonment. Because of the strong edaphic differences between marine, glacial, and peat deposits, it is likely that they must have originally supported very different vegetation types. Although our knowledge of the pre-European vegetation cover on marine deposits is still scarce, historical data indicate that large non-forested areas, including bogs, were covering extensive surfaces of the clay plain (Jean and Bouchard 1987; Bouchard and Jean in press). As for glacial deposits, historical data (Bouchard et al. 1989; Simard and Bouchard 1996) and field studies in a unique old-growth forest remnant (Brisson et al. 1992; 1994) provide strong evidences of forest composition at the time of settlement. Shade-tolerant species such as *Fagus grandifolia* and *Tsuga canadensis* along with *Acer saccharum* appear to have been co-dominant on mesic sites in the pre-European landscape, whereas the current tree cover is dominated by species of intermediate shade tolerance such as *Ulmus americana, Fraxinus* spp., and *Thuja occidentalis*, or gap-phase species such as *Ostrya virginiana* and *Carya cordiformis* (figure 7). *Thuja occidentalis*, in particular, has been shown to be associated with grazed sites, where it tends to maintain a dense cover that delays reforestation by deciduous species (de Blois and Bouchard 1995). The long-term effects of grazing practices on vegetation may be more persistent than any other disturbances in our landscape.

Foster et al. (1998) examined historical and current relationships between environmental gradients and forest composition in central New England and concluded to broad scale homogenization of forest patterns across substrate and climate gradients. The lack of historical evidences about forest composition on types of deposits others than the glacial ones in our area does not, at the present, allow us to reach the same broad conclusion, although our findings partly hint at similar patterns. Because of differential land-use dynamics following European settlement and different recovery time following disturbances, however, it seems that tree composition has become more heterogeneous, at least on the main substrate type now supporting the remnant natural vegetation (glacial deposits). These findings emphasize strongly the complex interactions between environmental gradients, land-use history, and vegetation assemblages. Land-use activities may result in different patterns depending on the scale of observation and the type and length of environmental gradient sconsidered (e.g., non-discriminant vegetation types across substrate gradient submitted to similar broad-scale human disturbances, increased heterogeneity within environmentally homogeneous substrate showing spatially differentiated land-uses).

Herbaceous and shrub species remain subject to environmental control

If the measured environmental variables have a marginal influence on tree distribution, the same cannot be said of herbaceous and shrub species which show a significant environmental component. These results are consistent with those of Meilleur et al. (1992) who found herbaceous and shrub species to be better ecological indicators of geomorphic features and soil conditions than are tree species in our region. Life history differences between the separate strata may explain the different responses to environmental heterogeneity. Longer lag time between the responses of tree species to disturbances or changes in environmental conditions compared to that of herbaceous or shrub species can lead to different responses in a multidimensional environmental space. In our study, however, the selected environmental variables remain relatively stable. Herbs are also sensitive to local (small-scale) environmental differences that may not influence trees, which can smooth out such differences because of their size (Austin and Nicholls 1988). The finer spatial grain at which herbaceous species have been sampled may have enhanced our ability to detect environmental relationships.

The significance of spatial context

The inclusion of variables that take into account the spatial context or neighboring of patches is relatively recent in vegetation models (Rescia et al. 1994; Bergeron et al. 1997; Roche et al. 1998; Harrison 1999; Liu and Ashton 1999). Depending on the scale of measurements, context can be used to evaluate different processes, ranging from adjacency constraints to broad-scale regional patterns. More importantly, it has to show relevance to the species at hand. Here, we chose to relate it to fine-scale edge-mediated effect that have been shown to affect plant species performance and recruitment (Matlack 1994b; Jules and Rathcke 1999). Gradients of light intensity, air temperature, soil and litter moisture (Matlack 1993), the influence of adjacent management practices such as agricultural herbicides used at the forest/crop interface (Kleijn and Snoeijing 1997; Boutin and Jobin 1998), and the proximity of propagule sources for revegetation (Matlack 1994a; Grashof-Bokdam and Geertsema 1998; Liu and Ashton 1999) are some of the main processes driving compositional changes in these conditions. An ongoing study on herbaceous and shrub species of hedgerows in our landscapes indeed shows a strong influence of adjacent land-cover on vegetation composition, when controlling for environmental effects (de Blois et al. submitted).

Except for herbaceous species at older sites, there is no unique contribution of context to vegetation distribution in most of our models. Failure to detect contextual effects could be related to the spatial scale at which context has been evaluated, but our data suggest that it is mostly related to the overwhelming influence of land-use history. Given the importance of human activities, it is likely that the vegetation in the majority of plots is still showing the influence of past or current management practices that have opened up the canopy, selectively removed species by grazing or logging, modified light conditions and competitive interactions, and allowed the introduction and maintenance of species of little or intermediate shade tolerance. Most plots have yet to recover from these disturbances.

Nevertheless, when we consider older less-disturbed sites, the context has a significant influence on overall herbaceous and shrub species composition. Although this result requires further investigations at the species level to distinguish among alternative hypotheses, the sharp gradient in environmental conditions between mature forest, brushland, and field is likely to influence species distribution, either by restricting forest interior species (Jules and Rathcke 1999) or by facilitating recruitment of edge opportunists. Matlack (1994b) reported edge-orientated pattern to persist for more than 100 years after side canopy closure. Another process specific to our landscapes, however, may have contributed to the observed patterns. Pan et al. (1999) detected for the same time period frequent fine-scale land-cover changes, mostly from forest to crop, occurring at the boundary between deposits. Hence even relatively stable plots that have remained forested during the reference period and that are found at the glacial/marine interface – i.e. plots that are more likely to be surrounded by open field - may have been subjected to edge fluctuations related to agricultural intensification. Herbaceous species are likely to adapt rapidly to such effect, whereas the response of tree species may be lagging, though increase in vegetative or lateral growth of tree species at the edge are often reported, leading to a change in density rather than in composition (Murcia 1995).

In the mixed landscape, the glacial patches have always been isolated from one another by the marine matrix (figure 1). Therefore, these patches have probably always showed marked differences in species composition in relation to the surrounding vegetation types, although the nature and the extent of the edge gradient are still unknown. Agricultural activities in the marine matrix have marked the influence of soil conditions, most likely intensifying edge effects at the glacial/marine interface. Following disturbances, rates and patterns of recovery and subsequent species dynamics under these conditions may differ from those observed in the glacial landscape where patches are less isolated. Low recruitment of slow dispersers as distance from a propagule source increases (Dzwonko and Loster 1992; Dzwonko 1993; Matlack 1994a) and the persistence of invasive species in small patches enhanced by a low interior-to-edge ratio can all help delay natural successional processes (de Blois and Bouchard 1995).

Finally, the inclusion of contextual variables in vegetation models should always be considered with care. Our results showing a link between context and plot environmental and historical conditions highlight the importance of identifying and explaining the common spatial variation shared by these sets of variables in order to extract their unique contribution to species distribution. Consequently, ecological studies should aim to control either experimentally or statistically for the spatial correlation effects that could be related to the configuration of land-uses and the underlying environmental characteristics of the landscape. This is becoming increasingly important as we move from site to landscape studies that are likely to integrate more complex factors and interactive effects.

CONCLUSION

Our models based on a non-parametric approach have highlighted the relative importance of processes structuring vegetation and landscape patterns. The main land-covers (forest, crop, etc.) are largely constrained by geomorphic deposits. Uncultivated vegetation patches, despite environmental and contextual differences, have been submitted to similar disturbances. Within uncultivated patches, vegetation patterns are related to land-use history, a constant for our two landscapes. Unlike tree species, herbaceous and shrub species remain under environmental control and show the effect of context in older plots. Human influences have therefore replaced natural catastrophic events as the main ecological disturbance, obscuring abiotic relationships for tree species. Spatially differentiated land-uses seem to have increased the heterogeneity of the vegetation cover, at least on glacial deposit.

Wooded uncultivated habitats in agricultural areas have economical as well as ecological functions and the challenge is to reconcile both in an intensively managed landscape. From a conservation perspective, knowing the environmental and human influences that drive compositional changes is essential to evaluate the contribution of these landscape elements to the maintenance of ecological processes and vegetation diversity. From a management point of view, a landscape perspective integrating environmental, historical and contextual influences can help inform and orient management strategies and efforts in the manner that will be most productive. Finally, evaluating the relative importance of controlling processes in different landscapes or for different taxa could provide significant insights into a broad theory of landscape and vegetation dynamics and a basis to compare and contrast landscapes across space and time.

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Chapitre 4

FACTORS AFFECTING PLANT SPECIES DISTRIBUTION IN HEDGEROWS OF SOUTHERN QUEBEC

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de Blois, S., G. Domon, & A. Bouchard. Factors affecting plant species distribution in hedgerows of southern Quebec.

