UNIVERSITÉ DU QUÉBEC À MONTRÉAL

# ANALYSE SPATIOTEMPORELLE D'UN TERRITOIRE AGROFORESTIER : QUAND LES CONDITIONS PAYSAGÈRES DU PASSÉ ET DU PRÉSENT S'UNISSENT POUR INFLUENCER LES COMMUNAUTÉS FORESTIÈRES

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# DÉDICACE

À Léa et Nito, sources d’inspiration infinies

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# RÉSUMÉ

L'objectif général de cette thèse est de faire l'étude de communautés forestières d'arbres et d'arbustes sous l'angle de leur mémoire écologique et, plus précisément, de leur relation avec des legs paysagers et différents filtres écologiques ayant agi au fil du temps et à travers différentes échelles spatiales. Le territoire forestier du sud du Québec, hautement fragmenté et où les activités liées à l'agriculture et l'exploitation forestière ont façonné les paysages depuis 200 ans, se révèle un territoire idéal pour nos travaux.

Le chapitre 1 vise à évaluer si les communautés actuelles d'arbres et d'arbustes situées dans des paysages forestiers hautement fragmentés possèdent une mémoire écologique. Plus précisément, nous posons la question à savoir si les communautés actuelles sont liées aux conditions de peuplement et de paysage du passé à travers la présence de legs, tels que des patrons dans l'abondance, la richesse et la diversité des arbres et arbustes, qui auraient persisté au fil du temps. Nous examinons l'influence de plusieurs filtres écologiques agissant à l'échelle locale, du peuplement et du paysage sur les communautés actuelles d'arbres et d'arbustes. Pour les filtres à la dispersion à l'échelle du peuplement et du paysage, notre investigation couvre quatre périodes à l'intérieur des 85 dernières années, soit le passé lointain (1930-40), intermédiaire (1958), récent (1983) et le temps présent (2015). Les résultats montrent que les perturbations et la structure du paysage constituent des facteurs importants influençant les patrons de diversité et d'abondance des communautés d'arbres et d'arbustes et que leur influence persiste à travers le temps jusqu'à 57 à 85 ans plus tard. Ces communautés sont ainsi caractérisées par une mémoire écologique prenant la forme d'un délai de réponse suite à des changements survenus dans le passé dans la structure du paysage. Les résultats montrent également que les conditions d'habitat plus récentes ou actuelles pouvaient aussi être importantes pour expliquer l'abondance de certaines espèces d'arbres et d'arbustes, laissant entrevoir que des filtres écologiques plus récents (ex., perturbations, conditions biotiques et abiotiques) avaient la capacité d'effacer la mémoire lointaine des communautés.

Le chapitre 2 vise d'abord à déterminer si les communautés forestières d'arbres possèdent une mémoire écologique à travers leurs patrons de traits fonctionnels qui seraient liés aux conditions d'habitat du passé. Il vise également à déterminer si une trajectoire d'évolution du paysage hautement perturbée peut conduire à une érosion de la diversité des traits fonctionnels de réponses et à un filtrage des traits de réponses dans les communautés d'arbres actuelles. Cette trajectoire implique une altération des legs au sein du paysage au fil du temps, en raison de l'importance des milieux ouverts perturbés sur le territoire. Nos résultats indiquent que la structure fonctionnelle des communautés étudiées porte une mémoire écologique liée aux conditions d'habitat des années 1930-40 et 1958, mais que les conditions plus récentes ou actuelles sont également importantes. L'analyse des trajectoires de paysages indique par la suite que l'altération des legs paysagers, à travers des perturbations continues au fil du temps, peut conduire à une érosion de la diversité de réponses et à un filtrage des traits de réponses favorisant les espèces qui possèdent des graines se dispersant sur de plus longues distances par le vent ou les mammifères. Les trajectoires moins perturbées (davantage forestières au fil du temps) favorisent quant à elles une plus grande diversité de réponses et les espèces dispersant leurs graines par les oiseaux et capables de se reproduire végétativement. Ainsi, les espèces des communautés situées au sein de paysages historiquement plus perturbés possèdent une meilleure capacité de colonisation, mais une persistance locale plus faible à travers le mécanisme de reproduction végétative.

Le chapitre 3 investigue la relation entre les arbres résiduels actuels distribués au sein des paysages agricoles et les patrons des communautés forestières locales, tant au niveau spécifique que fonctionnel. Nous avons donc cartographié les arbres reliques présents en 2015 dans le paysage et les avons inclus dans le couvert forestier. Nos résultats montre d'abord que les arbres résiduels dans le paysage ont un effet positif sur la connectivité et que leur contribution relève surtout de leur rôle en tant que pas japonais. Nos résultats indiquent également qu'il existe une relation entre les arbres résiduels et les patrons des communautés d'arbustes en ce qui a trait à leur diversité spécifique et la diversité de leurs traits de réponses liés à la dispersion des graines et la reproduction. Les arbres résiduels sont également associés aux patrons des communautés d'arbres en ce qui concerne quatre traits fonctionnels de réponses, soit : la proportion d'espèces se reproduisant végétativement par drageonnement à partir de la couronne des racines, se reproduisant surtout de manière sexuée, dispersant leurs graines par les oiseaux et dispersant leurs graines par le vent. Les arbres résiduels persistants (présents en 2015 et en 1983) ne se sont toutefois pas révélés plus importants que les arbres reliques non-persistants (présents seulement en 2015). L'association entre les patrons des communautés forestières et les arbres résiduels suggère que ces derniers peuvent agir comme sources de propagules et favoriser le déplacement des animaux dispersant les propagules vers les forêts adjacentes, bien qu'ils pourraient aussi être le résultat de la dispersion des propagules en provenance de ces forêts. Dans les deux cas, les arbres reliques sont interconnectés avec les forêts dans le paysage et pourraient contribuer à leur mémoire écologique externe. Dans ce contexte, leur rôle ne devrait donc pas être négligé.

En somme, cette thèse permet de faire progresser nos connaissances quant à la profondeur temporelle de la mémoire des communautés forestières suite à la modification du paysage qui les entoure. Elle illustre également les effets que peuvent avoir les perturbations historiques continues sur les communautés forestières actuelles et nous permet d'anticiper une perte de résilience des forêts face à de futures perturbations. Enfin, en explorant les liens qui unissent les arbres reliques situés en milieux perturbés aux communautés forestières, cette thèse pave également la voie à de futures études qui viseraient à déterminer plus précisément le rôle que pourraient jouer ces legs du paysage dans l'augmentation de la résilience et de la capacité d'adaptation des forêts dans un contexte de changements globaux.

Mots clés : communautés d'arbres et d'arbustes, traits fonctionnels de réponses, mémoire écologique, structure et perturbations historiques du paysage, arbres reliques.

# INTRODUCTION GÉNÉRALE

Ce projet de doctorat en biologie se situe à l'intersection de plusieurs champs disciplinaires. Il s'insère en effet dans un contexte d'écologie des communautés végétales terrestres, d’écologie des méta-communautés et d’écologie du paysage. L'écologie des communautés se veut l'étude des patrons dans la distribution, l’abondance et l’interaction des espèces qui co-occurrent dans le temps et l'espace (McGill et al., 2006). L’écologie des méta-communautés met l’emphase sur un ensemble de communautés locales interreliées par la dispersion d’espèces qui peuvent interagir entre elles (Leibold et al., 2004). De son côté, l’écologie du paysage étudie l’effet de la structure du paysage sur les processus écologiques à travers différentes échelles. Un paysage peut être défini comme une mosaïque de reliefs, d’écosystèmes, d’habitats et d’usages à l’intérieur d’un territoire pouvant varier en superficie selon le processus ou les organismes étudiés (ex., quelques kilomètres carrés à quelques centaines de kilomètres carrés) (With, 2019). L’écologie du paysage met donc l’emphase sur l’hétérogénéité spatiale, l’influence de celle-ci sur les processus biotiques et abiotiques ainsi que les interactions et les échanges à travers les paysages hétérogènes (Turner & Gardner, 2015).

## 0.1 Structure et assemblage des communautés

### 0.1.1 Structure des communautés

Une communauté représente le niveau d'organisation qui inclut des organismes de différentes espèces vivant dans un même espace à un moment particulier et qui interagissent entre eux et avec les différents éléments constituant leur environnement (Roughgarden, 2009; Vellend, 2010). Elles sont caractérisées par des patrons qui peuvent se décliner en termes d'identité, d’abondance et de diversité des espèces, ainsi que d’identité et de diversité des traits fonctionnels des espèces.

Les traits fonctionnels sont des caractéristiques morphologiques, physiologiques ou phénologiques mesurables au niveau d’un individu, de la cellule à l’organisme entier, sans qu’il ne soit fait référence à aucun autre niveau d’organisation ni à aucun facteur du milieu (Violle et al., 2007). La variation de ces traits à l’échelle des individus influence la structure des communautés et contribue au fonctionnement général des écosystèmes (Chapin III et al., 2012;

Díaz & Cabido, 2001; Eviner & Chapin III, 2003; Garnier & Navas, 2013; Grime, 2001; Naeem et al., 2012; Prinzing et al., 2008; Wardle, 2002). Par exemple, il peut s'agir de traits des feuilles (ex. épaisseur et quantité d'azote) ou des racines (ex. morphologie et longueur). Ces traits sont des *traits d'effets* et peuvent affecter des processus comme la productivité primaire nette, la décomposition et l'accumulation de la litière, le transfert et le stockage du carbone ainsi que le bilan hydrique des forêts (Garnier et al., 2004; Garnier & Navas, 2013; Lavorel & Garnier, 2002). Les espèces peuvent être assemblées en *groupes fonctionnels* selon leurs traits d'effets, ceux-ci pouvant alors comprendre, par exemple, des organismes pollinisateurs, des prédateurs, des espèces qui dispersent les graines ou d'autres fixatrices d'azote (Folke et al., 2004).

Par ailleurs, les traits qui déterminent la façon dont les espèces répondent à des perturbations ou à des changements dans les conditions environnementales sont qualifiés de *traits de réponses* (Garnier & Navas, 2013; Lavorel & Garnier, 2002; Naeem & Wright, 2003; Suding et al., 2008; Suding & Hobbs, 2009). Ainsi, la *diversité de réponses* consiste en la variabilité des réponses aux perturbations ou aux changements environnementaux parmi les espèces d'une communauté (Elmqvist et al., 2003; Suding & Hobbs, 2009; Walker, 1995). La réponse des plantes en réaction à des perturbations et à des variations du climat, du $CO_2$ ou de la disponibilité des ressources du sol peut passer, à titre d'exemple, par une variation dans le cycle de vie, la masse des graines ou le mode de régénération (ex. capacité à drageonner et à faire des rejets de souches) (Lavorel & Garnier, 2002).

### 0.1.2 Règles d'assemblage des communautés

La structure des communautés est affectée par quatre processus fondamentaux, soit 1) la dérive, 2) la spéciation, 3) la dispersion et 4) la sélection (Vellend, 2010). La dérive consiste en des changements aléatoires dans l'abondance relative des espèces causés par la nature stochastique des processus tels la mortalité et la natalité, alors que la spéciation constitue l'apparition de nouvelles espèces. La dispersion concerne pour sa part le mouvement des organismes et des propagules à travers les communautés. Enfin, la sélection relève du taux de survie ou de reproduction différentiel des différentes espèces en fonction des conditions biotiques et abiotiques auxquelles elles sont exposées. Les processus de dispersion et de sélection, qui sous-tendent les travaux de cette thèse, impliquent une série de contraintes à la coexistence des espèces qui sont conceptualisées sous la forme d'une combinaison de filtres organisés de manière hiérarchique et agissant à différentes échelles spatiales pour favoriser ou défavoriser les espèces (Götzenberger et al., 2012). Au nombre de trois, ces filtres sont 1) un filtre à la dispersion à l'échelle du paysage, 2) un filtre abiotique lié aux conditions environnementales locales ou aux perturbations abiotiques et 3) un filtre biotique lié aux interactions entre les différentes espèces présentes au sein d'une communauté (Figure 0.1) (Garnier & Navas, 2012, 2013; Götzenberger et al., 2012; Lavorel & Garnier, 2002; Lortie et al., 2004; Suding et al., 2008; Vellend, 2010).

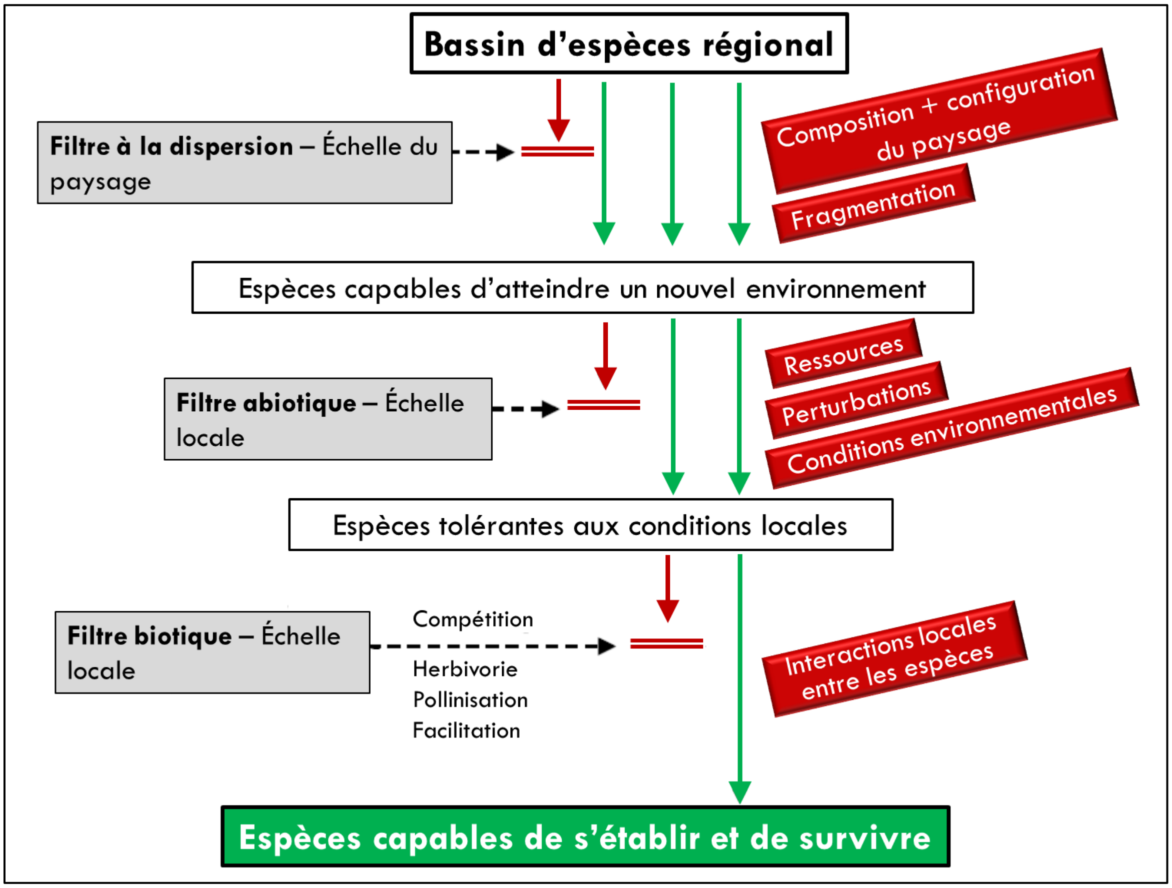

Figure 0.1. Règles d'assemblage des communautés selon une série de filtres écologiques organisés de manière hiérarchique et agissant à différentes échelles spatiales pour favoriser ou défavoriser les espèces (figure adaptée de Lortie et al., 2004).