SUMMARY

Woody linear features of farmlands have received much attention as pools of diversity in European countries, but they have, in comparison, been little considered in eastern North American ecological studies. Here, we evaluate the relative contribution of environmental conditions, history of management practices, and adjacent land–uses on herb and shrub species distribution in woody hedgerows of agricultural landscapes of Southern Quebec, Canada. We pay particular attention to forest herbs and weed species and identify the multiple factors that explain their presence. We also take into account the geographic coordinates of the samples in order to get a measure of the amount of spatial structuring in the species data and explanatory factors.

Our results show significant differences in composition related to the influence of all sets of factors considered, even when spatial effects are partialled out. Agricultural practices (from intensive crop to fallow land) in adjacent land-uses are especially influential, but our analysis also shows that they correlate with deposit type, increased level of disturbances, and narrower hedgerows. As intensity of agricultural practices in adjacent fields increases, presence of opportunist weed species increases within hedgerows. On the other hand, forest herbs are generally found in more stable structures adjacent to less intensively farmed fields. We discuss the results in terms of interactions between the different determinants of plant diversity in hedgerows, and conclude at the necessity to distinguish between confounding factors to devise proper conservation strategies. To be effective, such

strategies will have to take into account the ecological as well as the agricultural exploitation context in which linear features are found.

INTRODUCTION

Non-agricultural habitats are critical to the conservation of biological diversity and ecological processes in farmlands. They often provide the only elements of structural and biological diversity in landscapes that have otherwise lost most of their natural habitats to agriculture (Burel 1996). Along with their conservation value, some of these habitats also play important ecological functions that can help maintain the sustainability of agricultural activities. Woody linear features such as windbreaks, for instance, play a significant role in controlling soil erosion and have been introduced in many agricultural areas for this purpose (Kort 1988). Field margin strips that increase structural complexity in a landscape may harbor beneficial predators that can provide pest control in adjacent fields (Thies & Tschamtke 1999). Such structural features that can contribute both to the sustainability of ecological processes and the maintenance of agricultural productivity have therefore become the focus of attention in the ecology of agricultural landscapes.

Hedgerows have been the object of several ecological and agronomic investigations, most of them in Europe. In Britain and France, in particular, hedgerows have been part of farming systems for centuries (Baudry et al. 2000). They were deliberately introduced often to mark boundaries between different land-uses or property lines. Awareness of their cultural and ecological values (Oreszczyn & Lane 2000) has increased with the realization that such habitats were under threat with the intensification of agricultural activities (Macdonald & Jonhson 2000). In eastern North America, however, most hedgerows have spontaneously developed along field margins and fences after forest clearance for agriculture. Their composition and dynamics are little known most likely because they have not been given the same ecological and cultural importance that their European counterparts have received. In general, they are still perceived by landowners as marginal structures that can become a nuisance when fields need to be widened or ditches need to be maintained. Worse, they are often seen as refuges for species of weedy propensity that can invade adjacent crops. A novel concern may also arise from the spread of genetically modified crops in agricultural landscape. Non-agricultural habitats may harbor wild relatives of plant species that could integrate the new genes or carry pollen of transgenic insecticidal crops harmful to non-target species (Jesse & Obrycki 2000). Such perceptions are maintained because we still have little data to assess the contribution of non-agricultural habitats to plant diversity and their possible conservation function in agricultural landscapes. Meanwhile, hedgerows in our region are under threat, especially when they border crops in lowland areas where agriculture is the most intensive (Schmucki et al. in prep.).

In eastern North America, floristic composition of hedgerows has been compared to that of other types of habitats such as forest edges or woodlots (Fritz & Merriam 1994; Jobin et al. 1996), and has been assessed along with forest edges for the effect of adjacent agricultural practices (Jobin et al 1997; Boutin & Jobin 1998). Particular attention has also been given to the presence of forest species in relation to hedgerow function as habitat corridors (Fritz & Merriam 1993, Corbit et al. 1999). No study, however, has yet explained species distribution in relation to the various environmental, historical or spatial factors that are likely to interact in such an intensively managed system.

Plant species distribution in hedgerows is certainly influenced by several factors acting at different temporal and spatial scales (Forman & Baudry 1984; Le Coeur et al. 1997). Soil or light conditions within the hedgerow will influence species colonization and survival as in any other plant habitat. Light conditions often correlate with hedgerow structure and the presence of trees or shrubs (Marshall & Arnold 1995). Environmental conditions may in turn be modified by frequent disturbances when management activities are conducted to control hedgerows and prevent their spread into adjacent fields (e.g., elimination of shrubs or trees). Because of their very structure and narrow width, however, hedgerows are likely to be impacted by practices in adjacent parcels more than any other habitats (Jobin et al. 1997; Le Coeur et al. 1997; Boutin & Jobin 1998). The more intense the agricultural activities in adjacent fields, the more frequent are likely to be interventions to control the spread of hedgerows. Also, frequent tillage and heavy use of herbicides and fertilizers in intensive farming systems can selectively favor some species to the detriment of other (Kleijn & Snoeijing 1997; Marrs & Frost 1997). Environmental conditions and management practices within the hedgerows, as well as the type of adjacent land-uses, are all likely to determine plant species composition. It is therefore important to evaluate the relative contribution of these factors and to take into account their possible interactions for a better assessment of hedgerow diversity and function in the landscape.

In this study, we evaluate the relative contribution of environmental conditions, history of management practices, and adjacent land–use on overall herb and shrub species distribution in woody hedgerows of agricultural landscapes of Southern Quebec, Canada. We pay particular attention to forest herbs and weed species and identify the multiple factors that explain their presence. We also take into account the geographic coordinates of the samples to get a measure of the amount of spatial structuring in the species data and explanatory factors.

METHODS

Study area

This study and others (Pan et al. 1999; de Blois et al. in press; Schmucki et al, in prep.) have been initiated to understand the landscape and vegetation dynamics in agroforested landscapes of southern Quebec. The study area is located in Godmanchester, a rural municipality of 139 km^2 within the Haut-Saint-Laurent region in the southernmost part of the Province of Quebec (figure 8). The region is part of the deciduous forest of the Great Lakes and St-Lawrence River system (Rowe 1972). Mesic forests are generally dominated by *Acer saccharum*, with *Carya cordiformis, Ostrya virginiana, Tilia americana, Fagus grandifolia*, and *Tsuga canadensis* (Brisson et al. 1988; Meilleur et al. 1994).

Following European settlement in the 19th century, the region has been under intensive exploitation, first for timber and then for agriculture (Simard & Bouchard 1996; Bouchard & Domon 1997; Paquette & Domon 1997). Today, land-cover and land-uses correlate with soil conditions that are strongly determined by geomorphic deposit type (mostly glacial and marine deposits) (Pan et al. 1999). Uncultivated vegetation patches and low-intensity agricultural practices (e.g., pasture) are often confined to the numerous moraine islets and ridges of glacial origin. More intensive agricultural activities related to dairy farming and grain and cereal production are concentrated in the rich lowlands covered with marine clay deposits left by the ancient Champlain sea. Land-use dynamics in this area is typical of many other agricultural or agroforested landscapes in eastern North America. Land parcels are generally rectangular and lie parallel to each other.

Hedgerows, all of spontaneous origin, usually mark current or ancient property lines, or sub-divide parcels with different covers or crops. In the marine lowlands, they sometimes run along drainage ditches that appeared, for the most part, in the middle of the 20th century. On glacial substrates, they mostly run along old rock fences or barbwires that were likely put in place in the 19th century when agricultural activities expanded in the region. Schmucki et al. (in prep.) compared the spatial and temporal (1958 – 1999) dynamics of three hedgerow networks, located in three landscape units that differed by the nature and spatial arrangement of their geomorphic features. They observed changes in land-use patterns and hedgerow characteristics with marked differences between glacial and marine landscapes.

Field sampling and data collection

For the purpose of this study, we defined hedgerows as linear features that border farmlands and include woody species. Such features are often organized in complex networks within the landscape and can be submitted to different environmental and management influences that operate at several spatial scales (Schmucki et al. in prep.). For instance, the same linear feature located on a homogeneous deposit can be bordered by different land-uses (e.g., cash crops, fodder crop, fallow land) on one or both sides. Within a similar adjacent land-use, a hedgerow section may have been submitted to differential treatments, either related to past land-use practices when the land was subdivided differently or because of current selective intervention conducted on a small portion of the hedgerow. Our sampling scale was chosen to take into account these possible sources of variability. Because marine and glacial deposits are strong determinants of land-use cover and hedgerow dynamics in the landscape (Pan et al. 1999; Schmucki et al. in prep.), and of understory vegetation cover in woodlands (de Blois et al. in press), hedgerows were selected on these two types of substrates using geomorphic maps and aerial photographs. Within a linear feature, sampling of vegetation cover was done using contiguous 25 m long transects running along the midline. Sampling plots, which all showed a single type of land-cover on each side, were then treated as independent sampling units, but geographic coordinates were included in our vegetation model to take into account possible spatial correlation effects. Sampling was conducted in spring and summer of 1997. A total of 158 plots were retained for analyses.