#### 0.1.2.1 Filtre à la dispersion

À l'échelle du paysage, le filtre à la dispersion relève notamment des événements stochastiques pouvant y survenir ainsi que de la composition et de la configuration spatiale de ce dernier (de Bello et al., 2013; Garnier & Navas, 2012; Lortie et al., 2004). Les paysages étant hétérogènes, les différents usages et habitats du territoire ainsi que leur configuration spatiale peuvent favoriser ou empêcher la dispersion, particulièrement lorsque les propagules des espèces végétales sont dispersées par les animaux (With, 2019). L'hétérogénéité du paysage influence ainsi le processus de dispersion des espèces entre les communautés locales formant des méta-communautés (Leibold et al., 2004; With, 2019). La dispersion entre ces communautés est fondamentale, notamment pour la colonisation de nouveaux habitats, pour la recolonisation d'habitats ayant été perturbés, pour le maintien du flux génétique entre les populations des différentes espèces présentes dans ces communautés et, de manière plus générale, pour la persistance et la coexistence des espèces dans le paysage (Garnier & Navas, 2012; Leibold et al., 2004; With, 2019).

Pour la végétation forestière en milieu agricole, la perte nette d'habitat se traduit directement par une réduction de la taille des populations et du nombre d'espèces à mesure que la superficie des parcelles diminue (Kiviniemi, 2008; Turner & Gardner, 2015) et peut ainsi affecter directement le bassin régional d'espèces disponibles pour coloniser les communautés locales. Pour sa part, la fragmentation du couvert forestier, qui représente la subdivision d'un habitat continu en plus petits morceaux survenant dans les écosystèmes par l'entremise de perturbations naturelles ou anthropiques (Andrén, 1994), peut constituer un filtre à la dispersion des propagules de certaines espèces en réduisant la connectivité dans le paysage. La fragmentation peut ainsi altérer ce processus fondamental, à l'instar du processus de pollinisation, notamment lorsque l'isolement des parcelles d'habitat empêche les pollinisateurs et les animaux qui dispersent les propagules de s'y rendre (Aguilar & Galetto, 2004; Chapman et al., 2003; Cordeiro & Howe, 2003; Cramer et al., 2007; Herrera & García, 2010; Ibáñez et al., 2014; McEuen & Curran, 2004; Ozinga et al., 2009; Rogers et al., 2021; Tewksbury et al., 2002). Conséquemment, la perte et la fragmentation de l'habitat à travers le paysage peuvent engendrer une réduction de la disponibilité des propagules, une plus faible colonisation des parcelles d'habitat, une augmentation du risque d'extinction locale et un isolement génétique des populations vivant au sein des communautés isolées (Aguilar et al., 2006; Grashof-Bokdam, 1997; Honnay et al., 2008; Honnay & Jacquemyn, 2007; Ibáñez et al., 2014; Joshi et al., 2006; Soons & Heil, 2002).

#### 0.1.2.2 Filtre abiotique

À une échelle plus locale (ex., dans un peuplement forestier), le filtre abiotique correspond quant à lui à la disponibilité des ressources (ex. éléments nutritifs), aux conditions environnementales qui prévalent (ex. pH et température du sol) ainsi qu'au régime de perturbations abiotiques (ex. sévérité et fréquence) (Garnier & Navas, 2012, 2013; Grime, 2006; Lavorel & Garnier, 2002; Suding et al., 2008). L'ensemble de ces éléments déterminent les conditions locales d'habitat et influencent quelles espèces sont capables de s'y établir et d'y survivre en fonction des traits de réponses qu'elles possèdent (Grime, 2006). Par exemple, au sein des forêts fragmentées, il existe un microclimat différent dans les forêts de bordures comparativement aux conditions qui prévalent à l'intérieur de la forêt (Brotons et al., 2001; Matlack & Livaitis, 1999; McCollin, 1998). Le taux d'humidité y est en effet plus faible et la radiation solaire plus élevée, ce qui se reflète sur la structure de la végétation et sur les espèces animales et végétales présentes dans ce type de milieu (Esseen & Renhorn, 1998; Matlack & Livaitis, 1999; Villard, 1998).

Le filtre lié aux ressources engendre une convergence des traits impliqués dans l'utilisation de ces ressources par les espèces puisque celles capables de tolérer ces conditions possèdent des traits similaires, ce qui se traduit par une réduction de la diversité fonctionnelle (Bernard-Verdier et al., 2012; Cornwell & Ackerly, 2009; de Bello et al., 2009). Par contre, le filtre des perturbations fait plutôt intervenir les traits liés à la régénération et engendre une divergence de ces derniers puisque les espèces possèdent des stratégies de reproduction et d'établissement variées (Grime, 2006).

#### 0.1.2.3 Filtre biotique

Toujours à une échelle locale, les relations interspécifiques, telles que la compétition, la prédation et le mutualisme, exercent un filtre biotique supplémentaire influençant les espèces qui sont capables de survivre au sein des communautés (Garnier & Navas, 2013; Lavorel & Garnier, 2002). L'influence du filtre biotique est généralement détectable à une échelle très locale, soit celle à laquelle les individus doivent cohabiter et partager les ressources (de Bello et al., 2013). Dans les peuplements forestiers isolés en milieu agricole, le filtre biotique peut affecter la performance individuelle des plantes lorsque, par exemple, la surabondance de certains herbivores cause un surbroutage de la végétation (Elzinga et al., 2005; Kolb, 2008) ou lorsque la perte de pollinisateurs due à l'isolement des parcelles d'habitat engendre une diminution du succès reproducteur des espèces présentes (Aguilar & Galetto, 2004).

Les interactions interspécifiques peuvent conduire à une convergence ou une divergence des traits fonctionnels au sein d'une communauté. La convergence des traits est d'abord possible par l'entremise du principe d'exclusion compétitive. Celui-ci stipule que « dans un environnement stable et homogène, deux espèces utilisant la même ressource limitante ne peuvent coexister, l'une d'entre elles finissant par exclure l'autre selon leur hiérarchie compétitive » (Garnier & Navas, 2013). Ce principe d'exclusion compétitive est notamment évoqué pour expliquer la plus faible biodiversité dans les forêts de fin de succession comparativement aux forêts de début ou milieu de succession. À l'inverse, le filtre biotique peut également conduire à une divergence fonctionnelle selon le principe de la limitation de la similarité fonctionnelle, qui stipule que « des espèces ne peuvent coexister que si elles occupent des niches écologiques différentes […] limitant ainsi l'effet négatif des interactions biotiques sur leur performance » (MacArthur & Levins, 1967). Une augmentation de la divergence fonctionnelle peut également résulter de processus biotiques tels que la facilitation, qui peuvent maintenir la présence de compétiteurs plus faibles (Perronne et al., 2017).

## 0.2 Lorsque le passé est garant du futur

Bien que les filtres écologiques actuels puissent avoir une grande influence sur la composition et la structure des communautés, l'effet des conditions (filtres) passées n'est toutefois pas à négliger, surtout pour les organismes possédant une très grande persistance due, par exemple, à leur longévité ou leur capacité à se reproduire végétativement. Il est désormais clair que des événements ou des conditions historiques affectent les patrons contemporains décelés au sein des communautés (Turner & Gardner, 2015). La capacité qu'ont ces événements et conditions passés à influencer les patrons actuels ou futurs d'une communauté a été décrite en termes de mémoire (Padisak, 1992; Peterson, 2002) et est intimement liée à la présence de legs (Johnstone et al., 2016).

Une communauté possède une mémoire dite interne des conditions passées lorsqu'il subsiste, en son sein, des legs biologiques qui en témoignent. Il peut s'agir d'espèces ayant persisté à travers le temps ou de legs suite à une perturbation tels que des arbres semenciers, des banques de graines dans le sol et des champignons mycorhiziens. Une communauté possède également une mémoire externe, qui réfère à la présence de legs dans le paysage ayant la capacité d'influencer son développement (Bengtsson et al., 2003; Perry, 1995). Ces legs sont notamment constitués des peuplements sources situés dans le paysage et des espèces qui y vivent dont les semences peuvent coloniser ladite communauté (Johnstone et al., 2016).

Les legs paysagers actuels peuvent avoir été influencés par des événements ou conditions du passé. Par exemple, le bassin d'espèces sur un territoire est influencé par la structure actuelle du paysage (filtre à la dispersion actuel; Garnier & Navas, 2012), mais peut aussi refléter l'effet des filtres à la dispersion passés ayant façonné le bassin d'espèces au fil du temps. Les legs au sein d'une communauté ou dans le paysage peuvent aussi avoir été altérés par l'utilisation anthropique d'un territoire à travers le temps. Il peut notamment s'agir d'une altération de la structure du sol, une réduction des arbres morts au sein d'une forêt, un changement dans la composition en espèces des peuplements ou une réduction de l'hétérogénéité ou de la connectivité du paysage forestier. Ces legs altérés et leurs effets peuvent ainsi perdurer à travers plusieurs décennies, voire des centaines et milliers d'années, comme en témoignent les études de Dupouey et al. (2002) et Dambrine et al. (2007). Ces auteurs ont en effet montré que les activités agricoles pratiquées en Europe il y a environ 2000 ans avaient induit des changements au niveau des éléments nutritifs du sol et de la diversité des espèces végétales qui étaient encore perceptibles de nos jours. L'ensemble de ces éléments démontre que l'aspect temporel est important à considérer dans l'étude des communautés et qu'il peut nous permettre de mieux comprendre leur dynamique.

## 0.3 Objectif général et contexte de la thèse

L'objectif général de cette thèse est de faire l'étude de communautés forestières d'arbres et d'arbustes sous l'angle de leur mémoire écologique et, plus précisément, de leur relation avec des legs paysagers et différents filtres écologiques ayant agi au fil du temps et à travers différentes échelles spatiales. Le territoire forestier du sud du Québec, hautement fragmenté et où les activités liées à l'agriculture et l'exploitation forestière ont façonné ses paysages depuis 200 ans, se révèle un territoire idéal pour nos travaux. En ce sens, des études conduites sur une portion du territoire couvert par cette thèse (municipalité de canton de Godmanchester, superficie d'environ 138 km$^2$) ont montré que les premiers colons s'y sont établis aux alentours des années

1800 (Bouchard & Domon, 1997), alors que l'exploitation forestière dans cette région y était déjà commencée (Brisson & Bouchard, 2006). À peine 50 ans plus tard, le déclin des activités forestières se faisait déjà sentir (Bouchard & Domon, 1997). Pendant cette courte période, l'ensemble des espèces prélevées auraient été exploitées jusqu'à l'épuisement des stocks (Simard & Bouchard, 1996). À la même époque, les forêts ont également été brûlées pour la production de potasse, le territoire forestier fraîchement défriché ayant par la suite été converti en terres agricoles (Brisson & Bouchard, 2006). C'est autour des années 1825 que l'agriculture s'est déployée sur le territoire, d'abord sur les dépôts morainiques, où le sol était mieux drainé, puis sur la plaine argileuse. Selon Domon & Bouchard (2007), l'agriculture a été à son apogée autour des années 1890 où elle occupait, en certains endroits, plus de 80 % du territoire. Vers 1950, les activités agricoles ont été concentrées sur la plaine argileuse, engendrant alors une déprise sur les sites morainiques. Une succession secondaire s'est alors amorcée, menant d'abord à une végétation caractéristique des terres en friche avant d'évoluer vers un stade de jeune forêt autour des années 1975-80. Au fil du temps, ces forêts de seconde venue ont fait l'objet de divers travaux allant d'une exploitation par coupe à diamètre limite à la récolte de bois de chauffage, en passant par des coupes d'assainissement d'érablières. L'activité humaine sur ce territoire depuis l'époque de la colonisation a profondément modifié la composition forestière, conduisant notamment à une augmentation de la prévalence de l'Érable à sucre (*Acer saccharum*) et une raréfaction du Hêtre à grandes feuilles (*Fagus grandifolia*) et du Bouleau jaune (*Betula alleghaniensis*) (Brisson et Bouchard, 2003). Nous posons donc, comme hypothèse générale, que cette trajectoire paysagère a généré des conditions spatiales ayant un effet sur le devenir des communautés forestières et que ce signal est toujours décelable aujourd'hui.

## 0.4 Structure et objectifs spécifiques de la thèse

Cette thèse est divisée en trois chapitres, dont chacun étudie le territoire selon une combinaison spatiotemporelle différente. Ainsi, le chapitre 1 combine les échelles spatiales locales, du peuplement et du paysage et quatre périodes temporelles allant de 1930 à 2015. Le chapitre 2 met l'emphase sur l'échelle du paysage en intégrant les différentes occupations du sol survenues au fil du temps en trajectoires d'évolution des paysages. Le chapitre 3 met quant à lui l'emphase sur le paysage analysé avec un grain (résolution) plus fin qui implique la détection d'arbres résiduels présents en 2015, qui pouvaient également exister en 1983. En ce qui a trait à la réponse des communautés, le chapitre 1 met l'accent sur les espèces d'arbres et d'arbustes, le chapitre 2 sur les traits fonctionnels de réponses des arbres et le chapitre 3 sur les espèces et traits fonctionnels de réponses des arbres et arbustes.

### 0.4.1 Objectifs et hypothèses du chapitre 1

Le chapitre 1 vise à évaluer si les communautés actuelles d'arbres et d'arbustes situées dans des paysages forestiers hautement fragmentés possèdent une mémoire écologique. Plus précisément, nous posons la question à savoir si les communautés actuelles sont liées aux conditions de peuplement et de paysage du passé à travers la présence de legs, tels que des patrons dans l'abondance, la richesse et la diversité des arbres et arbustes, qui auraient persisté au fil du temps. L'existence d'une mémoire montrerait que les communautés ne sont pas en équilibre avec les conditions d'habitat actuelles et seraient plutôt encore influencées par les conditions d'habitat du passé. Pour atteindre cet objectif, nous examinons l'influence de plusieurs filtres écologiques agissant à l'échelle locale, du peuplement et du paysage sur les communautés actuelles d'arbres et d'arbustes. Pour les filtres à la dispersion à l'échelle du peuplement et du paysage, notre investigation couvre quatre périodes à l'intérieur des 85 dernières années, que nous abordons sous les termes de passé lointain (1930-40), passé intermédiaire (1958), passé récent (1983) et temps présent (2015).

Nous posons l'hypothèse que les conditions passées liées aux échelles du peuplement et du paysage influencent l'abondance, la richesse et la diversité spécifiques des arbres et arbustes, révélant ainsi l'existence d'une mémoire écologique interne et externe. Plus précisément, nous prédisons que les conditions de peuplement et de paysage du passé lointain et intermédiaire sont importantes pour expliquer les patrons des communautés d'arbres et d'arbustes actuels, particulièrement pour les espèces possédant des valeurs de traits fonctionnels de réponses leur conférant une bonne persistance à travers le temps (ex., grande longévité, habileté à se reproduire végétativement et à former des banques de graines) et une bonne capacité de colonisation (ex., dispersion des graines sur de grandes distances). Nous prédisons également que les conditions de peuplement et de paysage plus récentes ou actuelles peuvent aussi être importantes pour expliquer les patrons des communautés d'aujourd'hui. Les perturbations récentes (ex., coupes forestières) pourraient en effet avoir modifié les patrons des communautés soit en prélevant directement les espèces qui étaient persistantes et liées aux conditions du passé, ou en modifiant indirectement les conditions d'habitat, affectant ainsi la survie de certaines espèces.

### 0.4.2 Objectifs et hypothèses du chapitre 2

Le chapitre 2 vise d'abord à déterminer si les communautés forestières d'arbres possèdent une mémoire écologique à travers leurs patrons de traits fonctionnels qui seraient liés aux conditions d'habitat du passé. Il vise également à déterminer si une trajectoire d'évolution du paysage hautement perturbée peut conduire à une érosion de la diversité des traits fonctionnels de réponses et à un filtrage des traits de réponses dans les communautés d'arbres actuelles. Cette trajectoire implique une altération des legs au sein du paysage au fil du temps, en raison de l'importance des milieux ouverts perturbés sur le territoire (ex. terres agricoles abandonnées transformées en friches et en zones de régénération dominées par une strate arbustive). L'altération de ces legs est susceptible d'avoir contribué à la diminution de la disponibilité des propagules et empêché leur dispersion à travers le paysage.