Cover of herbaceous and shrub species was recorded using the line intercept method. Some species that were difficult to distinguish when not in flowers or fruits were grouped (e.g., *Viola* spp.). Nomenclature follows Marie-Victorin (1964) and Gleason & Cronquist (1991). Hedgerow width, the perpendicular distance to the outermost edges of the hedgerow, was recorded at the midpoint (12,5 m). Adjacent land-use type was noted on each side of the plot. Land-use types included crops (mostly corn and soybean rotation), forage crops (alfafa or hay), fallow land, and pasture. Signs of disturbances in the plot including cut branches, stumps, traces of fire or herbicide treatments were noted.

We used aerial photographs from 1958, 1965, 1979, and 1992, along with field data collected in 1997 to evaluate plot management history. Plots were classified for each year as showing either a low vegetation cover (dominated by shrubs or low trees) or a high vegetation cover (mature trees). This dynamic measure of hedgerow structure was used as an indication of the stability of hedgerows and of the frequency of management practices to reduce tree cover in the plot.

Data analysis

We first computed the percent cover of each species in each plot, calculated as the total fraction of the line covered by a species x 100. To eliminate the effect of rare species on the correspondence analyses, we only retained the species that were present in at least 3 of the plots. As well, some species were grouped to facilitate ordination interpretation (for ex. *Trifolium repens*, *T. pratense; Medicago lupulina,* *M. sativa*). 89 species or taxa were retained for ordination analyses, whereas a total of 126 species or taxa were sampled.

We then conducted correspondence analyses (CA), canonical correspondence analyses (CCA), and partial CCA to evaluate the contribution of individual variables and sets of variables to herb and shrub species composition (terBraak 1986; Borcard et al. 1992; Palmer 1993). In CCA, the ordination axes are constrained to be linear combinations of the supplied set of environmental variables. Canonical eigenvalues give an indication of the amount of variation in the species data that is related to the supplied explanatory variables. Partial CCA allows one to remove, by multiple linear regressions, the effects of covariables. Significance of environmental variables and of canonical ordination axes was assessed using 999 Monte-Carlo permutation tests. Individual variables were selected using the selection procedure of the CANOCO program (terBraak & Smilauer 1998). Variables that were not significant at the 0.05 level in a model initially including all the variables were dropped from the final data set.

Selection of individual explanatory variables

Several explanatory variables were tested for their effect on species distribution. Three general categories of variables were tested: site environmental conditions, management history, and effect of adjacent land-uses.

Environmental conditions included the type of geomorphological deposit: marine or glacial (dummy binary variable), and hedgerow width (between 4.3 m and 11.3 m). Because deposit has only two states, only one needs to be coded. It was coded as marine deposit. These variables were included in an environmental matrix that was related to the species data using CCA. Significant environmental variables were then retained for further analyses.

For the *management history* matrix, we summarized historical data so as to reflect a gradient of intensity of disturbances related to management activities within the hedgerow: a) F_d is the number of times a plot was recorded as being dominated by a low vegetation cover during the reference period (1958, 1965, 1979, 1992, and 1997) (quantitative variable); higher values are an indication of frequent interventions to maintain low vegetation cover. b) L_d is the last year a plot was dominated by a low vegetation cover (quantitative variable); a plot may have shown a low cover only once in 1958, an indication of its stability, or only once in 1997, indicating more recent disturbances; plots that retained a high tree cover for all the years were given the arbitrary value of 1944, which is 1958 – 14 years, the largest value separating 2 periods. c) we also included a composite term defined by multiplying $F_d \times L_d$ (quantitative variable); this new variable takes into account the combined effect of the two previous terms; the higher values are assumed to be associated with more recent and more frequent disturbances.

Adjacent land-uses were classified so as to reflect a gradient of agricultural intensity. The categories were chosen after preliminary testing that included all the different combinations of land-use surveyed. Adjacent land-use categories included the following (from higher to lower intensity): 1) crop - one or both sides are corn and soybean rotation with frequent use of herbicides, chemical fertilizers, and tillage; 2) forage crop - both sides are characterized by hay (*Poa* spp., *Trifolium* spp., etc.) or alfafa (*Medicago sativa*), crops that usually require irregular use of chemical herbicides but some use of chemical fertilizers; 3) fallow land on one side and forage crop on the other; 4) both sides are fallow land; 5) one side is used as pasture. All the categories are mutually exclusive. These variables were included in an adjacency matrix that was related to the species data using CCA.

Relative influence of sets of explanatory variables

To evaluate the relative influence of a particular set of explanatory variables, we used partial CCA with each individual set as constraining variable while controlling for the effect of all other variables in the model. This step allowed us to test for significant effect while controlling for shared variation between the explanatory variables.

Spatial component of species variation

To get a measure of the amount of spatial structuring in species distribution and to extract the spatial component of our explanatory variables, we conducted a series of partial CCA using geographic coordinates and all explanatory variables alternatively as constraining variables and covariables (Borcard et al. 1992). We computed a matrix of spatial coordinates that initially included all 9 terms of a cubic polynomial equation of the x and y geographic coordinates and selected the most significant terms ($p < 0.001$) after running CCA. The 5 terms retained were x, y, xy, y^2, xy^2.

Presence of forest herbs and weed species

We used stepwise logistic regressions to identify the factors that could best predict the presence of forest herbs or of weed species. Are considered as forest herbs perennial, herbaceous plants generally characteristic of the shady interiors of forests in our area (Marie-Victorin 1964). Weeds were identified as such using published information (Anonymous, 1981; Frankton & Mulligan 1987; Uva et al 1997). Each sampling site was coded for presence/absence of forest herbs or weed species. To simplify the model, a new semi-quantitative variable that included all the adjacent land-use types was created. Adjacent land-use types were coded from 1 to 5 from the least to the most intensive agricultural practices: fallow land, pasture, fallow & forage, forage, and finally crop. The model included 4 variables: type of geomorphological deposit, hedgerow width, the management history composite variable ($F_d \times L_d$), and the new semi-quantitative adjacent land-use variable. Logistic regressions were performed using SAS (SAS 1989).

RESULTS

Selection of individual explanatory variables

Of all the explanatory variables initially selected and tested in CCA, all but one were found highly significant and were retained in the final data set for further analyses (table V). Forage crop as the sole adjacent land-use was found to be not significant and was therefore excluded. Deposit type, crop, and the combination of fallow land and forage crop as adjacent land-uses, were especially influential in their respective data sets (table V).

Relative influence of sets of explanatory variables

When controlling for all other influential variables, all sets of explanatory variables remained highly significant (p of canonical ordination axes = 0.001) (table VI). Each set therefore has a unique contribution to species variation. Because of its higher canonical eigenvalues, adjacent land-uses appear to have a greater contribution to herbaceous and shrub species distribution. It uniquely contributes to 9.4% of total species variation (0.565*100/6.0), whereas environmental conditions and management history respectively explain 5% (0.300*100/6.0) and 3.7% (0.223*100/6.0) of species variation, when controlling for all other variables (table VI).

Spatial component of species variation

All CCA and partial CCA, using all the variables in one data set and spatial coordinates in another, and setting each set alternatively as constraining variables and covariables, were found to be highly significant (p = 0.001) (table VII). When it is the only constraining data set, environmental, land-use, and history variables explain 25.1% of the total species variation (1.507*100/6.0). Details of this ordination are found in tables VII and VIII, and figure 9.

When controlling for spatial location, variation explained by all the variables drops to 17.0% (1.019*100/6.0) (table VII). Spatial location as the only constraining variable explains 16.6% of species variation (0.998*100/6.0). When controlling for all other variables, the value drops to 8.5 % (0.510*100/6.0). Variation partitioning therefore reveals that both sets share a common structure, but also uniquely contribute to species composition variation. Variation of the species data can be partitioned as follows: 1) non-spatial component of the environmental, history, and land-use variation: 17.0%; 2) shared variation between the spatial coordinates and all other variables: 8.1%; 3) unique contribution of spatial variation that is not shared by other explanatory variables: 8.5%; 4) total explained variation: 33,6%; 5) unexplained and stochastic variation: 66.4%.

Species composition

Figure 9 displays the ordination of species constrained by all 9 explanatory variables. Table VII and figure 9 clearly show the division between, on the one hand, species that tend to be associated with marine deposits, intensive adjacent land-uses (crop), higher intensity and frequency of disturbance events within the hedgerow, and narrower hedgerows, and, on the other hand, species associated with less intense agricultural practices (fallow land and pasture), less disturbances, and wider hedgerows.

To better highlight, these patterns, we classified each site according to the type of deposit - marine or glacial - and adjacent practices – crop or non-crop (forage, fallow land or pasture) (fig. 10). The resulting site ordination reveals a gradient of intensity of agricultural practices that tends to override deposit constraints for several sites adjacent to crop. Most sites that have forage on both sides, whether on marine or glacial deposit, group with sites adjacent to crop. As well, several glacial sites adjacent to crop tend to group with marine/crop sites, whereas most other glacial/crop sites show a compositional gradient that clearly separate them from other glacial sites.

Of all the species sampled, the majority were native species (63% native vs 37% introduced) with a relatively small proportion of annual or biennial species (14%). As we would expect, the proportion of introduced species is relatively high compared to other less disturbed habitats in North America. Woody species accounted for 21% of the flora. Forest species accounted for 22% of the flora. They were found in up to 72% of the plots. The most frequent were *Smilacina racemosa* (27%), *Sanguinaria canadensis* (27%), *Aster cordifolius* (27%), and *Viola* spp. (23%). *Trillium grandiflorum* (10%) and *Erythronium americanum* (9%) were also relatively common. Species considered as potential weeds of agricultural crops also accounted for 22% of the flora and were present in 77% of the plots. The most frequent were *Bromus inermis* (59%), *Taraxacum officinale* (31%), and *Arctium minus* (22%).

Species showed different distribution patterns in relation to our explanatory variables depending on their characteristics (figure 9). Whereas native species are found in all types of conditions, forest species are mostly associated with glacial habitats and tend to concentrate in the less disturbed sites associated with less intense adjacent agricultural practices (e.g., *Trillium spp.*, *Erythronium americanum*, *Aralia nudicaulis).* Species of weedy propensity, although found in all habitats, tend to concentrate in the more disturbed sites adjacent to intensive crops. They include introduced species as well as native opportunists (e.g., *Equisetum arvense, Asclepias syriaca*). Finally, the most common species were woody species, including *Vitis riparia* (89% of the sites), *Rubus idaeus* (77%) and *Prunus virginiana* (59%). The majority of woody species were associated with glacial habitats, the most commonly distributed being found in the center of the ordination (e.g., *Vitis riparia, Rubus idaeus*).

Stepwise logistic regression modeling the presence or absence of forest species retained only the variable measuring the intensity of adjacent land-uses as significant. The fitted model is:

$$\text{Forest} = -5.8873 + 1.1079 \text{ x (adjacent land-use)}$$

As for weed species, their presence or absence was best predicted in the logistic regression model by adjacent land-use and by the width of the hedgerow. All the other variables were not retained after selection. The model is:

$$\text{Weed} = -2.5915 + 0.4335 \text{ (Width)} - 0.5575 \text{ (Adjacent land-use)}$$

Both the intercept and the slope coefficients of the models were significant ($p < 0.05$).

Table V. Variables tested in each of the 3 explanatory data sets. Significance was tested with Monte-Carlo permutation tests (999 permutations). The non-significant (ns) variables in a model including all variables were excluded from the final set for subsequent partial and spatial analyses.

Variables and data sets	Variance explained	Significance (p)
Environmental conditions		
Deposit (MAR)	0.432	0.001
Hedgerow width (WIDTH)	0.258	0.001
Management history		
Compsite term (F_d) x (L_d)	0.178	0.001
Frequency of disturbance (F_d)	0.163	0.001
Last disturbance (L_d)	0.121	0.001
Ajacent land-uses		
Crop (CROP)	0.40	0.001
Forage crop & fallow land (FOR&FAL)	0.372	0.001
Pasture (PASTURE)	0.237	0.001
Fallow land (FALLOW)	0.187	0.001
Forage crop (FORAGE)	-	ns

Table VI. CCA and partial CCA analyses with one explanatory set as constraining variable and all the other factors as covariables. Significance of ordination axes was tested with Monte-Carlo permutation tests. All tests were highly significant (p = 0.001). The sum of unconstrained eigenvalues in a correspondence analysis (CA) of species data is 6.0. See table V for variable codes.

Constraining set	Covariables	Sum of all canonical eigenvalues
Environmental condition: MAR, WIDTH	-	0.572
Environmental condition: MAR, WIDTH	F_d, L_d, F_d x L_d, CROP, FOR&FAL, FALLOW, PASTURE	0.300
Management history: F_d, L_d, F_d x L_d,	-	0.527
Management history: F_d, L_d, F_d x L_d,	MAR, WIDTH, CROP, FOR&FAL, FALLOW, PASTURE	0.221
Adjacent land-use: CROP, FOR&FAL, FALLOW, PASTURE	-	0.884
Adjacent land-use: CROP, FOR&FAL, FALLOW, PASTURE	MAR, WIDTH, F_d, L_d, F_d x L_d,	0.565

Table VII: Contribution of all explanatory variables and spatial coordinates to species variation. Significance of ordination axes was assessed using permutation tests. The sum of unconstrained eigenvalues in a correspondence analysis (CA) of species data is 6.0. All tests were significant at the 0.001 level. See table V for variable codes.

Constraining variables	Covariables	Sum of all canonical eigenvalues
MAR, WIDTH, F_d, L_d, F_d x L_d, CROP, FOR&FAL, FALLOW, PASTURE	-	1.507
MAR, WIDTH, F_d, L_d, F_d x L_d, CROP, FOR&FAL, FALLOW, PASTURE	Spatial coordinates	1.019
Spatial coordinates	-	0.998
Spatial coordinates	MAR, WIDTH, F_d, L_d, F_d x L_d, CROP, FOR&FAL, FALLOW, PASTURE	0.510

Table VIII : Result of a CCA ordination of species data constrained by all environmental, historical, and land-use variables showing the amount of variation explained by each individual variable and correlation with the first 2 canonical axes All the variables and canonical axes were found significant at the 0.001 level (999 permutation tests). * Eigenvalue are shown below each axis. See table V for variable codes.

Variable	Variation explained	Axis 1 (0.499*)	Axis 2 (0.304*)	Axis 3 (0.238*)	Axis 4 (0.167)
MAR	0.432	-.8629	.3612	-.2542	-.0990
CROP	0.400	-.8107	-.4328	-.0035	.2842
FOR&FAL	0.372	.7180	.1610	-.6647	-.0251
WIDTH	0.258	.5530	-.3678	-.2432	-.2713
PASTURE	0.237	.2011	.5588	.5020	.6143
FALLOW	0.187	.2508	.1158	.4917	-.6968
$(F_d) \times (L_d)$	0.178	.4058	.1385	-.4655	.0175
F_d	0.163	-.3194	.1864	-.5081	-.0323
L_d	0.121	-.3147	-.0234	-.3394	-.0342

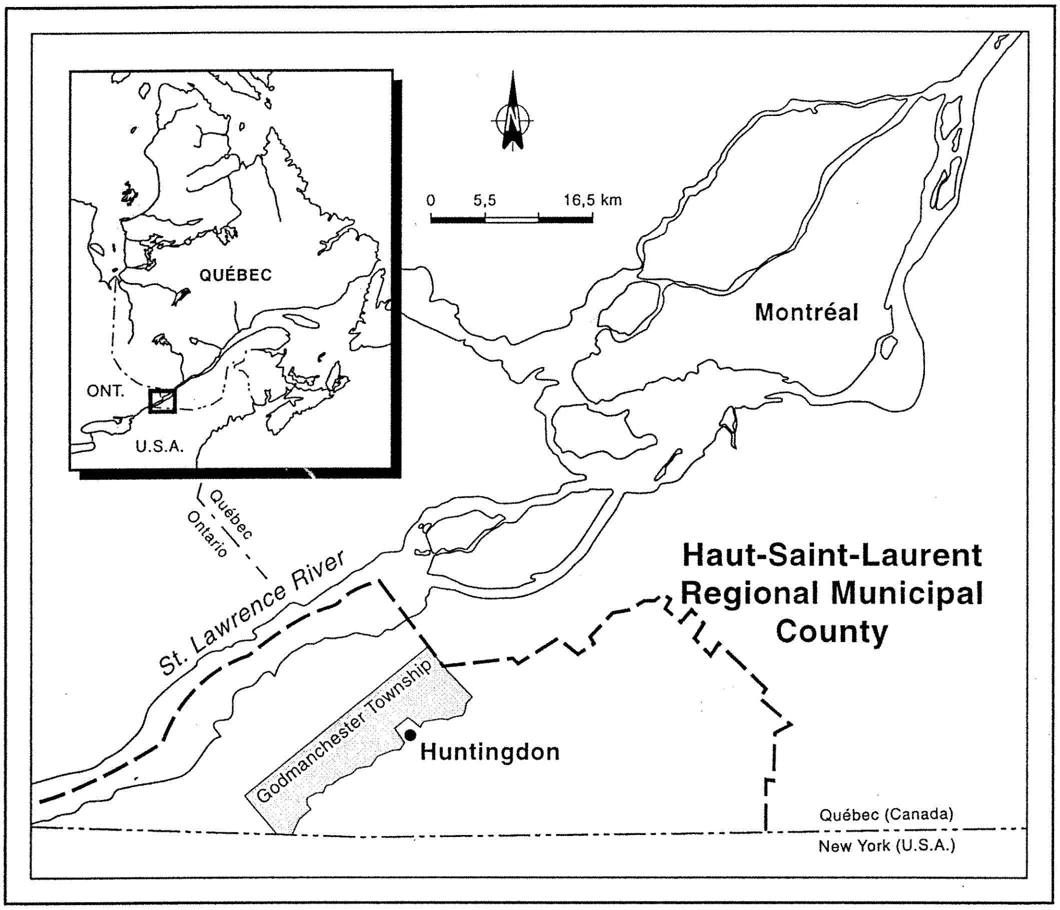

Figure 8: Location of study area.