Notre première hypothèse stipule que les conditions de peuplement et de paysage des années 1930-40 et 1958 sont importantes pour expliquer la diversité et la valeur des traits de réponses dans les communautés d'arbres actuelles. Nous posons également l'hypothèse que les communautés situées dans des paysages caractérisés par une trajectoire d'évolution hautement perturbée possèdent une diversité de réponses plus faible et des espèces ayant été filtrées en fonction de leurs traits de réponses. Ainsi, les espèces se reproduisant principalement de manière sexuée (par graines), capables de disperser leurs graines sur de plus grandes distances pour coloniser des sites isolés et dont les graines sont dispersées par le vent auraient été favorisées. À l'inverse, les communautés situées dans des paysages caractérisés par une trajectoire moins perturbée (avec une plus grande superficie forestière à travers le temps) possèderaient une plus grande diversité de réponses. Les espèces se reproduisant végétativement et dispersant leurs graines par les mammifères et les oiseaux auraient également été favorisées dans les paysages historiquement moins perturbés, dans la mesure où plusieurs de ces espèces sont sensibles à la fragmentation du couvert forestier et peuvent éviter les milieux ouverts lors de leurs déplacements.

### 0.4.3 Objectifs et hypothèses du chapitre 3

Le chapitre 3 investigue la relation entre les arbres résiduels actuels distribués au sein des paysages agricoles et les communautés forestières locales et, conséquemment, si ces arbres résiduels peuvent contribuer à la mémoire écologique externe de ces communautés. Nous posons la question à savoir si les arbres résiduels sont liés à la composition et la structure des communautés tant au niveau spécifique que fonctionnel. Dans le cadre de ce chapitre, nous avons donc cartographié les arbres résiduels présents en 2015 dans le paysage et les avons inclus dans le couvert forestier.

Nous posons l'hypothèse que les arbres résiduels dans le paysage sont associés aux communautés forestières d'arbres et d'arbustes (abondance relative, diversité et richesse spécifiques, diversité et valeurs de traits de réponses) en favorisant le déplacement des animaux qui dispersent les propagules d'arbres et d'arbustes et en tant que sources de propagules d'arbres. Nous posons aussi l'hypothèse que les arbres résiduels ayant persisté sur une plus longue période (arbres plus âgés) sont plus importants que ceux ayant persisté moins longtemps (arbres plus jeunes) pour expliquer les patrons des communautés forestières adjacentes. Nous anticipons toutefois que les arbres résiduels d'aujourd'hui pourraient expliquer seulement une fraction des patrons au sein des communautés d'arbres et d'arbustes, puisque ces communautés sont influencées par un amalgame de conditions liées au passé et au présent (Gagné, Doyon, et al., 2022; Gagné, Messier, et al., 2022).

## 0.5 Pertinence de la thèse pour l'avancement des connaissances

Les travaux de cette thèse viennent complémenter et apporter un éclairage nouveau sur la dynamique spatiotemporelle du territoire et ses effets sur les communautés végétales par rapport aux résultats issus d'études antérieures réalisées dans une portion de notre aire d'étude (ex., D'Orangeville et al. (2008) et de Blois et al. (2001)). Les travaux de cette thèse se démarquent de par la couverture d'un territoire plus vaste couvrant l'ensemble des MRC Le Haut-Saint-Laurent et Vaudreuil-Soulanges. Elle se démarque également de par la combinaison de multiples échelles spatiales et temporelles, où l'analyse du territoire s'étend sur une plage temporelle plus grande (1930 à 2015), incorpore plusieurs échelles d'influence (locale, peuplement, paysage [600 m et 2 km de rayon]), en plus d'inclure une variation du grain d'analyse (résolution), prenant en compte les diverses classes d'occupation du sol ainsi que la présence d'arbres résiduels distribués au sein du territoire agricole. Enfin, l’unicité de ce projet réside également dans l’étude des communautés forestières en combinant le niveau des espèces (abondance, diversité et richesse spécifiques) à celui des traits fonctionnels de réponses (valeurs et diversité des traits de réponses) afin de mieux comprendre les mécanismes sous-jacents aux patrons observés.

# CHAPITRE I

## DO CURRENT SHRUB AND TREE COMMUNITIES BEAR THE MEMORY OF PAST LAND USE IN RURAL AREAS?

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## 1.1 Abstract

There is a growing interest in investigating the impact of past landscape and stand conditions on current species patterns. Forests around the world are becoming increasingly fragmented and these communities of long living organisms can bear the memory of past events for a long period. Our main goal is to assess whether present-day shrub and tree communities, located in a fragmented temperate forest landscape resulting from two centuries of human activities in southern Quebec, Canada, carry internal and external memories due to the persistence of legacies from the past. More precisely, we ask whether present-day community patterns are linked to past stand and landscape conditions through the presence of remaining legacies (patterns in shrub and tree species abundance, richness and diversity) that would have persisted through time. We sampled shrub and tree communities within 64 sites. We then assessed historical and recent land use and forest disturbances at the stand and landscape scales around each site at four different times over the past 85 years by photointerpreting old aerial photographs and analyzing recent forest maps. This allowed us to determine to what extent antecedent stand and landscape conditions influenced the present-day community patterns. We show that the relative abundance of several tree and shrub species, as well as tree richness and diversity, are influenced by events or conditions that occurred in 1930-40 and 1958, hence revealing the existence of distant and intermediate ecological memories within these communities. We also show that some species, as well as shrub diversity and richness, lost their link with distant and intermediate past conditions. Hence, shrub and tree communities are still controlled by events or conditions that occurred in the past, but recent habitat conditions or events could have reset the ecological memory of some species. The observed time lag could lead to uncertainty in the outcome of forest or land management, since reorganization of communities following a time lag, combined with interactions with new stressors, might give rise to novel species assemblages that could be unrelated to previous communities.

Keywords: ecological memory, ecological filters, landscape structure, time lag, shrub and tree communities.

## 1.2 Introduction

Community assembly rules are generally defined as a series of biotic and abiotic constraints to species coexistence (Götzenberger et al., 2012; HilleRisLambers et al., 2012) that could be conceptualized as a combination of hierarchical filters acting at different spatial and temporal scales. At the landscape scale, the dispersal filter on plant communities is related to stochastic events and to landscape connectivity and structure that can facilitate or impede propagules dispersal (de Bello et al., 2013; Garnier & Navas, 2012; Lortie et al., 2004). This dispersal filter favors species with colonizing traits adapted to the landscape structure, and thus influences the regional species pool (Garnier & Navas, 2012). Such filter can have a profound impact on community assembly and dynamics, especially in landscapes where forests are embedded within a heavily agricultural matrix, and are characterized by a reduced and fragmented forest cover. In extreme cases, where connectivity has been drastically reduced by habitat conversion, remnant communities in isolated habitats may undergo extinction when immigration can no longer compensate for individual mortality (Hanski & Ovaskainen, 2002; Hobbs & Yates, 2003; Ibáñez et al., 2014; Tilman et al., 1994). At the local or stand scale, abiotic filters encompass resource availability (e.g., soil nutrients), environmental conditions (e.g., soil pH and temperature) and disturbance regime (e.g., severity and frequency), whereas biotic filters refer to interspecific positive and negative relationships such as facilitation, competition, predation, and mutualism (Garnier & Navas, 2012, 2013; Grime, 2006; Lavorel & Garnier, 2002; Suding et al., 2008). These abiotic and biotic filters define local habitat conditions and influence which species, and where within the landscape, they are likely to establish and thrive based on their functional traits (Grime, 2006).

Although present-day ecological filters may demonstrate a strong influence on the current community patterns, the temporal dimension also needs to be accounted for, particularly for long living organisms such as trees. The capacity of past events or states to influence present or future community responses has been referred to in the literature as the ecological memory of an ecosystem (Padisak, 1992; Peterson, 2002), and appears through the presence of legacies (Johnstone et al., 2016). The internal ecological memory refers to legacies at the micro- or stand-scale, such as the presence of certain biological structures (e.g., dead wood), organisms, or soil and vegetation patterns that either persist following a disturbance (Franklin et al., 2007) or are altered following a prolonged land-use change (Foster et al., 2003). On the other hand, the external ecological memory refers to legacies at the landscape scale that influence the dynamics of a habitat patch following a disturbance or throughout its development. These legacies represent the supply of information and material from the surrounding landscape (Johnstone et al., 2016) such as source areas and their propagules located outside a disturbed site (Bengtsson et al., 2003). Such landscape legacies originate from past dispersal filters: they were shaped by former land-use, which have constrained former species and propagule availability.

Ecological memory, through disturbance and landscape legacies, can affect how disturbed stands will recover and continue their temporal trajectory (Bengtsson et al., 2003; Perry, 1995). The memory can last for very long periods ranging from decades to thousands of years. For example, Flinn and Marks (2007) showed that former agricultural activities in the New York state resulted in a decrease in soil organic matter, carbon and phosphorus, and in an altered species composition of secondary forests 100 years later. Dupouey et al. (2002) and Dambrine et al. (2007) also showed that farming in western Europe during Roman times about 2000 years ago induced changes in soil nutrients and species diversity that are still perceptible today. Ecological memory can also be detected in populations or communities experiencing a time lag, where their current state reflects more correctly past habitat conditions than present ones (With, 2007). A time lag is then the time taken to reach a new equilibrium following a landscape disturbance or restoration, and can be related to both metapopulation decline and expansion (Jackson & Sax, 2010; Kuussaari et al., 2009; Nagelkerke et al., 2002; With, 2007). Studies conducted in several European countries and Brazil showed that such a time delay in the species response to historical landscape structure still exists after 36-49 years (Krauss et al., 2010), 40 years (Metzger et al., 2009), 50 years (Burel, 1992; Petit & Burel, 1998), 60 years (van Ruremonde & Kalkhoven, 1991), 70 years (Helm et al., 2006), 100 years (Lindborg & Eriksson, 2004), 120 years (Ellis & Coppins, 2007; Paltto et al., 2006) and about 130 years (Vellend et al., 2006). Hence, the concept of ecological memory implies a spatiotemporal perspective that includes ecological filters at different spatial and temporal scales and implicitly recognizes the importance of past land-use and forest disturbances in shaping the current community composition and structure.

In the present study, our main goal is to assess whether present-day shrub and tree communities, located in a fragmented forest landscape resulting from two centuries of human activities in southern Quebec, Canada, carry internal and external memories due to the persistence of legacies from the past. More precisely, we ask whether present-day community patterns are linked to past stand and landscape conditions through the presence of remaining legacies (patterns in shrub and tree species abundance, richness and diversity) that would have persisted through time.

To achieve this goal, we examine the influence of several local biotic and abiotic filters (e.g., soil pH and sapling density) and dispersal filters associated with stand and landscape composition, configuration, connectivity and disturbances on the local present-day shrub and tree communities. Our investigation of dispersal filters extends over four different times in the past 85 years, which we refer to as distant past (1930-40), intermediate past (1958), recent past (1983) and current time (2015). We hypothesize that past conditions pertaining to both the stand and landscape scales influence the current shrub and tree specific abundance, richness, and diversity, hence revealing the existence of internal and external memories. More precisely, we predict that distant and intermediate past stand and landscape conditions are important for explaining the present-day shrub and tree community patterns, especially for species with response functional trait values that would have promoted their persistence (e.g., longer lifespan, and the ability to reproduce vegetatively and build seed banks), and colonization (e.g., long-distance seed dispersal by either mammals, birds or wind). Colonization is indeed important to reducing the risk of local extinction and reaching new unoccupied sites, both ensuring regional species persistence over time (Ozinga et al., 2007). We also predict that more recent or current stand and landscape conditions can be important in explaining present-day shrub and tree community patterns. Indeed, recent forest disturbances (e.g., forest logging) could have changed community patterns either by directly removing species that were persistent and linked with past conditions, or by indirectly modifying habitat conditions for species in the understorey, hence affecting their survival.

## 1.3 Study area

The study area is located in the Montérégie region in southern Quebec, Canada, and covers about 983 km$^2$ (98 259 ha). It is located between 45.0 and 45.5° north, and between -74.4 and -73.8° west (Figure 1.1). The mean annual temperature ranges from 5.6 to 7.4°C and the mean total annual precipitation ranges from 896 to 1120 mm. The topography is mostly flat with a maximum elevation of 40 m, except for the Rigaud (220 m) and Covey hills (343 m). The bedrock is mostly composed of dolomite and sandstone with some areas composed of limestone or granite. Surface deposits vary across the study area and are composed of marine, moraine, sand, gravel, and glacial till. Forest stands of this region are part of the sugar maple and bitternut hickory bioclimatic zone (Robitaille & Saucier, 1998) and are dominated by a variety of species, according to their successional stages, such as sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), white ash (*Fraxinus americana*), American basswood (*Tilia* *americana*), eastern white cedar (*Thuja occidentalis*), grey birch (*Betula populifolia*) and large-tooth aspen (*Populus grandidentata*). In this region, agricultural areas were at their peak around the 1890s, before starting to decline in the 1950s (Domon & Bouchard, 2007). The present-day forest of this region covers about 26-36% of the territory and is highly fragmented and scattered within an agricultural matrix with few large forest remnants such as those located on the Rigaud hill (> 5 000 ha) and around the Covey hill close to the Canada-United States border (> 10 000 ha). Within the 2 km-buffer zones that we have studied, forest cover generally increased over time between 1930-40 and 2015 (Figure 1.2), and the present-day forest cover varies from less than 5% to more than 80% (Annex A).

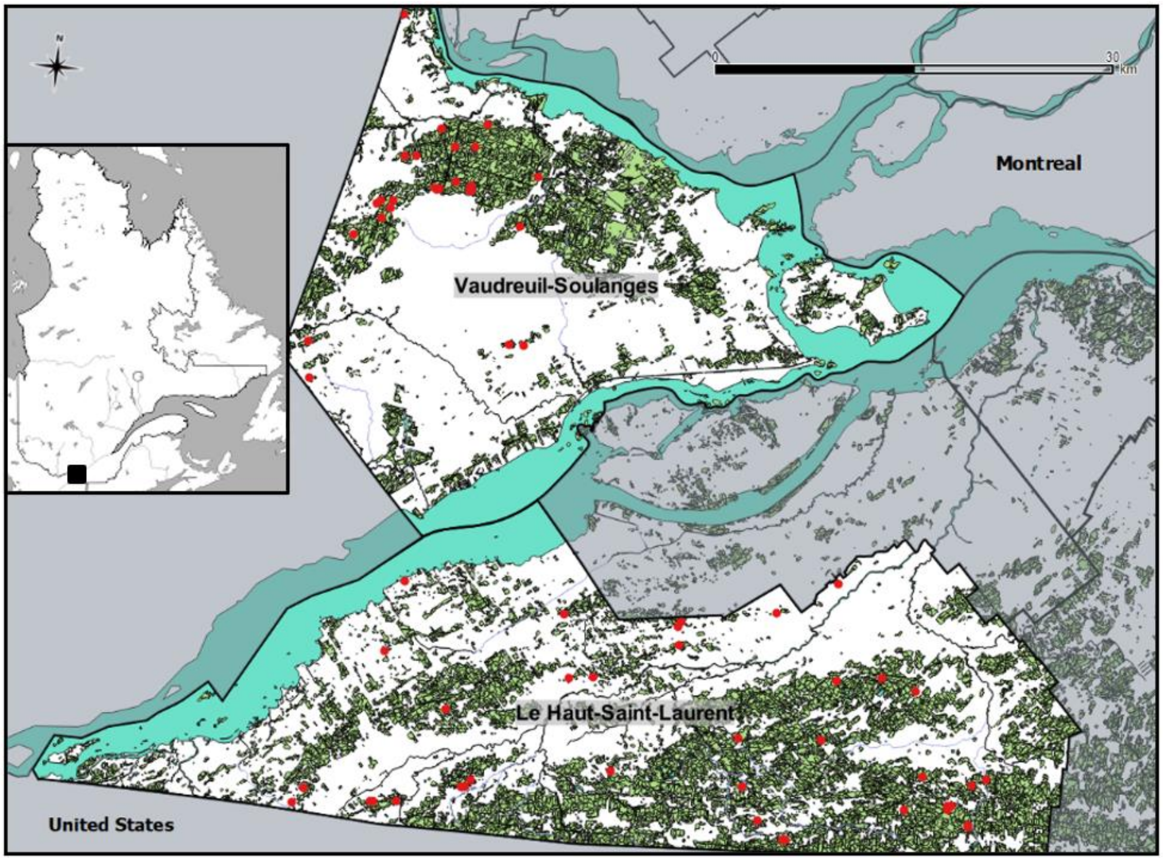

Figure 1.1. The study area and sampling sites (red dots) located in the regional county municipalities of Vaudreuil-Soulanges and Le Haut-Saint-Laurent, Quebec, Canada. Forests are represented by green patches.