Figure 9: Ordination of plant species in relation to explanatory variables. Quantitative variables are represented as arrows and ordinal variables by their centroids. Forest species are underlined, whereas potential weed species are in italic. AAN *Apocinum androsaemifolium;* ACA *Asarum canadense;* ACO *Aster cordifolius;* ACT *Actaea spp.;* AGR *Agrimonia gryposepala;* AMA *Aster macrophyllus;* AMI *Achillea millefolium;* AMN *Arctium minus;* ANU *Aralia nudicaulis;* APE *Adiantum pedatum;* AST *Aster spp.;* ASY *Asclepias syriaca;* BIN *Bromus inermis;* BNI *Brassica nigra;* CAL *Cornus alternifolia;* CAR *Carex spp.;* CAV *Cirsium arvense;* CLU *Circaea lutetiana;* COB *Cornus obliqua;* CRA *Cornus racemosa;* CSC *Celastrus scandens;* CSP *Crataegus spp.;* CST *Cornus stolonifera;* CTH *Caulophyllum thalictroides;* DCA *Daucus carota;* DDP *Dentaria diphylla;* DSP *Dryopteris spinulosa;* EAM *Erythronium americanum;* EHE *Epipactis helleborine;* EQU *Equisetum spp.;* ERI *Erigeron spp.;* FVI *Fragaria virginiana;* GAL *Geum aleppicum;* GLA *Galium lanceolatum;* GPA *Galium palustre;* GTE *Galeopsis tetrahit;* HIE *Hieracium spp.;* HPE *Hypericum spp.;* HVI *Hydrophyllum virginianum;* ICA *Impatiens capensis;* LAL *Lychnis alba;* LCO *Lotus corniculatus;* LVU *Linaria vulgaris;* MAL *Melilotus alba;* MCA *Maianthemum canadense;* MCD *Menispermum canadense;* MLU *Medicago lupulina; M. sativa;* ORE *Osmunda regalis;* OST *Oxalis stricta;* PAQ *Pteridium aquilinum;* PMA *Plantago major;* PNI *Prunus nigra;* POL *Polygonum spp.;* PPT *Poa spp.; Phleum pratense;* PPU *Polygonatum pubescens;* PQU *Parthenocissus quinquefolia;* PRC *Potentilla recta;* PSA *Pastinaca sativa;* PVI *Prunus virginiana;* RAC *Ranunculus acris;* RAL *Rhamnus alnifolius;* RAM *Ribes americanum;* RCA *Rubus canadensis;* RCT *Rhamnus catharticus;* RCY *Ribes cynosbati;* RID *Rubus idaeus;* ROC *Rubus occidentalis;* ROD *Rubus odoratus;* RRA

Rhus radicans; RTY *Rhus typhina;* SAL *Spiraea alba;* SCA *Sanguinaria canadensis;* SCU *Silene cucubalus;* SDU *Solanum dulcamara;* SMA *Sannicula marilandica;* SOL *Solidago spp.;* SPU *Sambuscus pubens;* SRA *Smilacina racemosa;* SSP *Salix spp.;* TER *Trillium erectum;* TGR *Trillium grandiflorum;* TOF *Taraxacum officinale;* TRE *Trifolium repens; T. pratense;* VCA *Viburnum cassinoides;* VCR *Vicia cracca;* VLE *Viburnum lentago;* VRI *Vitis riparia;* VSP *Viola spp.;* ZAM *Zanthoxylum americanum.*

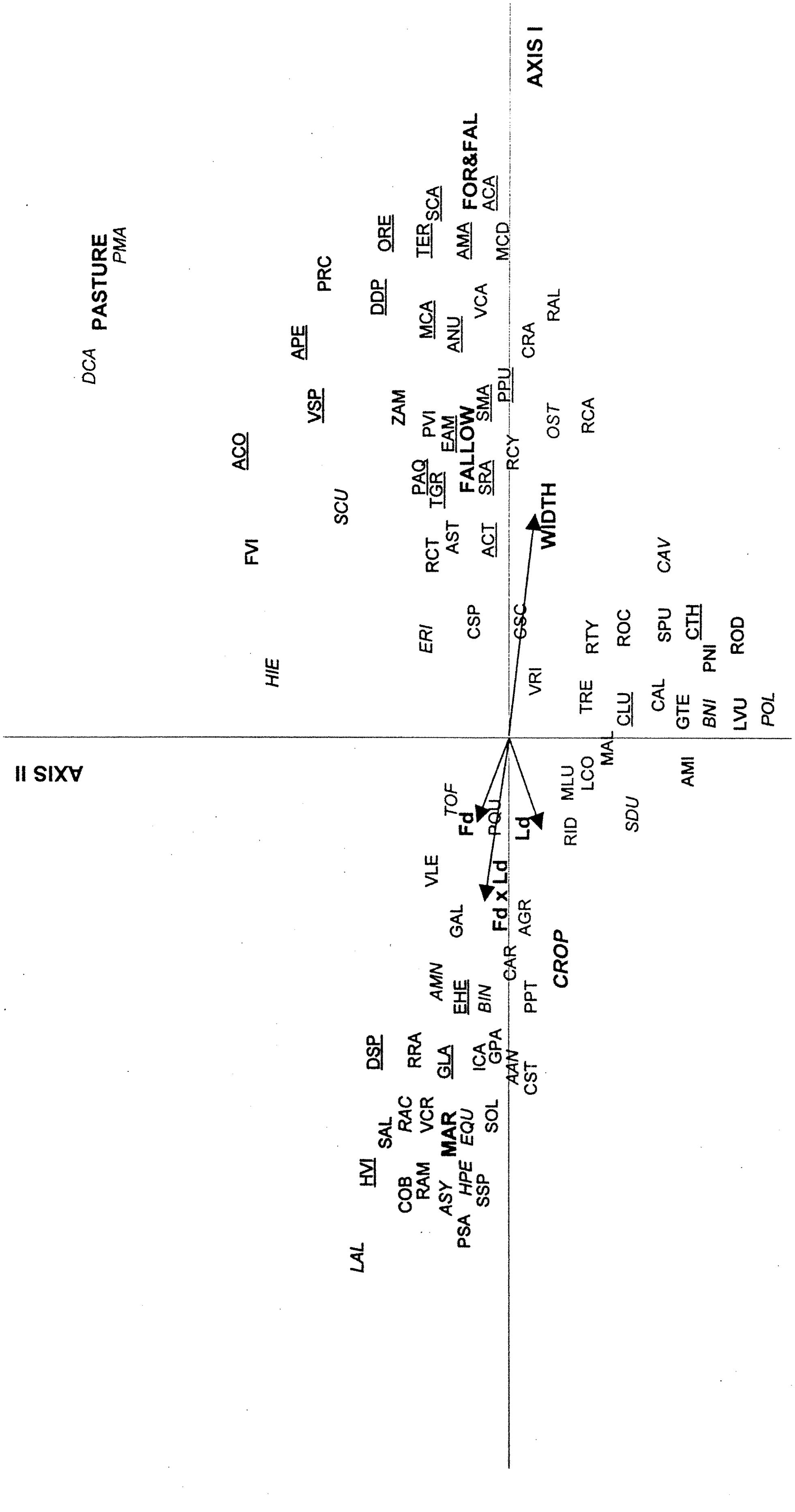
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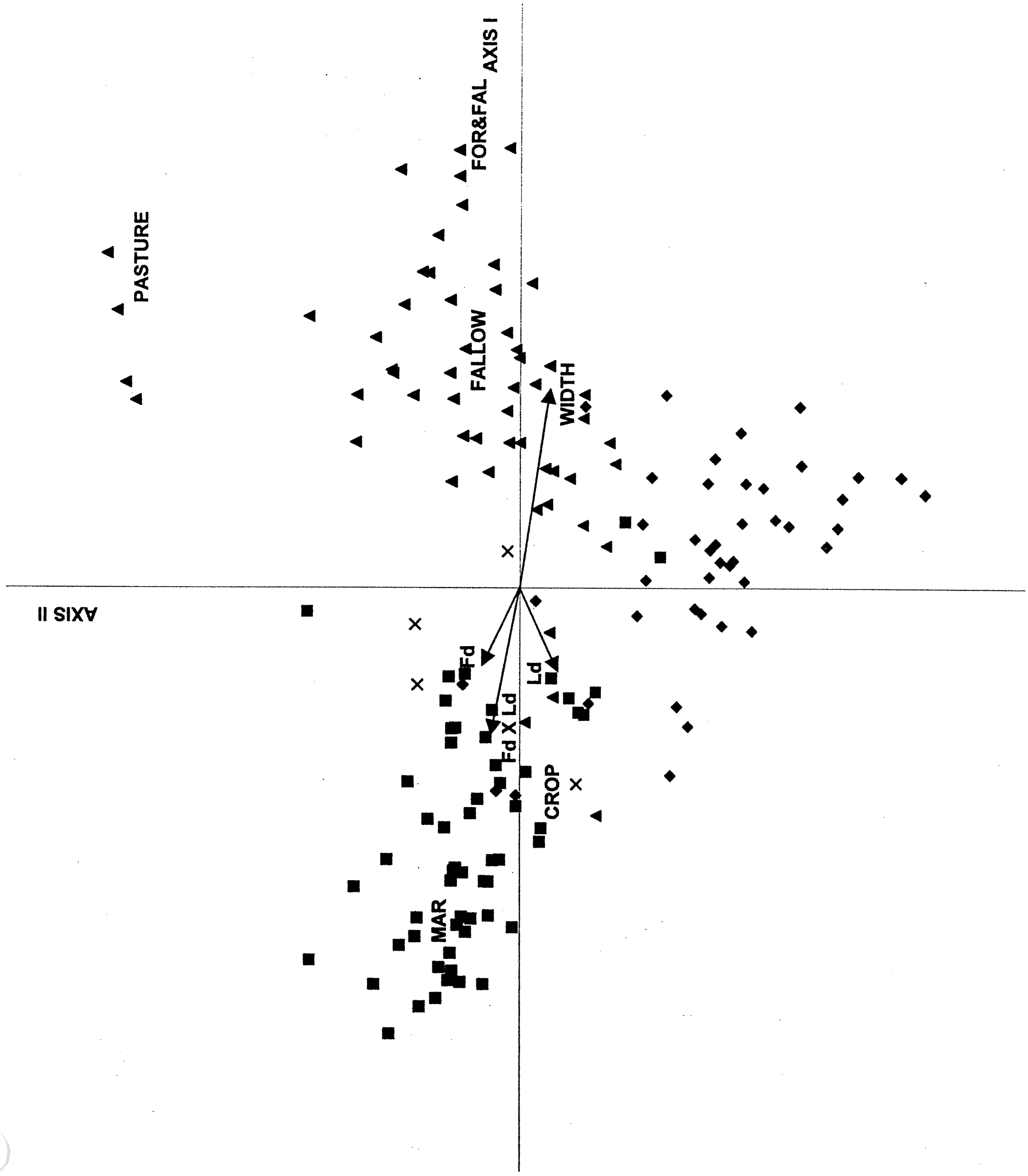
Figure 10: Ordination of sites in relation to explanatory variables. Sites have been classified as: ■ Crop –Marine; ◆ Crop-Glacial; ✕ Non-crop-Marine; ▲ Non-crop-Glacial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DISCUSSION

Effect of explanatory variables

In our study area, the geomorphic deposit is considered a stable environmental feature determining edaphic conditions. It has been used in ecological classification studies to predict both regional vegetation types (Meilleur et al. 1992; Meilleur et al. 1994; Nolet et al. 1995) and land-use patterns (Paquette & Domon 1997; Pan et al. 1999). Predictability remains poor for tree species (Leduc et al. 1992), however. Herb and shrub species of woodlands, on the other hand, have been shown to relate to environmental conditions, even when other factors such as land-use history or land-use context (e.g., plots adjacent to fields) are controlled for (de Blois et al. in press). This is also true of herb and shrub species in hedgerows, and our results indicate that deposit type is a determinant factor. Part of this influence has to do with the edaphic constraint imposed by marine or glacial deposits. We do not expect species intolerant to heavy clay soil and poorer drainage generally associated with marine deposit to be found in these habitats. For instance, several species tolerant of more hydric conditions (e.g., *Spiraea alba*, *Cornus obliqua*, *Salix spp.*) are characteristic of the hedgerows found on marine sites, whereas species of more xeric habits such as *Zanthoxylum americanum* or *Rhus typhina* are mostly associated with glacial sites. In the latter case, erection of stone fences or piling of rocks or other field debris tends to enhance xeric conditions for understory species.

Part of the species variation associated with the differences between marine and glacial sites, however, can also be related to the management practices within the hedgerows. Because of their better agricultural potential, soils of marine origin are generally intensively cultivated. In our samples, plots associated with marine soils also tend to be more disturbed than hedgerows associated with glacial sites. Schmucki et al. (in prep.) conducted a study in the same territory to understand hedgerow dynamics in relation to geomorphic deposits and changes in land-uses. They observed greater fluctuations in the vegetation structure of hedgerows (dominance by tall trees vs low trees or shrub cover) in hedgerows associated with marine landscapes than with hedgerows associated with glacial conditions. Our results corroborate these findings and highlight the consequences for plant species distribution.

Intensification of agricultural practices requires more frequent and more drastic interventions to prevent hedgerows from encroaching on agricultural land when tillage is frequent or to clean up drainage ditches that often border hedgerows on clay soils. Shading from trees can also have a negative influence on yield (Sparkes et al. 1998). As a consequence, hedgerows are not only more disturbed, but they are also generally narrower. On the other hand, hedgerows on glacial deposits seem more stable, even when surrounded by crop, than hedgerows in the lowlands. They are often associated with stable structures such as ancient stone fences that were established when land was initially cleared for agriculture in the 19th century. Hedgerow management in this case is more selective and less drastic, with trees being cut here and there when they become a nuisance for adjacent cultures.

Weeds in hedgerows

Because hedgerows are by definition an all-edge habitat, we expect light-requiring species to do well. But opportunist species (e.g., *Asclepias syriaca, Panistica sativa, Taraxacum officinale*), some of them weeds of agricultural crops, will do even better in hedgerows when the level of disturbance increases. Our results show that increased levels of disturbances in hedgerows correlate with the more intensive agricultural practices, and the consequence is to facilitate invasion by opportunist weed species characteristic of unstable habitat.

Both the direct management practices within the hedgerows that contribute to reduce width and tree cover, and the indirect effects of inputs from adjacent fields (e.g., herbicides, fertilizers) interact to increase opportunity for weed invasion. Corn (maize) and soybean rotation commonly involves greater input of herbicides and fertilizers, and more frequent tillage than other less intensive agricultural uses (Boutin & Jobin 1998). When sampling species in hedgerows, we witnessed on many occasions direct herbicide application in the hedgerows, signs of recent herbicide application, or drift from application in adjacent corn fields. Jobin et al. (1997) and Boutin & Jobin (1998) compared species composition of woodlot edges and hedgerows, and noted more species of introduced origin and weedy propensity in habitats directly adjacent to intensively farmed fields compared to less intensively farmed habitats (forage crop or pasture). Agrochemical drifts from herbicides and fertilizers have been shown to affect species composition and community structure of arable field boundaries, and the establishment of buffer zones has been suggested as a mitigation measure, mainly to protect habitats and sensitive species (Kleijn & Snoeijing 1997; Kleijn & Verbeek 2000). Our results suggest that, in our area, such measures could also contribute to reduce opportunities for weed invasion. But it will make sense to do so only if hedgerows are treated as a stable component of the agroecosystem rather than as a nuisance to agricultural activities, and if other mechanical interventions to reduce tree cover are also reconsidered.

Forest herbs in hedgerows

In our region as in many other temperate parts of the world, agriculture developed on land that was previously forested. Today most remnant forest fragments are found on glacial deposits whereas the marine lowland has been virtually cleared of natural vegetation. The evidence that hedgerows can provide a surrogate habitat for forest species remains equivocal (Fritz & Merriam 1993; Corbit et al. 1999; McCollin et al. 2000), but the ability to provide such refuge is seen as one of the main incentives for conservation of these linear features in agricultural landscapes that have lost forest species.