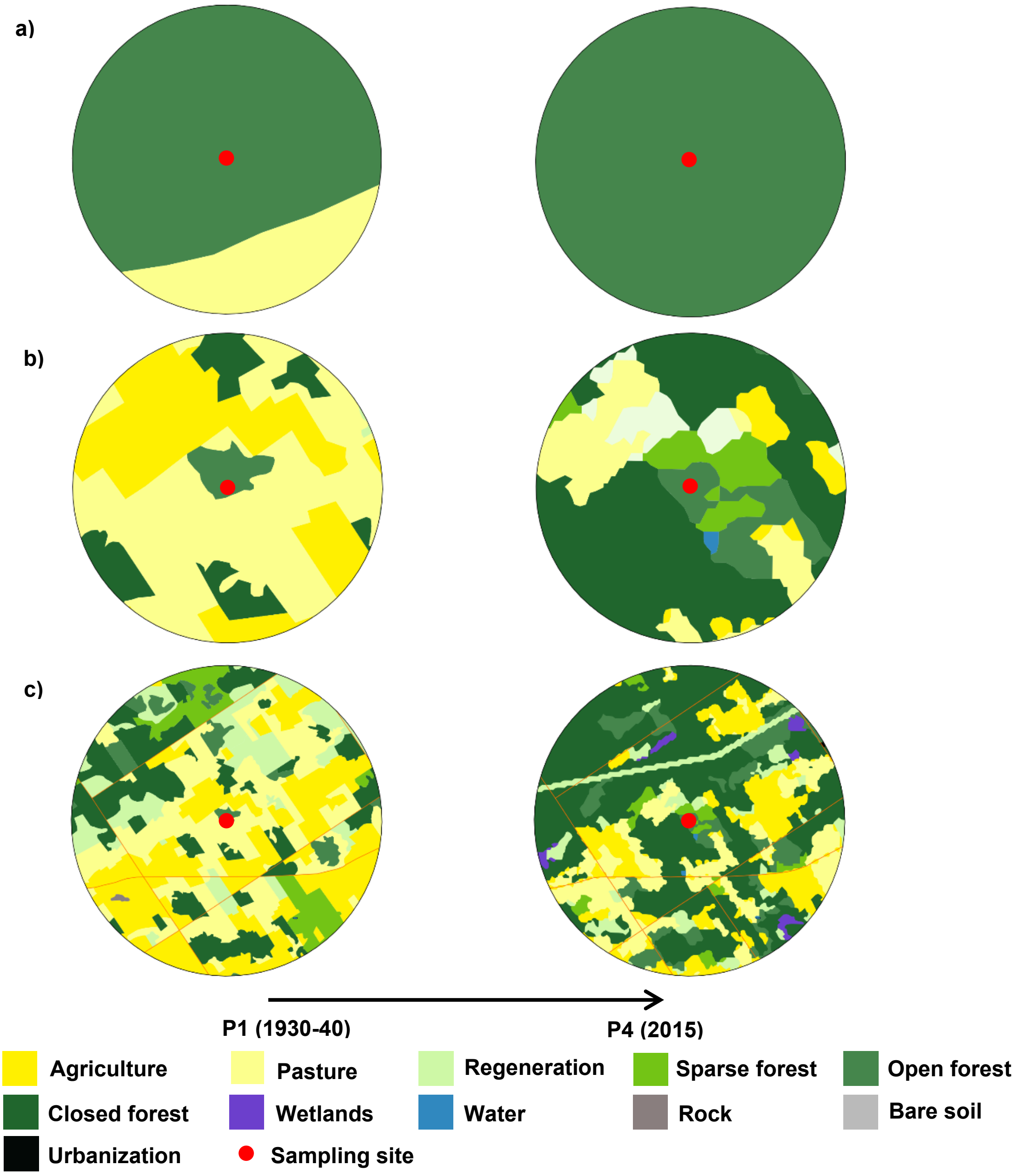

Figure 1.2. Evolution of forested areas between 1930-40 (P1) and 2015 (P4) for one of our 64 sampling sites within the 60 m-buffer zone (a), 600 m-buffer zone (b) and 2 km-buffer zone (c).

## 1.4 Methodology

Two main methods were used in this study. First, field sampling of forest communities in the study area was done to assess the current tree and shrub abundance, diversity and richness, and biophysical variables at the local scale (30 m radius) in 64 sampling sites. Second, photointerpretation of old aerial photographs and analyses of recent forest maps were done to assess stand and landscape historical explanatory variables. We investigated three spatial scales (60 m, 600 m, and 2k m radii), four periods in time and the intervening years between each of these periods. The 60 m buffer represents the stand scale at which short-distance seed dispersal and local disturbances occur. The 600 m and 2 km buffers represent the landscape scale and encompass different scales of influence of ecosystem processes, such as long-distance seed dispersal. The use of multi-scale nested buffer zones allows us to assess the amount of habitat and other landscape characteristics in local landscapes, as recommended in Fahrig (2013) when the appropriate scale is unknown. The four periods are as follow: P1 – distant past (1930-40), P2 – intermediate past (1958), P3 – recent past (1983), and P4 – current time (2015). The intervening years are as follows: A1 – distant past (before 1930-40), A2 – intermediate past (between 1930-40 and 1958), A3 – recent past (between 1958 and 1983), and A4 – very recent past (between 1983 and 2015). The choice of the four periods was dependent on data availability, and time periods about 15 to 30 years apart were selected which allowed us to witness land-use changes and forest evolution. Land use was assessed for the five time periods, whereas forest disturbances were associated with the intervening years.

### 1.4.1 Site selection

During the spring and summer 2015, 64 sites were established within mature forest patches to sample tree and shrub communities. Using ecoforestry maps (Ministère des Ressources naturelles et de la Faune [MRNF], 2009), sites having homogeneous pedological and topographic characteristics, as well as representing a diversity of historical forest disturbances and land uses such as clearcutting, agriculture, and pasture, were chosen. Site selection was based on recent ecoforestry maps (MRNF, 2009), on-site physical evidence of past use (presence of recent or old cut stumps, fences, sugar shacks or signs of maple syrup production), and discussions with private landowners. Tree communities in the sampling sites had various profiles, ranging from early to late-successional assemblages.

### 1.4.2 Response variables based on tree and shrub sampling

From the centre of each sampling site, trees were sampled using the prism sweep technique using a factor 1 prism. All trees with a diameter at breast height (DBH) greater than 9.1 cm were accounted for during the prism sweep and tree species were identified. The basal area was obtained by summing the number of stems that were included in the sampling site during the sweep (i.e., stems whose images saw through the prism were within the real stems), and then multiplying the number of stems by the prism factor (one in this case). The basal area was calculated for each tree species. A total of 27 tree species were present in the sampling sites (Table 1.1). Information on shrubs was collected within four circular subplots with a 2.5 m radius (total area of 78.5 $m^2$) located 20 m from the central point of the sampling sites in four directions (north, south, east and west). Within these subplots, shrubs were counted and species were identified. For shrubs, all stems that were emerging from the same location (e.g., from a main stem that would have sprouted close to the ground) were considered as a single individual, while stems emerging from the ground in different locations were considered as separate individuals. A total of 31 shrub species were present in the sampling sites (Table 1.1). In this study, shrubs include all woody species of shrubs, subshrubs and vines as defined in the PLANTS Database (U.S. Department of Agriculture & National Resources Conservation Service, 2016).

From this information, tree and shrub relative abundance was computed for each species based on its relative basal area and relative density, respectively. Tree and shrub richness and diversity were also calculated, where the diversity index corresponded to the effective number of species (Jost, 2006) and was based on the Shannon-Wiener index using the relative basal area and the relative frequency for all trees and shrubs, respectively.

### 1.4.3 Local-scale explanatory variables

To characterize local conditions (abiotic and biotic filters), two soil samples of the A horizon (Soil Classification Working Group, 1998) were randomly collected within a 30 m radius. The soil pH was measured with a digital pH meter and the soil texture was assessed through a tactile method (Méthot et al., 2014) and classified using the Canadian system of soil classification (Soil Classification Working Group, 1998). The percentage of canopy closure was also visually assessed in the centre of each 2.5 m radius subplot up to 0.5 and 1.5 m above ground. All visual assessments were done by the same three observers for all sampling sites, who previously calibrated their observations and assessments in order to ensure the same interpretation. Further calibration was also carried out throughout the field work. Within the four circular 2.5 m radius subplots, tree saplings (stem DBH ≤ 9.1 cm) were also counted and characterized as to species and DBH. Finally, tree seedlings (stem DBH < 2 cm) were counted within four circular 1.5 m subplots (total area of 28.3 $m^2$) nested within the 2.5 m subplots and were characterized according to their species and a combination of height and DBH. Tree seedlings and saplings are important to include as local-scale explanatory variables for explaining shrub diversity, richness and relative abundances because they can compete with shrubs for resources such as light (e.g., tree saplings are often taller than shrubs in our study area), and could thus influence shrub community patterns. With this information, we calculated the tree sapling and seedling total density (all species included) and diversity. The diversity indices were computed in the same way as for shrubs.

### 1.4.4 Explanatory variables based on historical land use and forest disturbances

#### 1.4.4.1 Classification and assessment of historical land use and forest disturbances

Land use included abandoned agricultural field, agriculture, closed forest (forest cover ≥ 60%), open forest (forest cover ≥ 25% and <60%), pasture, regeneration, sparse forest (forest cover <25%) and urbanization. Forest disturbances were divided between severe and partial disturbances, where the former mainly includes forest clearcutting, while the latter primarily includes partial logging and ice storms. Forest disturbances were indicated on recent ecoforestry maps, while they were photointerpreted on older aerial photos based on the canopy opening (most trees were removed after a clear-cut, while we could detect a residual forest cover after a partial harvesting). Maple syrup production over the years is also a type of partial forest disturbance at the stand scale but was considered separately since it is a binary variable (presence/absence) for which the exact area and period were not possible to assess.

In this study, all land-use classes are related to habitat composition at the stand or landscape scale, and all but one are also related to disturbances. For example, agricultural and regeneration areas are both the result of a severe disturbance that removed all trees from a particular site, while open forests are instead associated with partial disturbances. Areas in regeneration could be the result of either a clearcut or a slow forest recovery following agricultural abandonment, while open forests could result from partial logging or from natural disturbances, such as ice storms. Closed forest is the only land-use class associated with undisturbed habitat. Moreover, landscape fragmentation in this study is a result of landscape disturbances and does not reflect natural geographical barriers.

The assessment of historical land use and forest disturbances was done through data integration from multiple sources. First, photointerpretation of 185 historical aerial photographs was conducted with a mirror stereoscope for the years 1930-40 and 1958. To achieve this, acetates were superimposed on the aerial photographs to reproduce land-use classes and forest disturbances in at least a 2 km buffer around each of the 64 sampling sites (Annex B). Drawn acetates were then scanned, georeferenced with Global Mapper (Blue Marble Geographics, 2016), and vectorized with QGIS (QGIS Development Team, 2016) in order to create new shapefiles. We validated the photointerpretation results during field sampling of the 64 sites and with a postal survey intended for the 52 landowners where our sampling sites were located that invited them to share their knowledge about past and current land use (Annex C). Among others, we were interested in gathering information about past logging activities. About 40% of the landowners, 21 in total, responded to the survey. This information confirmed the adequacy of the photointerpretation.

Second, georeferenced ecoforestry maps of the second forest inventory, using aerial photographs from the year 1983 (Ministère de l'Énergie et des Ressources [MER], 1984), were used to extract relevant information related to land use and forest disturbances. Since each map was a georeferenced image, it was also necessary to vectorize them to obtain new shapefiles of land use and forest disturbances.

Third, data originating from Landsat satellite images (30m-resolution) that were available in a raster format for the year 2013 (Bissonnette & Lavoie, 2015) were used and converted into a vectorized polygon format with QGIS (QGIS Development Team, 2016). This layer contained information about agricultural lands, urban areas, forest areas, wetlands, and other non-forest land-use classes. In addition, very recent forest disturbances (e.g., partial logging, clearcutting) from an updated version of the 2009 ecoforestry maps (MRNF, 2015) were added to the Landsat layer. Finally, other very recent forest disturbances (in 2015 or slightly before) that occurred close to the sampling sites and that were detected during field work were also added to this layer.

#### 1.4.4.2 Stand and landscape explanatory variables

Most variables represent a combination of three components: 1) a factor related to habitat structure, connectivity or disturbance, 2) a spatial scale (30 m [local scale, field-surveyed], 60 m [stand scale], 600 m or 2 km buffers [landscape scales]), and 3) a temporal scale (one of the four time periods; Annex D). Factors related to stand composition or disturbance include the area of each land-use class and disturbance type within the 60 m-radius. Measures of landscape structure, disturbance and functional connectivity include the area of each land-use class and disturbance type within the 600 m- and 2 km-radii, the distance to the nearest forest disturbance, the mean distance to forest disturbances, the distance to the nearest forest edge, the distance to the nearest pasture, the length of forest edges, the length of roads, and the probability of connectivity index (PC; Saura & Pascual-Hortal, 2007). All distance variables were computed from the centre of each sampling site. The PC index was computed based on the grey squirrel's (*Sciurus carolinensis*) dispersal ability in open ground between two habitat patches (less than 500-1000 m; Fitzgibbon, 1993) and on its perceptual range in a fragmented agricultural landscape (about 300 m; Zollner, 2000). Squirrels are good seed dispersal vectors and the lack of functional connectivity for this species and similar species is likely to impact tree and shrub seed dispersal across the landscape.

Some variables were computed at both the stand and landscape scales for each of the four periods, while some others were computed only at the landscape scale (Annex D). All data preparation, shapefile manipulations and spatial analyses for computing stand- and landscape-scale explanatory variables were conducted with Global Mapper (Blue Marble Geographics, 2016), QGIS (QGIS Development Team, 2016) and FME (Safe Software, 2016). The probability of connectivity index was obtained using Conefor (Saura & Torné, 2009).

## 1.5 Statistical analyses

Principal component analyses (PCA) were first conducted with our set of standardized continuous explanatory variables. To do so, we split the variables in the following 13 groups based on their spatial and temporal scales, and did a PCA for each of these groups for shrubs (n=59) and trees (n=64):

1) local – *P4*,
2) stand – *P1*,
3) stand – *P2*,
4) stand – *P3*,
5) stand – *P4*,
6) landscape (composition + disturbances; LCD) – *P1*,
7) LCD – *P2*,
8) LCD – *P3*,
9) LCD – *P4*,
10) landscape (configuration + connectivity; LCC) – *P1*,
11) LCC – *P2*,
12) LCC – *P3*, and
13) LCC – *P4*.

We used the broken-stick method to decide which dimensions to keep in each group, combined with the Kaiser-Guttman approach to avoid underestimating the number of interpretable dimensions that can sometimes happen with the broken-stick method (Jackson, 1993). The dimensions and associated variables kept for the 13 groups are shown in Tables 1.2 (trees) and 1.3 (shrubs). To complete the groups of explanatory variables, we added the following categorical variables: soil texture (Trees_1 and Shrubs_1 models), maple syrup production over time (Trees_5 model), and maple syrup production over time and successional stage (Shrubs_5 model).

Subsequently, we modelled each response variable against the 13 sets of explanatory variables described above and compared the models with the Akaike's information criterion ($AIC_c$) to identify those with the highest strength of evidence (Burnham & Anderson, 2002). The best and competing models, with a $\Delta$ $AIC_c < 2$, are those that are shown and discussed in the Results section.