Colonization by forest herbs may depend on the proximity of available propagules (Dzwonko 1993; Matlack 1994; Grashof-Bokdam & Geertsema 1998; Corbit et al. 1999; Kleijn & Verbeek 2000), but survival ultimately rests on the environmental conditions within the hedgerows (Fritz & Merriam 1993). Forest herbs in our samples were mostly found near the less intensive agricultural uses and within wider hedgerows on glacial deposits. Because forest herbs are generally associated with interior mesic conditions, they are more likely to be found on glacial sites than on marine sites, and within hedgerows that can provide minimal "interior" habitat. In hedgerows of New Jersey, forest herbs were more frequent in wider hedgerows (8-12 m) than in narrower omes (Forman & Baudry 1984). Corbit et al. (1999), on the other hand, found no significant effect of width but a relatively high frequency of forest herbs in hedgerows that were mostly < 7 m. Failure to detect width effect may be related to a narrow range of widths in their study. However, they suggest that, regardless of width, the relative stability of hedgerows in their landscape could be a more determinant factor to explain forest species richness. This would also be true of our plots on glacial deposit.

Forest herbs were less frequent even on glacial deposits when the hedgerows were surrounded by crop. This suggests that disturbances or inputs from agricultural fields impose constraints on forest herbs. Some of the selective disturbances associated with agricultural fields in the glacial landscape (e.g., cutting trees, trimming branches) may have enough impact to affect forest herb survival but were not taken into account in our quantitative evaluation of disturbances.

Nevertheless the relatively high frequency of forest herbs that we found in our hedgerows implies that at least some forest herbs require minimal interior conditions to survive and are able to withstand some levels of disturbances (e.g., *Trillium grandiflorum, Erythronium americanum*). In Britain, McCollin et al. (2000) investigated the autecological and habitat characteristics of forest species in relation to their frequency in hedgerows and woodlands and found significant differences in ecological requirements for species most frequent in hedgerows. They concluded that hedgerows contain only a narrow range of woodland types and that environmental conditions in hedgerows were probably not suitable for several woodland species, a conclusion also reached by Fritz & Merriam (1993) for hedgerows within low intensity farmland in eastern Ontario. In central New York state, Corbit et al. (1999) highlighted the similarity of composition between forest herbs of hedgerows and proximate woodlands. Several species mentioned in this paper were also found in our samples, including *Circaea lutetiana*, *Smilacina racemosa*, *Erythronium americanum* and *Trillium grandiflorum*. They also found, however, that some taxa were notably infrequent in hedgerows (e.g., *Prenanthes* spp.). Other studies also mentioned species unique to woodlands or forest edges, but not found in hedgerows (Fritz & Merriam 1994; Jobin et al. 1996; Boutin & Jobin 1998). These findings and ours suggest that hedgerows may serve as surrogate habitats in the landscape for a subset of woodland species but, given their structural characteristics, they may not provide the proper conditions for those species most likely to be affected by the loss of undisturbed interior habitats in farmlands.

The fragmentation of the original forest cover by agriculture, seen in the light of the theory of island biogeography, has raised the question of the potential function of hedgerows as corridors linking isolated forest habitats (Baudry 1988; Fritz & Merriam 1993; Corbit et al. 1999). Evidence regarding this function is still scarce and rather ambiguous. Although distance effects have been noticed (Baudry 1988; Corbit et al. 1999), the question has not yet been considered in relation to the whole landscape structure or even in relation to the demography of forest species in the patches. We did not specifically address this question, but our results and some features of our landscape and hedgerows bring about relevant observations. To disperse through hedgerows, forest species must find the proper environmental conditions to sustain their growth and life cycle. For instance, hedgerows on marine depositS in the agricultural lowlands would not necessarily provide the proper edaphic conditions to link forested glacial islets interspersed in the same landscape. If edaphic conditions are right (i.e., hedgerow and forest are found on similar edaphic conditions), hedgerow management in relation to adjacent agricultural activities become crucial, especially when intensive agricultural practices are used. Comparing hedgerows for their proximity to forest sources in relation to their ability to harbor forest species without controlling for adjacent land-use effects may hide important patterns. For instance, less intense agricultural uses may correlate with the proximity of forests. Even then, it is likely that the corridor function would be relevant for only a subset of species that can withstand edge condition and some level of disturbances. It remains to be seen whether these species are also the ones that show the best dispersal abilities and could therefore be less in needs of corridors.

Even if we know little about the metapopulation dynamics of forest herbs in fragmented landscape, we know that hedgerows do facilitate forest herb dispersal in general. For instance, Schmucki et al. (in prep.) have shown that some hedgerows in a landscape dominated by glacial deposits often disappear by becoming integrated into adjacent fallow lands when these lands revert to forests. Given the relatively broad representation of forest herbs in linear features adjacent to fallow lands in our samples, hedgerows, in this case, will serve as propagule sources to facilitate the rapid recolonization of abandoned patches by forest species.

Spatial structure

Spatial patterns of species dispersal can explain in part some of the spatial effect that was retained after controlling for other explanatory variables. Adjacent sites are more likely to share the same set of species simply because species will disperse relatively close to their parents. Also there is a significant spatial component of species variation that is related to our explanatory variables. For example, a good part of spatial environmental variation is related to the spatial arrangement of geomorphic deposits. Nearby sites are commonly on the same type of deposit. Other factors not measured in this study that can show strong spatial patterns include selective management activities conducted by individual owners and relationship to woodlands in the landscape. Yet, even when spatial patterns and all the measured explanatory variables are taken into account, there is still a fairly high unexplained proportion of species variation, some of which could be attributed to nondeterministic fluctuations or to controlling factors not included in our study. For instance birds are strong dispersal agents for most of the shrub species sampled. The presence of well-grown, dead or decaying trees is beneficial to many species, providing nest holes, foraging sites and perches (Hinsley & Bellamy 2000), and may correlate with patterns of shrub distribution, especially in the glacial landscape. Finally, high amounts of unexplained variation is not uncommon when trying to model any natural phenomena, but the incidence of human effects that are often inherently hard to quantify will likely contribute to increase this amount in our ecological models (see for instance Borcard et al. 1992 on forest vegetation; Le Cœur et al 1997 on hedgerow vegetation).

CONCLUSION

Several interrelated factors determine plant species distribution in hedgerows of farmlands in southern Quebec. While constraining species distribution, edaphic conditions imposed by geomorphic deposits also influence structural characteristics of hedgerows (e.g., stable rock fences in glacial landscape vs unstable field boundaries in marine landscape) and adjacent land-uses. Greater intensity of agricultural practices in adjacent parcels corresponds to more frequent and drastic control interventions within hedgerows, as well as more agrochemical inputs from farming activities. All these factors contribute to the differential distribution of plant species, facilitating the invasion of opportunist weed species in narrow hedgerows bordering crops on marine deposits and allowing forest herbs to survive in wider hedgerows bordering the less intense agricultural uses on glacial deposits.

Our findings have important consequences for management and conservation of hedgerows in agricultural landscapes. First of all, hedgerows provide habitat for a wide range of indigenous species, including some forest species. The very fact that they can sustain populations of forest species can by itself justify their maintenance in agricultural landscapes, regardless of their possible function as corridors linking isolated forest habitats. But the habitat requirements necessary for the survival of most mesophytic forest species may not be found in hedgerows in the most intensively cultivated area (i.e. landscape dominated by marine deposits). There, management should focus on the factors that will help reduce weed invasion that seems to be enhanced by current practices (e.g., establishment of buffer zone, reduced input of pesticides and fertilizers, limited control interventions). This could be an incentive for the farmers who manage linear features with the added benefit of maintaining much needed habitats for indigenous plant and animal species in biologically poor landscapes. Because we have little evidence of natural vegetation type in the marine lowlands in our area, non-agricultural linear features may indeed provide an opportunity to reintroduce some poorly represented vegetation types in the landscape. To be effective, however, conservation objectives will have to take into account the ecological as well as the agricultural exploitation context in which linear features are found. Unfortunately, our field observations suggest that relatively few farmers are so far ready to give up prime agricultural land to maintain non-agricultural habitats unless economic incentives or legislative constraints are involved.

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CHAPITRE 5

DISCUSSION ET CONCLUSION GÉNÉRALES

En écologie végétale, la nature a d'abord été pensée en terme de gradient montrant des variations plus ou moins continues dans l'espace. À de grandes échelles spatiales, les espèces s'ordonnent principalement le long de gradients climatique et édaphique. Suite à une perturbation, ces mêmes conditions environnementales détermineront l'évolution d'un site vers une composition plus ou moins en équilibre avec le milieu. C'est la notion de climax. Ces deux aspects, déterminisme environnemental et potentiel climacique, ont constitué la base traditionnelle de la plupart des études de végétation au vingtième siècle, de la simple analyse de gradients à l'ambitieuse cartographie écologique.

Dans les travaux présentés ici, la perspective est nettement différente. Le paysage est l'objet d'intérêt et sa délimitation dans l'espace détermine l'échelle d'observation. Il est défini comme une mosaïque composée d'éléments distincts : une matrice, des îlots, des composantes linéaires. La configuration de ces éléments permet de distinguer un paysage d'un autre. Les paysages et leurs éléments ayant des structures différentes, il est possible que la végétation associée à ces structures montre elle aussi une dynamique distincte ou soit soumise à des influences variables. De plus, ces influences sont largement déterminées non pas par des processus naturels mais bien par les activités humaines. Il s'agit donc d'évaluer la contribution des divers éléments du paysage à la diversité végétale, une diversité qui devient le produit des relations homme-nature.

Dans une mosaïque agricole où les activités de production ont des intensités variables, la végétation semble être le produit d'interactions complexes entre les contraintes imposées par les conditions environnementales, l'historique d'occupation des sols et les pratiques d'aménagement, et enfin le contexte spatial. Plus intéressant encore, l'importance relative de ces facteurs et les modèles d'interaction entre ces derniers et la végétation varient à la fois en fonction des échelles d'observation, des attributs des espèces (arbres vs arbustes et herbacées), et enfin de la nature des composantes du paysage considérées (îlots vs haies). Ces résultats soulèvent plusieurs questions autant d'un point de vue fondamental qu'en regard des pratiques de gestion et d'aménagement des paysages et de la biodiversité.

Dans cette étude, les composantes de l'échelle sont déterminées par le grain, i.e. la superficie de l'unité d'échantillonnage, et l'étendue, i.e. la superficie totale de l'aire d'étude (Turner et al. 1989). Cette recherche a montré que pour une superficie d'échantillonnage maintenue constante (i.e. la composante " grain " liée à l'échelle) l'influence relative de différents processus structurants de la végétation variait en fonction des configurations et de l'étendue du paysage (voir chap. 3, figure 5). Par exemple, la composante environnementale est déterminante pour la composition des herbacées et arbustes des îlots dans le paysage glaciaire, mais non dans le paysage mixte fortement fragmenté. Les modèles d'interaction diffèrent aussi quand on considère les deux paysages simultanément (i.e la composante « étendue » liée à la notion d'échelle) par rapport à chacun des paysages pris individuellement. Ces résultats rappellent de façon manifeste la nécessité de tenir compte des relations entre l'échelle d'observation et les processus structurants de la variabilité biotique dans l'interprétation écologique. Voilà certainement une question fondamentale en écologie du paysage. Existe-il autant de modèles de relations qu'il existe d'échelles d'observation spatiale pour la région d'étude ? Un paysage peut-il se caractériser, au point de vue biologique, par la nature et l'intensité des interactions entre les déterminants de la variabilité végétale ? Pour un même modèle d'interactions dans des paysages différents, y a-t'il des patrons émergents, des réponses communes au niveau des espèces ou des associations végétales, ou au niveau de leurs caractéristiques ? Pour une échelle spatiale déterminée, ces modèles de relations sont-ils stables ? Par exemple, il est permis d'avancer, sur la base de notre connaissance de l'historique d'exploitation de la forêt précoloniale, que ces mêmes analyses auraient donné des résultats fort différents au 19 $^{\text{ième}}$ siècle. Ces questions restent à explorer pour une variété de paysages anthropiques, ce qui pourrait permettre des avancés théoriques dans le domaine de l'écologie du paysage et ses rapports à l'écologie végétale.

Un autre constat intéressant est la réponse différente des formes biologiques, espèces arborescentes, herbacées ou arbustives. Les modèles proposés sont donc dépendants des caractéristiques des espèces végétales. Aux échelles d'observation auxquelles mes travaux ont été conduits, les variables abiotiques mesurées ont une influence déterminante sur la répartition des espèces herbacées et arbustives autant dans les îlots que dans les haies. Cependant, les espèces arborescentes des îlots ne retiennent pas l'effet des conditions environnementales, peu importe la configuration des paysages. Il serait intéressant de voir si les arbres des haies montrent les mêmes tendances. De même, l'influence du contexte spatial est plus importante pour les espèces herbacées et arbustives que pour les espèces arborescentes. Par contre les variables historiques sont déterminantes pour tous les types de végétation, et d'ailleurs aussi à toutes les échelles d'observation, ce qui confirme le fort pouvoir explicatif de ces variables. La végétation de ces paysages est définitivement le reflet des activités humaines.

Enfin, les modèles proposés varient aussi en fonction des éléments de paysages (i.e. îlots vs haies). En considérant toutes les parcelles dans l'étude des îlots, la variabilité végétale des herbacées et des arbustes est fonction avant tout des conditions environnementales et de l'historique des sites. Ces facteurs jouent aussi pour les haies mais, dans ce cas, c'est l'incidence des activités adjacentes qui semble la plus déterminante et serait donc le facteur à considérer dans une perspective de conservation de la diversité ou d'aménagement dans ces paysages. La haie n'est pas un élément indépendant de la mosaïque dans laquelle elle se trouve. Enfin, bien que dans cette étude seule la nature des occupations du sol adjacentes ait été prise en compte dans l'évaluation du contexte spatial, d'autres mesures à l'échelle du paysage (e.g., proximité de sites semblables, connexion aux boisés pour les haies) pourraient aussi avoir une contribution à la variabilité végétale. Cela reste à vérifier dans des travaux futurs.

Au-delà de toutes ces considérations, un élément reste omniprésent dans tous les niveaux d'analyse : c'est l'influence des activités humaines. La végétation est la résultante des interventions passées, et si le déterminisme environnemental demeure, c'est en toile de fond pour favoriser certaines occupations ou permettre certaines modalités d'intervention plutôt que d'autres. Dans cette perspective, les boisés, les friches et les haies peuvent être vus comme des composantes à part entière du paysage agricole au même titre que les champs cultivés ou les pâturages et non pas comme des entités indépendantes de la mosaïque où ils se trouvent ou comme les seuls vestiges d'une certaine nature sauvage. Ceci étant dit, ces composantes présentent quand même une biodiversité plus importante que celle des parcelles en culture ou en pâturage et à ce titre, elles sont aussi plus que de simples espaces agricoles résiduels. Leur rôle unique de réservoir de biodiversité dans des paysages anthropiques doit être définitivement pris en compte dans leur gestion.

Comme la végétation actuelle est le reflet des activités passées, la diversité végétale future sera déterminée par les pratiques de gestion et d'aménagement en cours. Ce qui est différent aujourd'hui, c'est qu'on connaît maintenant dans une bonne mesure les conséquences à long terme des pratiques - par exemple l'influence persistante du pâturage sur la dynamique d'un site - et que l'évolution du paysage en regard de la diversité biologique peut se poser maintenant en termes de choix concrets et d'objectifs précis. Force est de constater cependant que ces objectifs restent encore loin d'être clairement définis.

Jusqu'à maintenant, il semble que la préservation de la valeur écologique d'un site dépende plus d'une certaine passivité des utilisateurs que d'un choix individuel ou collectif réfléchi. Moins perturbé, le boisé ou la haie où l'on intervient peu ou pas, simplement par manque d'intérêt ou à cause d'un faible potentiel d'exploitation, devient un réservoir d'espèces de milieux stables. Le danger dans ce cas est que cette fonction peut changer à tout moment si le contexte d'exploitation ou les conditions économiques changent. En voici un exemple : certains producteurs en manque d'espace pour épandre les excédents de fumier utiliseront les petits boisés pour ce faire avec les conséquences qu'on peut facilement imaginer pour la flore. Ce genre de pratique appelle une question primordiale. Quelle doit être la fonction première des boisés ou des haies dans un paysage agricole ? Ces éléments doivent-ils avant tout supporter (ou subir) les activités de production (agriculture, foresterie) ? Ont-ils aussi des fonctions écologiques qu'il faut activement préserver (encore faudrait-il d'abord clairement les évaluer) ?

Une partie des réponses à ces questions repose certainement sur la capacité de pouvoir réconcilier au lieu d'opposer, à l'échelle des paysages, les objectifs de conservation et d'exploitation. Dans la vision large de l'écologie du paysage, cela implique nécessairement un certain décloisonnement des disciplines. Par exemple, pour ce qui est des questions de conservation, l'écologiste mettra naturellement l'accent sur la rareté des espèces ou le caractère exceptionnel de certains peuplements. Dans cette optique, ne seraient dignes d'intérêt pour l'écologiste dans un territoire agricole que les habitats comportant un caractère unique. Or, faut-il négliger pour autant les autres composantes de la diversité dans le paysage ? Mais accepter d'élargir ses perspectives, c'est aussi accepter de tenir compte d'un ensemble de facteurs d'ordre biologique certes, mais aussi d'ordre agronomique, économique, politique, social ou culturel. Le défi est de taille et, pour l'écologiste, il repose sur la capacité non seulement d'analyser les interactions complexes entre les différentes composantes des paysages à des échelles spatiales pertinentes, mais aussi de s'ouvrir à d'autres perspectives qui ne peuvent que venir enrichir la compréhension de ces interactions. L'objectif ultime n'est-il pas de maintenir des paysages productifs et viables, des lieux de vie où nature et culture s'enrichissent mutuellement ?

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