For shrubs, multiple linear regressions were used to model the following response variables: shrub diversity, shrub richness, the relative abundance of *Cornus alternifolia*, and the 4th root-transformed relative abundance of *Ilex mucronata*, *Parthenocissus quinquefolia*, *Rhamnus cathartica*, *Ribes spp.*, *Rubus spp.*, *Toxicodendron radicans*, *Vitis riparia*, and *Zanthoxylum americanum*. For shrub diversity, shrub richness, *Parthenocissus quinquefolia*, *Rhamnus cathartica*, *Rubus spp.*, *Toxicodendron radicans*, and *Zanthoxylum americanum*, we needed to account for spatial autocorrelation that was present in the residuals for one or several of their 13 models. In these cases, we used linear spatial lag regression models (Florax & Nijkamp, 2003). When spatial lag models failed to adequately address spatial autocorrelation in residuals, we used linear spatial error models instead (Florax & Nijkamp, 2003). In spatial lag models, the regression coefficients must be interpreted with caution because of the "spatial spillover effect" (Golgher & Voss, 2016). The spatial spillover effect occurs when one change in an explanatory variable in one location changes the response variable in that location, but also in its neighbors, meaning that the impact of a change in one explanatory variable is spatially spread out. For these models, we thus need to report the direct effects (how a response variable in a specific location changes with a change in explanatory variables in this same location), the indirect effects (how a response variable in a specific location changes with a change in explanatory variables elsewhere), and the total effects (the sum of the direct and indirect effects). Finally, for *Amelanchier spp.*, *Prunus virginiana* and *Viburnum lentago*, multiple Firth penalized logistic regressions were conducted to model the presence/absence of the species, their low overall occurrence and often low relative abundance preventing us to use linear regressions. This logistic regression is an appropriate approach for small sample size and low frequency data (Firth, 1983; Nemes et al., 2009). The remaining 18 shrub species (Table 1.1) were not modeled individually because of their very low overall occurrence and relative abundance.

For trees, multiple linear regressions were used to model the following response variables: tree diversity, tree richness, and the relative abundance of *Acer rubrum*, *Acer saccharum*, *Ostrya virginiana*, *Populus spp.*, *Thuja occidentalis*, *Tilia americana,* and *Tsuga canadensis*. For tree richness, *Acer rubrum*, and *Tilia americana,* we used linear spatial lag regression models to account for spatial autocorrelation that was present in the residuals for one or several of their 13 models (Florax & Nijkamp, 2003). We also used multiple Firth penalized logistic regressions to model the presence/absence of *Betula alleghaniensis*, *Fagus grandifolia*, and *Fraxinus americana*. The remaining 15 tree species (Table 1.1) were not modeled individually because of their very low overall occurrence and relative abundance.

For the linear regression models, the following assumptions were tested: normality, homoscedasticity and collinearity of residuals, outliers, relationship linearity, and spatial autocorrelation. The normality of residuals was visually assessed with Q-Q plots (Fox & Weisberg, 2019), while their homoscedasticity was tested with the Breusch-Pagan studentized test (Breusch & Pagan, 1979). To improve the normality and homoscedasticity of residuals, some response variables were 4th root-transformed. When residuals were still heteroscedastic, the standard error and confidence intervals of the coefficients were measured with a robust method based on a heteroscedasticity-corrected covariance matrix of the model parameters (Fox & Weisberg, 2019; Hayes & Cai, 2007). The collinearity of residuals was tested with the Variable Inflation Factors test (VIF; Fox & Weisberg, 2019). As expected, collinearity was absent from our explanatory variables data sets since we modelled PCA dimensions, which are orthogonal relative to each other. Influential outliers were detected with the residual vs. leverage plots showing the Cook's distance (Fox & Weisberg, 2019). When needed, sampling sites with a Cook's distance greater than 0.5 were removed. The linearity of the relationship was verified with the component + residual plots (Fox & Weisberg, 2019). Finally, residual spatial autocorrelation was tested with the Moran's test, which used a weighted list created with the k nearest neighbors' method from the spatial coordinates of the sampling sites (Dormann et al., 2007). Spatial lag models and spatial error models were used to address residual spatial autocorrelation, when needed (Florax & Nijkamp, 2003).

For the Firth logistic regression models, we tested the presence of influential outliers with the Cook's distance (Martín & Pardo, 2009) and, when needed, removed sampling sites showing a Cook's distance greater than 0.5. We also visually inspected the scatterplots between the logit of each response variable and each of their continuous explanatory variables to ensure these relationships were linear (Hosmer et al., 2013). This condition was met for all logistic regression models.

All statistical analyses were completed with R (R Core Team, 2017) with the following packages: Hmisc (Harrell & Dupont, 2017), stats (R Core Team, 2017), car (Fox & Weisberg, 2019), moments (Komsta & Novomestky, 2015), spdep (Bivand et al., 2013a; Bivand & Piras, 2015), AICmodavg (Mazerolle, 2020), lmtest (Zeileis & Hothorn, 2002), logistf (Heinze et al., 2022), spatialreg (Bivand et al., 2013a, 2013b, 2021; Bivand & Piras, 2015), and sandwich (Zeileis, 2004; Zeileis et al., 2020).

## 1.6 Results

Among the 14 response variables that were modeled for shrubs, we report results for 12 of them, for which at least one model was significant before proceeding with the model selection (Table

1.4). For *Amelanchier spp.* and *Vitis riparia*, none of their 13 models was significant, so we did not conduct the model selection. Thus, results for these species are not shown in Table 1.4 and will not be discussed further. For trees, we were able to model 12 response variables (Table 1.5), of which one (the relative abundance of *B. alleghaniensis*) did not have at least one significant model. In this case, we did not conduct model selection and will not discuss the results.

For shrubs, the best and competing models for seven response variables involve only present-day or very recent conditions at either the local scale (Shrub diversity), the stand scale (Shrub richness, *C. alternifolia* and *I. mucronata*), the landscape scale (*R. cathartica* and *Ribes spp.*) or at both the stand and landscape scales (*T. radicans*). On the other hand, the best and competing models for two response variables involve only past conditions, *P. virginiana* being influenced by intermediate and recent past landscape conditions and *Z. americanum* being influenced only by distant past landscape conditions. In between, the best and competing models for three response variables involve present-day or very recent and past conditions. Indeed, *P. quinquefolia* is influenced by present-day and very recent local and stand conditions as well as distant past stand conditions. *Rubus spp.* Is influenced by present-day and very recent landscape conditions and intermediate past landscape conditions. Finally, *V. lentago* is influenced by present-day and very recent landscape conditions as well as distant and intermediate past landscape conditions. Here, results for *C. alternifolia* must be interpreted with caution since neither of its competing models are significant, and the production of maple syrup over time is the only significant explanatory variable. Moreover, spatial models for which only the spatial parameter was significant (Shrubs_4 for *Rubus spp.* and *T. radicans*) and those where the only significant PCA dimension was mostly related to latitude and longitude (Shrubs_12 for *T. radicans* and Shrubs_8 for *V. lentago*) were not taken into account in the results reported above (Table 1.4).

For trees, the best and competing models for three response variables involve only present-day or very recent conditions at the local scale (*A. rubrum* and *T. occidentalis*) or the stand scale (*A. saccharum*). At the opposite, the best and competing models for seven response variables involve only past conditions at either the stand scale (*O. virginiana*) or the landscape scale (Tree diversity, *F. grandifolia*, *F. americana*, *Populus spp.*, *T. americana*, and *T. canadensis*). Among these response variables, four are influenced only by distant or intermediate past conditions (Tree diversity, *O. virginiana*, *Populus spp.*, and *T. canadensis*) and three respond only to recent past conditions (*F. grandifolia*, *F. americana*, and *T. americana*). In between, the best and competing models for one response variable (Tree richness) involve present-day or very recent as well as past conditions at both the stand and landscape scales, past conditions being related to the distant time period.

## 1.7 Discussion

### 1.7.1 Past and current habitat conditions can drive today's shrub and tree community patterns

In this study, we first predicted that distant and intermediate past stand and landscape conditions were important for explaining the present-day shrub and tree community patterns, especially for species with response functional trait values promoting their persistence and colonization over time. We showed that several shrub and tree species in the present-day communities, as well as tree diversity and richness, were still related to past stand and landscape conditions, hence revealing the existence of an internal and external memory. These species and community structure are biological legacies from the past that have persisted to this day in the sampled communities. We also predicted that more recent or current stand and landscape conditions could be important as well for explaining present-day community patterns because of direct removals of persistent species that were previously linked to past conditions, or because of indirect habitat modifications affecting their survival. In this regard, we showed that even species with functional trait values providing them with a long-term persistence could have their ecological memory reset by present-day or very recent ecological filters.

#### 1.7.1.1 Shrubs

In our study, shrub species exhibiting a relationship with distant and intermediate past conditions (*P. quinquefolia*, *P. virginiana*, *Rubus spp.*, *V. lentago*, and *Z. americanum*) display variable lifespan and ability to produce persistent seed banks (Aubin et al., 2012; Haeussler & Coates, 1986). However, all these species do have in common the ability to spread vegetatively either through rhizome, stolon or root sprouting (Crowder et al., 2004; Munter et al., 2018; Niering et al., 1986; Reinartz & Popp, 1987; U.S. Department of Agriculture & National Resources Conservation Service, 2016), *Z. americanum* and *V. lentago* being even able to form long-lasting clonal stands (Munter et al., 2018; Niering et al., 1986; Reinartz & Popp, 1987). Some of these species show a moderate to rapid vegetative spread rate (U.S. Department of Agriculture & National Resources Conservation Service, 2016), while they all have bird-dispersed seeds and, in some cases, mammal-dispersed seeds (Aubin et al., 2012). In comparison, shrub species that are solely associated with present-day or very recent past conditions (*I. mucronata*, *R. cathartica*, *Ribes spp.*, and *T. radicans*) also display variable lifespan and ability to produce persistent seed banks, and they all have bird- and mammal-dispersed seeds (Aubin et al., 2012). The difference between species associated with distant and intermediate past and those with the very recent or present-day conditions appears to stem from the species ability to spread vegetatively either from root, rhizome or stolon sprouting and from their spreading rate. This is especially obvious when comparing species with a similar lifespan from the two groups (*Rubus spp.* vs. *Ribes spp.* [short]; *P. virginiana*, *Z. americanum* and *P. quinquefolia* vs. *I. mucronata* [moderate]; *V. lentago* vs. *R. cathartica* and *T. radicans* [long]). For all these comparisons, species associated with distant and intermediate past conditions have a greater ability to spread vegetatively and/or at a faster rate compared to species that are only associated with very recent past or present-day conditions (Aubin et al., 2012; Barnes & Wagner, 2004; Converse, 1984; Crowder et al., 2004; Gale, 2000; Heneghan et al., 2006; Knight, 2005; Moss and Wellner, 1953; Munter et al., 2018; Niering et al., 1986; Reinartz & Popp, 1987; U.S. Department of Agriculture & National Resources Conservation Service, 2016). However, there is still uncertainty regarding the effect of seed persistence in soil seed banks for some species, mainly those for which persistence was noted as +5 years and for which more precise information was not available.

Despite a certain persistence ability, species responding only to very recent past or present-day conditions could be in equilibrium with those conditions and their memory could have been reset. For instance, *Ribes spp.* generally establish in early forest succession, within canopy openings of various sizes. As the canopy openings close and the light intensity decreases, *Ribes spp.* become less vigorous and lose their sexual reproduction capacity (Zambino, 2010). In our study, all sampled forests had a present-day closed canopy, but the sampling sites were at various distances from forest edges and from non-forested habitat in the surroundings. In this context, the individuals that were sampled may be those who survived where the habitat conditions (abiotic filter) were the most suitable such as closer to forest edges (for the increased light intensity) and away from pastures (where the browsing pressure is reduced), as shown in our results. This highlights the fact that present-day or very recent habitat conditions might filter species based on functional traits that were not accounted for in the present analysis.

#### 1.7.1.2 Trees

In the present-day tree communities, all species have the potential to be associated with distant and intermediate past conditions if only by their long lifespan. Indeed, all but two species have a lifespan greater than 100 years and some can even reach 800 years, like *T. canadensis* (Burns & Honkala, 1990a, 1990b; Loehle, 1988; MRN, 2013). Among species that were analysed individually, most are also able to reproduce vegetatively, although their ability to do so varies greatly in relation to tree species, size and age (Aubin et al., 2012; Burns & Honkala, 1990a, 1990b; Del Tredici, 2001; U.S. Department of Agriculture & National Resources Conservation Service, 2016; Wagner et al., 2010). In this regard, the ability of *P. tremuloides*, within the *Populus spp.* group, to form large clonal colonies through root sprouting is well known (Del Tredici, 2001). On the other hand, most tree species analysed individually do not have the capacity to build persistent soil seed banks, with the exception of *F. americana* whose seeds can still be viable after five years (MRN, 2013). They also disperse their seeds in different ways, some having wind-dispersed seeds (*A. rubrum*, *A. saccharum*, *F. americana*, and *Populus spp.*), the others having a combination of wind-, bird-, mammal- or gravity-dispersed seeds (Aubin et al., 2012).

In this context, among the three species associated with distant and intermediate past conditions, *Populus spp.* stand out by their well-developed clonal spread ability, while *T. canadensis* stands out by its lifespan that is way longer than that of other species. Nonetheless, *O. virginiana* does not stand out from other species that are associated with more recent stand or landscape conditions with regards to the response traits discussed above. This emphasizes the fact that external factors, such as changes in habitat conditions, targeted forest harvesting, or other stressors or disturbances (abiotic filter) might have reset the ecological memory of some species, but not all. Indeed, while *O. virginiana* is not the most sought-after species for harvesting because of its relatively small size and scattered distribution (Coladonato, 1992), neither is *T. canadensis*, whose wood contains a lot of knots, is somewhat brittle and is then considered of lower value compared to some hardwood species (Carey, 1993). These characteristics could have allowed these species to regenerate and persist either as companion or co-dominant species in late-successional stands over time. For their part, *Populus spp.* could have been cleared-cut in the past decades and still be occurring in present-day communities, hence retaining their relationship with distant past conditions, since logging can stimulate root sprouting and favor the clonal spread of these species (Del Tredici, 2001).

In our study, three species were only related to conditions that were measured in 2015 despite their great longevity. In this regard, *A. saccharum* was only related to maple syrup production over time at the stand scale (positive relationship), as measured in 2015. This result tells us that continuous stand management for maple syrup production over time appears to have completely reset the ecological memory of this species and erased all other links with past landscape conditions. The situation is different for *A. rubrum* and *T. occidentalis*, that were both influenced by soil pH as measured in 2015 (positive relationship for *T. occidentalis* and negative relationship for *A. rubrum*). Soil pH is a long-lasting soil condition that can be altered by agricultural activities, as shown in Blondeel et al. (2018) where post-agricultural forest stands had a higher soil pH compared to stands with a continuous forest cover over time. Similarly, Falkengren-Grerup et al. (2006) showed that soil pH was lower in stands that had a continuous forest cover over time compared to stands that were previously cultivated before forest regenerated, and that this difference was still perceptible after 80 years. In our study, soil pH could be a proxy indicating the past local conditions in which *A. rubrum* and *T. occidentalis* established. Indeed, our data show that *A. rubrum* occurs mostly in stands that were forested since before the 1930s (with a lower soil pH), while *T. occidentalis* occurs mostly in stands that were characterized by land uses such as agriculture, pasture or regeneration in 1930-40, 1958 and sometimes until 1983 (with a higher soil pH). This interpretation is compatible with the study of de Blois & Bouchard (1995) who showed that stands of *T. occidentalis* in southern Quebec were associated with pastures, where they would have been avoided by cattle grazing compared to other species, which would have provided them with a competitive advantage and allowed them to establish in those agricultural sites.

### 1.7.2 Community patterns show a time lag in their response to changes in habitat conditions

Our results indicate that some species in the present-day shrub and tree communities, as well as tree diversity and richness, may experience a time lag in their response to changes in landscape structure that occurred some time ago (Kuussaari et al., 2009; Nagelkerke et al., 2002; With, 2007). This is consistent with other studies showing that wood inhabiting fungi, forest lichens and understorey herbaceous and shrub species (Ellis & Coppins, 2007; Kolk & Naaf, 2015; Paltto et al., 2006; van Ruremonde & Kalkhoven, 1991; Vellend et al., 2006), natural or semi-natural grassland species (Krauss et al., 2010; Lecoq et al., 2021; Lindborg & Eriksson, 2004), and alvar grassland species (Helm et al., 2006) all experienced a time lag following an intensive habitat fragmentation episode. For trees, our results are similar to those reported by Metzger et al. (2009), who showed that both shade intolerant and tolerant tree species were responding to past rather than current landscape structure.

As shown in our study, communities where time lags can occur are generally characterized either by long-living species, species able to reproduce vegetatively, and, in some cases, by species producing long-lasting seedbanks (Hylander & Ehrlén, 2013; Lindborg, 2007; Nagelkerke et al., 2002; With, 2007). All these traits can allow individuals to remain or regenerate in local sites long after landscape alteration has occurred, and survive in a non-equilibrium dynamics (Hanski & Ovaskainen, 2002). However, external factors, such as forest harvesting and forest fragmentation, could break the link between persistent species and past conditions and create a new equilibrium between more recent or present-day habitat conditions and community composition and structure, as reported in the present study.

### 1.7.3 A colonization credit or an extinction debt?

Two hypotheses can be formulated to help interpret the observed time lags found in this study. Firstly, species associated with the time period ranging from 1930-40 to 1958 could experience a time lag related to a colonization credit (Jackson & Sax, 2010; Nagelkerke et al., 2002; With, 2007). Indeed, the abandonment of agricultural activities in some areas began around the 1950s and forests were then able to recover (Domon & Bouchard, 2007). A colonization credit implies a slow population increase of these species until they reach a new equilibrium with the present, more forested landscape. The alternative and opposite hypothesis implies that some highly persistent species could be associated with older periods for which no data were available. In this case, these species could be relics associated with landscape structure prevailing during the European settlement period (circa 1785 and after), when forests were more abundant and less fragmented (Domon & Bouchard, 2007). If this hypothesis holds, it means that the observed time lags for these species is related to extinction debts that are still not fully paid (Hanski & Ovaskainen, 2002; Jackson & Sax, 2010; Kuussaari et al., 2009; Tilman et al., 1994), and that further species decline should be expected in the future until communities are in tune with present, less abundant and more fragmented habitats. It is not possible to determine which scenario is the most accurate, yet the results nevertheless strongly suggest that a readjustment in community structure and composition will happen, and may have already begun for some species.

### 1.7.4 How to deal with time-delayed forest communities?

Forests in our study are still influenced by past habitat conditions, which translates into the observed time lags for some individual species abundance, as well as tree specific diversity and richness. In the absence of certainty regarding the duration of these time lags and whether they are related to a colonization credit or to an extinction debt, it is difficult to promote precise conservation or management guidelines. However, what is certain is that a time lag does bring about uncertainty in the outcome of forest or land management. Two apparently similar forest communities may indeed be on different trajectories because of their respective past memories, and may evolve differently in the future even in the absence of any new disturbance (Perring et al., 2016). Therefore, should we manage a forest containing species expected to decline in the future in the same way as another forest with species expected to increase? How will these transient time-delayed communities interact with stressors such as global change that may affect local abiotic filter, and thus further influence their trajectories (Perring et al., 2016)? The reorganization of communities following a time lag, combined with interactions with new stressors, might give rise to new species assemblages referred as novel ecosystems by some authors (Bürgi et al., 2017; Hobbs et al., 2014; Kellman, 1996). In this situation, the least we can do is foster a greater landscape connectivity and a higher local habitat quality (Nagelkerke et al., 2002; Ramalho & Hobbs, 2012) in order to reduce local extinction and enhance colonization. In this context, approaches that identify, preserve or restore existing key forest patches with key tree species to promote short- and long-distance movement corridors could prove to be necessary in highly fragmented landscapes (Messier et al., 2019; Rayfield et al., 2016). However, preserving the existing remnant forest patches scattered throughout intensive agricultural areas may not be enough to enhance local connectivity. Complementary and more pro-active approaches should receive more attention, such as managing the functional diversity of tree and shrub communities using a functional complex network approach (Craven et al., 2016; Messier et al., 2019), and implementing agroforestry practices (Jose, 2012; Schroth et al., 2004; Torralba et al., 2016) that aim at reintroducing species with particular traits by means of hedgerows, fencerows, windbreaks, and riparian forest buffer restoration.

## 1.8 Conclusion

Community structure and composition are driven by a complex spatiotemporal dynamics. In this study, we showed that past land use and disturbances were important in shaping current shrub and tree communities. Indeed, conditions related to the years 1930-40 and 1958 are still affecting shrub and tree communities 57 to 85 years later. However, more recent or present-day conditions also turned out to be important in shaping forest communities. Their influence indeed appears to have reset the ecological memory of some species or, in other words, disrupted their link with past conditions. Our results thus teach us that our current land and forest management practices may have an impact on communities that could last for several decades or even centuries in the future. At the same time, forest and land management could be a powerful tool to reset the ecological memory of present-day forest communities to help them adapt more rapidly to a changing environment.

Since current tree and shrub communities may not be in equilibrium with present-day habitat conditions, we recommend incorporating past landscape trajectories or states in future research aiming to understand the impact of ecological drivers on present-day communities. This is true especially in heavily fragmented landscapes having experienced profound and rapid changes in their structure over time (Nagelkerke et al., 2002; With, 2007). When historical data are available, this approach could then provide a much deeper understanding of community responses to habitat conditions.

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## 1.11 Tables

Table 1.1. List of tree and shrub species present in the sampling sites (n=59 for shrubs and n=64 for trees) and number of sites where each species occurs. Species in bold are those for which their relative abundance was modelled. All species were included in the calculation of species diversity and richness.

| **Trees** | **Nb of sites where species occurs** | **Shrubs** | **Nb of sites where species occurs** |
|---|---|---|---|
| *Abies balsamea* | 1 | *Acer pensylvanicum* | 6 |
| ***Acer rubrum*** | 24 | *Acer spicatum* | 2 |
| ***Acer saccharum*** | 49 | ***Amelanchier spp.*** | 10 |
| ***Betula alleghaniensis*** | 10 | ***Cornus alternifolia*** | 35 |
| *Betula papyrifera* | 4 | *Cornus stolonifera* | 3 |
| *Betula populifolia* | 1 | *Corylus cornuta* | 1 |
| *Carya cordiforma* | 8 | *Crataegus spp.* | 6 |
| ***Fagus grandifolia*** | 15 | *Diervilla lonicera* | 3 |
| ***Fraxinus americana*** | 20 | *Dirca palustris* | 4 |
| *Fraxinus nigra* | 2 | *Frangula alnus* | 1 |
| *Fraxinus pennsylvanica* | 2 | ***Ilex mucronata*** | 16 |
| ***Ostrya virginiana*** | 20 | *Lonicera canadensis* | 4 |
| *Picea glauca* | 1 | *Menispermum canadense* | 2 |
| *Pinus strobus* | 6 | ***Parthenocissus quinquefolia*** | 22 |
| ***Populus balsamifera***[a] | 2 | ***Prunus virginiana*** | 10 |
| ***Populus grandidantata***[a] | 9 | ***Rhamnus cathartica*** | 17 |
| ***Populus tremuloides***[a] | 11 | ***Ribes spp.*** | 28 |
| *Prunus serotina* | 9 | ***Rubus allegheniensis***[b] | 5 |
| *Quercus alba* | 1 | ***Rubus idaeus***[b] | 19 |
| *Quercus macrocarpa* | 2 | ***Rubus odoratus***[b] | 5 |
| *Quercus rubra* | 7 | *Rubus pubescens* | 7 |
| *Salix nigra* | 1 | *Sambucus racemosa* | 6 |
| ***Thuja occidentalis*** | 14 | *Taxus canadensis* | 1 |
| ***Tilia americana*** | 18 | ***Toxicodendron radicans*** | 14 |
| ***Tsuga canadensis*** | 23 | *Vaccinium angustifolium* | 2 |
| *Ulmus americana* | 4 | *Vaccinium myrtilloides* | 2 |
| *Ulmus rubra* | 7 | *Viburnum cassinoides* | 6 |
| | | *Viburnum lantanoides* | 1 |
| | | *Viburnum opulus var. Americanum* | 1 |
| | | ***Viburnum lentago*** | 11 |
| | | ***Vitis riparia*** | 22 |
| | | ***Zanthoxylum americanum*** | 13 |

[a] These species were pooled for the analyses.

[b] These species were pooled for the analyses.

Table 1.2. Principal component analyses (PCA) dimensions that were retained for each of the 13 models for trees. Models are labeled Trees_1 to Trees_13. Each of them includes a specific set of explanatory variables based on their spatial and temporal scale. The correlation of each explanatory variable with each PCA dimension is shown, as well as the percentage of variance explained by each dimension (in parentheses).

| **Trees_1**<br>**Local**<br>**P4** | | |
|---|---|---|
| **Variables** | **Dim.1 (56%)** | **Dim.2 (36%)** |
| Latitude | 0.775 | -0.566 |
| Longitude | -0.944 | -0.053 |
| Soil pH | 0.445 | 0.872 |

| **Trees_2**<br>**Stand**<br>**P1** | | | | |
|---|---|---|---|---|
| **Variables** | **Dim.1 (33%)** | **Dim.2 (27%)** | **Dim.3 (19%)** | **Dim.4 (13%)** |
| Latitude | 0.280 | -0.840 | -0.228 | -0.207 |
| Longitude | -0.682 | 0.601 | 0.085 | 0.134 |
| Agriculture area_3 root | 0.575 | -0.136 | 0.412 | 0.682 |
| Closed forest area | -0.844 | -0.417 | 0.141 | 0.018 |
| Pasture area | 0.317 | 0.405 | -0.823 | 0.138 |
| Regeneration area | 0.559 | 0.434 | 0.472 | -0.485 |

| **Trees_3**<br>**Stand**<br>**P2** | | | | |
|---|---|---|---|---|
| **Variables** | **Dim.1 (34%)** | **Dim.2 (28%)** | **Dim.3 (17%)** | **Dim.4 (14%)** |
| Latitude | -0.075 | -0.926 | 0.039 | -0.188 |
| Longitude | -0.484 | 0.790 | 0.101 | 0.125 |
| Agriculture area_3 root | 0.496 | -0.164 | 0.393 | 0.751 |
| Closed forest area | -0.935 | -0.093 | 0.000 | 0.095 |
| Pasture area_3 root | 0.476 | 0.132 | -0.839 | 0.158 |
| Regeneration area | 0.690 | 0.355 | 0.372 | -0.452 |

| **Trees_4**<br>**Stand**<br>**P3** | | | |
|---|---|---|---|
| **Variables** | **Dim.1 (43%)** | **Dim.2 (31%)** | **Dim.3 (19%)** |
| Latitude | -0.719 | 0.607 | 0.083 |
| Longitude | 0.924 | -0.111 | 0.021 |
| Agriculture area_3 root | -0.360 | -0.676 | 0.637 |
| Closed forest area | 0.457 | 0.647 | 0.591 |

| **Trees_5**<br>**Stand**<br>**P4 (A4 for forest disturbances)** | | | |
|---|---|---|---|
| **Variables** | **Dim.1 (42%)** | **Dim.2 (28%)** | **Dim.3 (22%)** |
| Latitude | -0.804 | 0.453 | 0.110 |
| Longitude | 0.912 | -0.063 | 0.033 |
| Closed forest area_power 3 | 0.255 | 0.677 | -0.688 |
| Partial forest disturbance area | 0.373 | 0.669 | 0.625 |

**Trees_6**
**Landscape (composition + disturbances)**
**P1 (A1 for forest disturbances)**

| **Variables** | **Dim.1 (24%)** | **Dim.2 (22%)** | **Dim.3 (13%)** | **Dim.4 (12%)** |
|---|---|---|---|---|
| Latitude | 0.089 | 0.904 | -0.017 | 0.030 |
| Longitude | 0.325 | -0.729 | -0.378 | 0.114 |
| Agriculture area_2km | -0.927 | 0.089 | 0.057 | 0.059 |
| Agriculture area_600m | -0.907 | 0.107 | -0.046 | 0.073 |
| Closed forest area_2km | 0.756 | 0.450 | -0.225 | -0.015 |
| Closed forest area_600m | 0.554 | 0.345 | -0.482 | 0.250 |
| Sparse forest area_2km | 0.401 | 0.655 | -0.050 | -0.114 |
| Sparse forest area_600m_3 root | 0.253 | 0.526 | -0.200 | -0.163 |
| Open forest area_2km | 0.445 | 0.478 | 0.524 | -0.345 |
| Open forest area_600m | 0.179 | 0.171 | 0.643 | -0.253 |
| Pasture area_2km | 0.407 | -0.688 | -0.117 | -0.479 |
| Pasture area_600m | 0.296 | -0.524 | 0.176 | -0.660 |
| Regeneration area_2km_3 root | 0.669 | -0.479 | 0.092 | 0.315 |
| Regeneration area_600m | 0.249 | -0.318 | 0.449 | 0.573 |
| Partial forest disturbance area_2km_3 root | -0.055 | -0.069 | 0.766 | -0.143 |
| Severe forest disturbance area_600m | 0.203 | 0.189 | 0.413 | 0.419 |
| Severe forest disturbance area_2km_3 root | 0.281 | -0.154 | 0.271 | 0.651 |

**Trees_7**
**Landscape (composition + disturbances)**
**P2 (A2 for forest disturbances)**

| **Variables** | **Dim.1 (29%)** | **Dim.2 (24%)** | **Dim.3 (11%)** | **Dim.4 (6%)** | **Dim.5 (6%)** |
|---|---|---|---|---|---|
| Latitude | -0.899 | 0.129 | -0.044 | -0.088 | 0.198 |
| Longitude | 0.707 | 0.292 | -0.370 | 0.242 | -0.037 |
| Agriculture area_2km | -0.067 | -0.867 | 0.101 | 0.045 | 0.231 |
| Agriculture area_600m | -0.086 | -0.868 | 0.013 | 0.144 | 0.034 |
| Closed forest area_2km | -0.604 | 0.715 | -0.177 | 0.038 | -0.036 |
| Closed forest area_600m | -0.533 | 0.553 | -0.416 | 0.241 | 0.006 |
| Sparse forest area_2km | -0.685 | 0.421 | 0.261 | -0.140 | 0.067 |
| Sparse forest area_600m_3 root | -0.599 | 0.488 | 0.125 | 0.040 | -0.066 |
| Open forest area_2km | -0.364 | 0.567 | 0.374 | -0.314 | -0.095 |
| Open forest area_600m_3 root | 0.026 | 0.373 | 0.545 | 0.158 | 0.080 |
| Pasture area_2km | 0.786 | 0.180 | 0.312 | -0.081 | -0.231 |
| Pasture area_600m | 0.546 | 0.188 | 0.588 | -0.303 | -0.280 |
| Regeneration area_2km | 0.676 | 0.517 | -0.147 | 0.167 | -0.132 |
| Regeneration area_600m | 0.601 | 0.248 | -0.140 | -0.373 | 0.462 |
| Partial forest disturbance area_600m | -0.118 | 0.026 | 0.572 | 0.537 | 0.299 |
| Partial forest disturbance area_2km_3 root | 0.343 | 0.276 | 0.379 | 0.327 | 0.410 |
| Severe forest disturbance area_2km | 0.482 | 0.632 | -0.206 | 0.330 | -0.033 |
| Severe forest disturbance area_600m | 0.392 | 0.364 | -0.171 | -0.363 | 0.587 |

**Trees_8**
**Landscape (composition + disturbances)**
**P3 (A3 for forest disturbances)**

| **Variables** | **Dim.1 (31%)** | **Dim.2 (17%)** | **Dim.3 (13%)** | **Dim.4 (12%)** | **Dim.5 (6%)** |
|---|---|---|---|---|---|
| Latitude | 0.156 | -0.046 | -0.843 | 0.234 | 0.087 |
| Longitude | 0.266 | -0.406 | 0.691 | -0.276 | 0.040 |
| Agriculture area_2km | -0.935 | -0.029 | -0.013 | 0.044 | -0.157 |
| Agriculture area_600m | -0.862 | -0.163 | 0.100 | 0.078 | 0.155 |
| Closed forest area_2km | 0.840 | -0.293 | -0.175 | -0.201 | 0.070 |
| Closed forest area_600m | 0.665 | -0.582 | -0.107 | -0.210 | 0.015 |
| Open forest area_2km | 0.565 | 0.557 | -0.158 | -0.390 | -0.104 |
| Open forest area_600m | 0.214 | 0.564 | -0.325 | -0.244 | -0.602 |
| Pasture area_2km | -0.053 | 0.666 | 0.295 | -0.387 | 0.417 |
| Pasture area_600m | -0.007 | 0.758 | -0.120 | -0.172 | 0.283 |
| Regeneration area_2km_3 root | 0.608 | 0.195 | 0.547 | 0.319 | -0.047 |
| Regeneration area_600m_3 root | 0.298 | 0.574 | 0.476 | 0.356 | -0.162 |
| Partial forest disturbance area_2km | 0.646 | -0.188 | -0.015 | -0.578 | 0.103 |
| Severe forest disturbance area_600m | 0.508 | 0.158 | 0.067 | 0.640 | 0.048 |
| Severe forest disturbance area_2km_3 root | 0.734 | -0.178 | 0.072 | 0.419 | -0.078 |
| Urban area_2km_3 root | 0.367 | 0.186 | -0.379 | 0.395 | 0.403 |

**Trees_9**
**Landscape (composition + disturbances)**
**P4 (A4 for forest disturbances)**

| **Variables** | **Dim.1 (31%)** | **Dim.2 (14%)** | **Dim.3 (12%)** | **Dim.4 (8%)** | **Dim.5 (7%)** |
|---|---|---|---|---|---|
| Latitude | 0.219 | -0.637 | 0.373 | 0.277 | 0.131 |
| Longitude | 0.195 | 0.349 | -0.673 | -0.110 | -0.218 |
| Agriculture area_2km | -0.842 | -0.342 | 0.096 | -0.166 | 0.027 |
| Agriculture area_600m | -0.842 | -0.283 | 0.101 | -0.009 | -0.084 |
| Closed forest area_2km | 0.879 | 0.055 | -0.249 | -0.006 | 0.025 |
| Closed forest area_600m | 0.796 | -0.014 | -0.444 | -0.092 | 0.125 |
| Sparse forest area_2km | 0.259 | 0.751 | -0.040 | -0.145 | -0.090 |
| Sparse forest area_600m | -0.004 | 0.638 | 0.320 | 0.067 | 0.258 |
| Open forest area_2km | 0.736 | 0.046 | 0.358 | -0.206 | 0.103 |
| Open forest area_600m | 0.454 | -0.011 | 0.503 | -0.354 | 0.248 |
| Pasture area_2km | -0.470 | 0.633 | -0.010 | 0.048 | 0.147 |
| Pasture area_600m | -0.449 | 0.539 | -0.016 | 0.050 | -0.102 |
| Regeneration area_2km | 0.221 | 0.467 | 0.714 | -0.166 | -0.045 |
| Regeneration area_600m | 0.338 | -0.021 | 0.662 | -0.275 | -0.271 |
| Partial forest disturbance area_2km | 0.783 | -0.369 | 0.049 | -0.002 | 0.008 |
| Partial forest disturbance area_600m | 0.835 | -0.100 | -0.291 | -0.122 | 0.338 |
| Severe forest disturbance area_2km | 0.246 | 0.225 | 0.045 | 0.577 | 0.431 |
| Severe forest disturbance area_600m | -0.392 | 0.035 | 0.120 | 0.383 | 0.604 |
| Urban area_2km_3 root | 0.460 | 0.063 | 0.120 | 0.625 | -0.323 |
| Urban area_600m_3 root | 0.413 | 0.076 | 0.243 | 0.583 | -0.492 |

**Trees_10**
**Landscape (configuration + connectivity)**
**P1 (A1 for forest disturbances)**

| **Variables** | **Dim.1 (28%)** | **Dim.2 (25%)** | **Dim.3 (17%)** | **Dim.4 (12%)** | **Dim.5 (9%)** |
|---|---|---|---|---|---|
| Latitude | 0.735 | 0.374 | -0.455 | 0.034 | -0.118 |
| Longitude | -0.229 | -0.359 | 0.797 | 0.299 | -0.003 |
| Distance to nearest forest edge | 0.550 | 0.048 | 0.304 | 0.230 | 0.657 |
| Mean distance to forest disturbances | 0.106 | 0.890 | 0.394 | -0.053 | -0.129 |
| Distance to nearest pasture_3 root | -0.036 | 0.265 | -0.349 | 0.848 | 0.071 |
| Distance to nearest forest disturbance | 0.131 | 0.868 | 0.422 | -0.003 | -0.170 |
| Length of forest edge_2km | 0.772 | -0.389 | 0.266 | -0.177 | 0.005 |
| Length of roads_2km | -0.415 | 0.451 | -0.185 | -0.373 | 0.570 |
| Probability of connectivity_2km_3 root | 0.904 | -0.104 | -0.047 | -0.072 | -0.004 |

**Trees_11**
**Landscape (configuration + connectivity)**
**P2 (A2 for forest disturbances)**

| **Variables** | **Dim.1 (29%)** | **Dim.2 (21%)** | **Dim.3 (16%)** | **Dim.4 (12%)** | **Dim.5 (9%)** |
|---|---|---|---|---|---|
| Latitude | 0.752 | -0.583 | 0.092 | 0.031 | -0.064 |
| Longitude | -0.195 | 0.809 | -0.168 | -0.406 | 0.162 |
| Distance to nearest forest edge_3 root | 0.647 | 0.374 | 0.105 | -0.245 | 0.464 |
| Mean distance to forest disturbances | 0.204 | 0.635 | 0.059 | 0.682 | -0.004 |
| Distance to nearest pasture _3 root | 0.425 | -0.037 | 0.700 | -0.365 | 0.130 |
| Distance to nearest forest disturbance | 0.397 | 0.429 | 0.625 | 0.236 | -0.349 |
| Length of forest edge_2km | 0.627 | 0.234 | -0.543 | 0.135 | 0.070 |
| Length of roads_2km | -0.436 | -0.262 | 0.292 | 0.443 | 0.655 |
| Probability of connectivity_2km_3 root | 0.812 | -0.234 | -0.319 | 0.108 | 0.129 |

**Trees_12**
**Landscape (configuration + connectivity)**
**P3 (A3 for disturbances)**

| **Variables** | **Dim.1 (24%)** | **Dim.2 (23%)** | **Dim.3 (17%)** | **Dim.4 (12%)** | **Dim.5 (8%)** |
|---|---|---|---|---|---|
| Latitude | -0.174 | -0.694 | 0.558 | -0.078 | 0.221 |
| Longitude | 0.621 | 0.535 | -0.275 | -0.101 | -0.357 |
| Distance to nearest forest edge_3 root | 0.533 | 0.203 | 0.631 | 0.205 | -0.119 |
| Mean distance to forest disturbances | -0.395 | 0.722 | 0.259 | -0.104 | 0.286 |
| Distance to nearest pasture _3 root | 0.290 | 0.342 | 0.569 | 0.531 | 0.006 |
| Distance to nearest forest disturbance | -0.703 | 0.546 | 0.267 | -0.089 | 0.007 |
| Length of forest edge_2km | 0.549 | 0.079 | -0.377 | 0.263 | 0.664 |
| Length of roads_2km | -0.352 | -0.440 | -0.126 | 0.639 | -0.229 |
| Probability of connectivity_2km | 0.531 | -0.357 | 0.413 | -0.450 | -0.010 |

| Trees_13<br>Landscape (configuration + connectivity)<br>P4 (A4 for forest disturbances) | | | | |
|---|---|---|---|---|
| **Variables** | **Dim.1 (27%)** | **Dim.2 (25%)** | **Dim.3 (16%)** | **Dim.4 (10%)** |
| Latitude | -0.726 | 0.364 | 0.350 | -0.115 |
| Longitude | 0.806 | 0.108 | -0.378 | 0.079 |
| Distance to nearest forest edge | 0.441 | 0.736 | -0.001 | -0.017 |
| Mean distance to forest disturbances | 0.489 | -0.148 | 0.718 | -0.148 |
| Distance to nearest pasture | -0.240 | 0.774 | 0.352 | -0.163 |
| Distance to nearest forest disturbance_3 root | -0.065 | -0.569 | 0.543 | -0.076 |
| Length of forest edge_2km | 0.661 | -0.231 | 0.459 | 0.342 |
| Length of roads_2km_3 root | -0.487 | 0.035 | 0.089 | 0.830 |
| Probability of connectivity_2km | 0.322 | 0.755 | 0.212 | 0.208 |

Table 1.3. Principal component analyses (PCA) dimensions that were retained for each of the 13 models for shrubs. Models are labeled Shrub_1 to Shrubs_13. Each of them includes a specific set of explanatory variables based on their spatial and temporal scale. The correlation of each explanatory variable with each PCA dimension is shown, as well as the percentage of variance explained by each dimension (in parentheses).

**Shrubs_1**
**Local**
**P4**

| **Variables** | **Dim.1 (25%)** | **Dim.2 (16%)** | **Dim.3 (13%)** | **Dim.4 (7%)** | **Dim.5 (7%)** | **Dim.6 (6%)** |
|---|---|---|---|---|---|---|
| Longitude | 0.066 | 0.444 | -0.579 | -0.416 | -0.395 | -0.107 |
| Latitude | 0.347 | -0.398 | 0.616 | 0.041 | 0.286 | -0.333 |
| Tree sapling density_2 root | 0.413 | 0.372 | -0.210 | 0.684 | -0.079 | -0.086 |
| Tree seedling density_ln | 0.240 | -0.716 | -0.263 | -0.026 | -0.161 | 0.032 |
| Tree seedling diversity | 0.412 | -0.434 | -0.257 | -0.005 | -0.023 | 0.290 |
| Tree sapling diversity | 0.664 | 0.236 | -0.234 | 0.373 | 0.074 | -0.244 |
| Tree diversity | 0.505 | 0.085 | 0.024 | -0.396 | 0.337 | -0.050 |
| Tree total basal area | -0.688 | 0.076 | 0.112 | 0.089 | -0.176 | -0.223 |
| Soil pH | -0.426 | -0.394 | 0.140 | 0.279 | 0.080 | 0.627 |
| % of canopy closure 0.5m above ground | 0.482 | 0.486 | 0.605 | -0.038 | -0.097 | 0.246 |
| % of canopy closure 1.5m above ground | 0.461 | 0.500 | 0.643 | -0.033 | -0.143 | 0.114 |
| % of ground covered by woody debris_logit | -0.537 | -0.098 | -0.066 | 0.060 | 0.535 | -0.253 |
| % of ground covered by herbaceous plants | 0.064 | -0.559 | 0.415 | -0.229 | -0.388 | -0.190 |
| % of ground covered by coniferous litter | -0.793 | 0.292 | 0.108 | 0.164 | -0.211 | 0.011 |
| % of ground covered by deciduous litter | 0.859 | -0.138 | -0.283 | 0.004 | 0.077 | 0.127 |
| % of ground covered by rocks_logit | -0.262 | 0.535 | -0.149 | -0.300 | 0.408 | 0.239 |

**Shrubs_2**
**Stand**
**P1**

| **Variables** | **Dim.1 (33%)** | **Dim.2 (26%)** | **Dim.3 (19%)** | **Dim.4 (13%)** |
|---|---|---|---|---|
| Longitude | -0.662 | 0.621 | 0.033 | 0.131 |
| Latitude | 0.236 | -0.869 | -0.150 | -0.192 |
| Agriculture area_3 root | 0.574 | -0.076 | 0.406 | 0.695 |
| Closed forest area | -0.862 | -0.367 | 0.164 | 0.028 |
| Pasture area | 0.332 | 0.296 | -0.866 | 0.111 |
| Regeneration area | 0.562 | 0.438 | 0.450 | -0.497 |

**Shrubs_3**
**Stand**
**P2**

| **Variables** | **Dim.1 (34%)** | **Dim.2 (27%)** | **Dim.3 (17%)** | **Dim.4 (14%)** |
|---|---|---|---|---|
| Longitude | -0.564 | 0.733 | 0.074 | 0.135 |
| Latitude | -0.003 | -0.925 | 0.108 | -0.177 |
| Agriculture area_3 root | 0.503 | -0.103 | 0.300 | 0.798 |
| Closed forest area | -0.924 | -0.152 | 0.005 | 0.097 |
| Pasture area_3 root | 0.425 | 0.110 | -0.879 | 0.071 |
| Regeneration area | 0.651 | 0.423 | 0.412 | -0.409 |

**Shrubs_4**
**Stand**
**P3**

| **Variables** | **Dim.1 (41%)** | **Dim.2 (28%)** | **Dim.3 (21%)** |
|---|---|---|---|
| Longitude | 0.707 | -0.570 | -0.139 |
| Latitude | -0.369 | 0.847 | -0.153 |
| Agriculture area_3 root | -0.294 | -0.117 | 0.930 |
| Closed forest area | 0.856 | 0.428 | 0.034 |
| Open forest area | -0.788 | -0.400 | -0.363 |

**Shrubs_5**
**Stand**
**P4 (A4 for forest disturbances)**

| **Variables** | **Dim.1 (41%)** | **Dim.2 (28%)** | **Dim.3 (22%)** |
|---|---|---|---|
| Longitude | 0.907 | -0.049 | 0.029 |
| Latitude | -0.798 | 0.452 | 0.123 |
| Closed forest area_power 3 | 0.233 | 0.675 | -0.697 |
| Partial forest disturbance area | 0.373 | 0.663 | 0.628 |

**Shrubs_6**
**Landscape (composition + disturbances)**
**P1 (A1 for forest disturbances)**

| **Variables** | **Dim.1 (24%)** | **Dim.2 (23%)** | **Dim.3 (13%)** | **Dim.4 (12%)** |
|---|---|---|---|---|
| Longitude | 0.099 | 0.760 | -0.348 | -0.289 |
| Latitude | 0.363 | -0.833 | -0.061 | 0.022 |
| Agriculture area_2km | -0.859 | -0.349 | -0.023 | 0.075 |
| Agriculture area_600m | -0.823 | -0.393 | -0.092 | 0.006 |
| Closed forest area_2km | 0.865 | -0.238 | -0.121 | -0.146 |
| Closed forest area_600m | 0.643 | -0.182 | -0.479 | -0.173 |
| Sparse forest area_2km | 0.601 | -0.488 | 0.094 | -0.024 |
| Sparse forest area_600m_3 root | 0.440 | -0.435 | 0.038 | -0.178 |
| Open forest area_2km | 0.572 | -0.319 | 0.605 | 0.154 |
| Open forest area_600m | 0.190 | -0.077 | 0.603 | 0.369 |
| Pasture area_2km | 0.210 | 0.743 | 0.340 | -0.413 |
| Pasture area_600m | 0.128 | 0.564 | 0.636 | -0.297 |
| Regeneration area_2km_3 root | 0.496 | 0.662 | -0.195 | 0.251 |
| Regeneration area_600m | 0.096 | 0.477 | -0.268 | 0.624 |
| Partial forest disturbance area_2km_3 root | -0.188 | 0.174 | 0.591 | 0.463 |
| Severe forest disturbance area_600m | 0.252 | -0.085 | -0.031 | 0.660 |
| Severe forest disturbance area_2km_3 root | 0.205 | 0.293 | -0.356 | 0.597 |

**Shrubs_7**
**Landscape (composition + disturbances)**
**P2 (A2 for forest disturbances)**

| **Variables** | **Dim.1 (29%)** | **Dim.2 (24%)** | **Dim.3 (11%)** | **Dim.4 (6%)** | **Dim.5 (6%)** |
|---|---|---|---|---|---|
| Longitude | 0.713 | 0.217 | -0.395 | 0.268 | -0.060 |
| Latitude | -0.883 | 0.208 | -0.041 | -0.011 | 0.194 |
| Agriculture area_2km | -0.107 | -0.858 | 0.121 | 0.061 | 0.249 |
| Agriculture area_600m | -0.156 | -0.858 | 0.052 | 0.155 | 0.016 |
| Closed forest area_2km | -0.555 | 0.756 | -0.179 | 0.056 | -0.032 |
| Closed forest area_600m | -0.508 | 0.576 | -0.417 | 0.240 | -0.025 |
| Sparse forest area_2km | -0.650 | 0.484 | 0.264 | -0.114 | 0.053 |
| Sparse forest area_600m_3 root | -0.630 | 0.514 | 0.164 | -0.040 | -0.107 |
| Open forest area_2km | -0.296 | 0.608 | 0.348 | -0.314 | -0.010 |
| Open forest area_600m_3 root | 0.153 | 0.346 | 0.578 | 0.173 | 0.156 |
| Pasture area_2km | 0.804 | 0.155 | 0.273 | -0.141 | -0.198 |
| Pasture area_600m | 0.584 | 0.207 | 0.532 | -0.364 | -0.234 |
| Regeneration area_2km | 0.704 | 0.503 | -0.112 | 0.153 | -0.241 |
| Regeneration area_600m | 0.581 | 0.230 | -0.165 | -0.304 | 0.522 |
| Partial forest disturbance area_600m | -0.111 | 0.044 | 0.594 | 0.571 | 0.147 |
| Partial forest disturbance area_2km_3 root | 0.353 | 0.271 | 0.413 | 0.321 | 0.333 |
| Severe forest disturbance area_2km | 0.518 | 0.586 | -0.192 | 0.337 | -0.069 |
| Severe forest disturbance area_600m | 0.396 | 0.385 | -0.231 | -0.166 | 0.632 |

**Shrubs_8**
**Landscape (composition + disturbances)**
**P3 (A3 for forest disturbances)**

| **Variables** | **Dim.1 (33%)** | **Dim.2 (17%)** | **Dim.3 (13%)** | **Dim.4 (11%)** | **Dim.5 (6%)** |
|---|---|---|---|---|---|
| Longitude | 0.215 | -0.540 | 0.647 | 0.162 | 0.087 |
| Latitude | 0.206 | 0.090 | -0.859 | -0.061 | 0.066 |
| Agriculture area_2km | -0.928 | 0.009 | -0.053 | -0.043 | -0.124 |
| Agriculture area_600m | -0.867 | -0.159 | 0.000 | -0.094 | 0.158 |
| Closed forest area_2km | 0.839 | -0.273 | -0.151 | 0.232 | 0.058 |
| Closed forest area_600m | 0.658 | -0.565 | -0.092 | 0.251 | 0.027 |
| Open forest area_2km | 0.576 | 0.562 | 0.005 | 0.414 | -0.111 |
| Open forest area_600m | 0.233 | 0.593 | -0.158 | 0.307 | -0.600 |
| Pasture area_2km | -0.028 | 0.632 | 0.467 | 0.230 | 0.430 |
| Pasture area_600m | 0.039 | 0.772 | 0.023 | 0.112 | 0.300 |
| Regeneration area_2km_3 root | 0.622 | 0.044 | 0.509 | -0.428 | -0.090 |
| Regeneration area_600m_3 root | 0.367 | 0.444 | 0.455 | -0.492 | -0.177 |
| Partial forest disturbance area_2km | 0.635 | -0.155 | 0.090 | 0.591 | 0.137 |
| Severe forest disturbance area_600m_3 root | 0.670 | 0.177 | -0.175 | -0.492 | 0.132 |
| Severe forest disturbance area_2km_3 root | 0.737 | -0.256 | -0.034 | -0.399 | -0.108 |
| Urban area_2km_3 root | 0.406 | 0.177 | -0.433 | -0.286 | 0.377 |

| Shrubs_9<br>Landscape (composition + disturbances)<br>P4 (A4 for forest disturbances) | | | | | |
|---|---|---|---|---|---|
| **Variables** | **Dim.1 (32%)** | **Dim.2 (14%)** | **Dim.3 (12%)** | **Dim.4 (9%)** | **Dim.5 (7%)** |
| Longitude | 0.166 | 0.357 | -0.663 | -0.167 | -0.207 |
| Latitude | 0.248 | -0.648 | 0.322 | 0.304 | 0.092 |
| Agriculture area_2km | -0.846 | -0.356 | 0.073 | -0.178 | 0.016 |
| Agriculture area_600m | -0.838 | -0.306 | 0.099 | -0.026 | -0.080 |
| Closed forest area_2km | 0.889 | 0.079 | -0.218 | -0.007 | 0.048 |
| Closed forest area_600m | 0.791 | 0.035 | -0.447 | -0.100 | 0.113 |
| Sparse forest area_2km | 0.246 | 0.770 | -0.013 | -0.136 | -0.130 |
| Sparse forest area_600m | 0.003 | 0.633 | 0.334 | 0.114 | 0.248 |
| Open forest area_2km | 0.748 | 0.028 | 0.324 | -0.215 | 0.113 |
| Open forest area_600m | 0.461 | -0.033 | 0.488 | -0.359 | 0.273 |
| Pasture area_2km | -0.490 | 0.638 | 0.030 | 0.068 | 0.156 |
| Pasture area_600m | -0.461 | 0.529 | 0.033 | 0.077 | -0.105 |
| Regeneration area_2km | 0.253 | 0.446 | 0.723 | -0.122 | -0.037 |
| Regeneration area_600m | 0.373 | -0.072 | 0.681 | -0.243 | -0.219 |
| Partial forest disturbance area_2km | 0.792 | -0.370 | 0.006 | -0.021 | 0.036 |
| Partial forest disturbance area_600m | 0.829 | -0.072 | -0.308 | -0.142 | 0.326 |
| Severe forest disturbance area_2km | 0.226 | 0.186 | 0.002 | 0.609 | 0.422 |
| Severe forest disturbance area_600m | -0.395 | -0.002 | 0.050 | 0.386 | 0.619 |
| Urban area_2km_3 root | 0.469 | 0.015 | 0.069 | 0.610 | -0.344 |
| Urban area_600m_3 root | 0.476 | 0.048 | 0.185 | 0.585 | -0.468 |

| Shrubs_10<br>Landscape (configuration + connectivity)<br>P1 (A1 for forest disturbances) | | | | | |
|---|---|---|---|---|---|
| **Variables** | **Dim.1 (29%)** | **Dim.2 (24%)** | **Dim.3 (16%)** | **Dim.4 (12%)** | **Dim.5 (9%)** |
| Longitude | -0.306 | -0.274 | 0.835 | 0.207 | 0.016 |
| Latitude | 0.811 | 0.125 | -0.438 | 0.109 | -0.133 |
| Length of forest edge_2km | 0.606 | -0.644 | 0.176 | -0.192 | 0.021 |
| Length of roads_2km | -0.231 | 0.549 | -0.247 | -0.369 | 0.569 |
| Probability of connectivity_2km_3 root | 0.825 | -0.376 | -0.094 | -0.044 | -0.001 |
| Distance to nearest forest edge | 0.528 | -0.158 | 0.274 | 0.207 | 0.673 |
| Mean distance to forest disturbances | 0.468 | 0.761 | 0.392 | -0.115 | -0.113 |
| Distance to nearest pasture_3 root | 0.026 | 0.319 | -0.191 | 0.877 | 0.071 |
| Distance to nearest forest disturbance | 0.491 | 0.736 | 0.410 | -0.074 | -0.148 |

**Shrubs_11**
**Landscape (configuration + connectivity)**
**P2 (A2 for forest disturbances)**

| **Variables** | **Dim.1 (28%)** | **Dim.2 (21%)** | **Dim.3 (17%)** | **Dim.4 (12%)** | **Dim.5 (10%)** |
|---|---|---|---|---|---|
| Longitude | -0.250 | 0.774 | -0.233 | -0.413 | 0.155 |
| Latitude | 0.820 | -0.447 | 0.191 | 0.051 | -0.084 |
| Length of forest edge_2km | 0.590 | 0.242 | -0.571 | 0.166 | 0.061 |
| Length of roads_2km | -0.418 | -0.352 | 0.239 | 0.380 | 0.683 |
| Probability of connectivity_2km_3 root | 0.850 | -0.162 | -0.264 | 0.120 | 0.097 |
| Distance to nearest forest edge_3 root | 0.575 | 0.479 | 0.099 | -0.246 | 0.459 |
| Mean distance to forest disturbances | 0.022 | 0.625 | -0.016 | 0.731 | 0.049 |
| Distance to nearest pasture_3 root | 0.380 | 0.084 | 0.746 | -0.273 | 0.170 |
| Distance to nearest forest disturbance | 0.162 | 0.531 | 0.649 | 0.261 | -0.342 |

**Shrubs_12**
**Landscape (configuration + connectivity)**
**P3 (A3 for forest disturbances)**

| **Variables** | **Dim.1 (24%)** | **Dim.2 (23%)** | **Dim.3 (17%)** | **Dim.4 (12%)** | **Dim.5 (8%)** |
|---|---|---|---|---|---|
| Longitude | 0.387 | 0.715 | -0.264 | -0.093 | -0.377 |
| Latitude | 0.107 | -0.727 | 0.527 | -0.095 | 0.195 |
| Length of forest edge_2km | 0.523 | 0.249 | -0.398 | 0.212 | 0.650 |
| Length of roads_2km | -0.202 | -0.502 | -0.111 | 0.690 | -0.179 |
| Probability of connectivity_2km | 0.621 | -0.207 | 0.375 | -0.441 | -0.024 |
| Distance to nearest forest edge_3 root | 0.454 | 0.352 | 0.629 | 0.205 | -0.099 |
| Mean distance to forest disturbances | -0.607 | 0.540 | 0.269 | -0.123 | 0.318 |
| Distance to nearest pasture_3 root | 0.220 | 0.435 | 0.562 | 0.500 | 0.036 |
| Distance to nearest forest disturbance | -0.837 | 0.276 | 0.296 | -0.085 | 0.007 |

**Shrubs_13**
**Landscape (configuration + connectivity)**
**P4 (A4 for forest disturbances)**

| **Variables** | **Dim.1 (27%)** | **Dim.2 (25%)** | **Dim.3 (17%)** | **Dim.4 (10%)** |
|---|---|---|---|---|
| Longitude | -0.601 | 0.543 | -0.377 | 0.060 |
| Latitude | 0.808 | -0.102 | 0.328 | -0.166 |
| Length of forest edge_2km | -0.660 | 0.233 | 0.485 | 0.296 |
| Length of roads_2km_3 root | 0.434 | -0.224 | 0.156 | 0.832 |
| Probability of connectivity_2km | 0.198 | 0.788 | 0.213 | 0.143 |
| Distance to nearest forest edge | 0.127 | 0.836 | -0.013 | 0.026 |
| Mean distance to forest disturbances | -0.458 | 0.168 | 0.723 | -0.145 |
| Distance to nearest pasture | 0.663 | 0.507 | 0.321 | -0.187 |
| Distance to nearest forest disturbance_3 root | -0.283 | -0.490 | 0.576 | -0.107 |

Table 1.4. Best and competing regression models following model selection with the $AIC_c$ for shrub diversity, richness and relative abundances. Significant explanatory variables for each model are in bold. The direct, indirect and total effects are provided for linear spatial lag models in addition to the parameter estimates.

| Response variable | Best models $\Delta AIC_c < 2$ | Model type | Spatial scale[a] | Temporal scale[b] | $\Delta AIC_c$ | Log likelihood | Adj. $R^2$ | p-value | Explanatory variable | Estimate[j] | Std. Error[j] | Confidence intervals | | Simulated p-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | 2.5 % | 97.5 % | |
| Shrub diversity | Shrubs_1 | Linear, spatial lag[d] | Local | P4 | 0.00 | -86.78 | N/A | N/A | **Rho (spatial parameter)** | **2.04E-01** | **8.42E-02** | **3.88E-02** | **3.69E-01** | **N/A** |
| | | | | | | | | | Soil texture (Loam vs. Clay) | 5.51E-01 | 3.41E-01 | -1.18E-01 | 1.22E+00 | N/A |
| | | | | | | | | | Direct effects | 5.71E-01 | 3.57E-01 | N/A | N/A | 1.09E-01 |
| | | | | | | | | | Indirect effects | 1.28E-01 | 1.06E-01 | N/A | N/A | 2.25E-01 |
| | | | | | | | | | Total effects | 7.00E-01 | 4.45E-01 | N/A | N/A | 1.16E-01 |
| | | | | | | | | | Soil texture (Organic matter vs. Clay) | 8.62E-01 | 7.15E-01 | -5.40E-01 | 2.26E+00 | N/A |
| | | | | | | | | | Direct effects | 8.96E-01 | 7.40E-01 | N/A | N/A | 2.26E-01 |
| | | | | | | | | | Indirect effects | 2.09E-01 | 2.16E-01 | N/A | N/A | 3.32E-01 |
| | | | | | | | | | Total effects | 1.11E+00 | 9.28E-01 | N/A | N/A | 2.33E-01 |
| | | | | | | | | | Soil texture (Sand vs. Clay) | 3.75E-01 | 6.28E-01 | -8.55E-01 | 1.61E+00 | N/A |
| | | | | | | | | | Direct effects | 3.32E-01 | 6.31E-01 | N/A | N/A | 5.98E-01 |
| | | | | | | | | | Indirect effects | 8.17E-02 | 1.60E-01 | N/A | N/A | 6.10E-01 |
| | | | | | | | | | Total effects | 4.14E-01 | 7.79E-01 | N/A | N/A | 5.95E-01 |
| | | | | | | | | | Dim.1 | -9.74E-02 | 6.84E-02 | -2.32E-01 | 3.67E-02 | N/A |
| | | | | | | | | | Direct effects | -1.01E-01 | 7.14E-02 | N/A | N/A | 1.59E-01 |
| | | | | | | | | | Indirect effects | -2.20E-02 | 1.95E-02 | N/A | N/A | 2.59E-01 |
| | | | | | | | | | Total effects | -1.23E-01 | 8.75E-02 | N/A | N/A | 1.62E-01 |
| | | | | | | | | | **Dim.2** | **-5.34E-01** | **9.16E-02** | **-7.14E-01** | **-3.55E-01** | **N/A** |
| | | | | | | | | | Direct effects | -5.51E-01 | 9.48E-02 | N/A | N/A | 6.10E-09 |
| | | | | | | | | | Indirect effects | -1.20E-01 | 5.68E-02 | N/A | N/A | 3.44E-02 |
| | | | | | | | | | Total effects | -6.71E-01 | 1.24E-01 | N/A | N/A | 6.30E-08 |
| | | | | | | | | | Dim.3 | 7.63E-02 | 1.06E-01 | -1.31E-01 | 2.84E-01 | N/A |
| | | | | | | | | | Direct effects | 7.90E-02 | 1.01E-01 | N/A | N/A | 4.32E-01 |
| | | | | | | | | | Indirect effects | 1.47E-02 | 2.43E-02 | N/A | N/A | 5.46E-01 |
| | | | | | | | | | Total effects | 9.37E-02 | 1.22E-01 | N/A | N/A | 4.41E-01 |
| | | | | | | | | | Dim.4 | -1.23E-01 | 1.32E-01 | -3.81E-01 | 1.35E-01 | N/A |
| | | | | | | | | | Direct effects | -1.31E-01 | 1.29E-01 | N/A | N/A | 3.10E-01 |
| | | | | | | | | | Indirect effects | -2.78E-02 | 3.22E-02 | N/A | N/A | 3.89E-01 |
| | | | | | | | | | Total effects | -1.59E-01 | 1.57E-01 | N/A | N/A | 3.11E-01 |
| | | | | | | | | | Dim.5 | 5.93E-02 | 1.38E-01 | -2.11E-01 | 3.30E-01 | N/A |
| | | | | | | | | | Direct effects | 5.97E-02 | 1.42E-01 | N/A | N/A | 6.74E-01 |
| | | | | | | | | | Indirect effects | 1.29E-02 | 3.50E-02 | N/A | N/A | 7.12E-01 |
| | | | | | | | | | Total effects | 7.26E-02 | 1.74E-01 | N/A | N/A | 6.76E-01 |
| | | | | | | | | | Dim.6 | 1.87E-01 | 1.41E-01 | -8.89E-02 | 4.62E-01 | N/A |

| Response variable | Best models $\Delta AIC_c < 2$ | Model type | Spatial scale[a] | Temporal scale[b] | $\Delta AIC_c$ | Log likelihood | Adj. $R^2$ | p-value | Explanatory variable | Estimate[j] | Std. Error[j] | Confidence intervals | | Simulated p-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | 2.5 % | 97.5 % | |
| | | | | | | | | | Direct effects | 1.95E-01 | 1.51E-01 | N/A | N/A | 1.97E-01 |
| | | | | | | | | | Indirect effects | 4.35E-02 | 4.30E-02 | N/A | N/A | 3.13E-01 |
| | | | | | | | | | Total effects | 2.38E-01 | 1.88E-01 | N/A | N/A | 2.06E-01 |
| Shrub richness | Shrubs_5[c] | Linear, spatial lag | Stand | P4/A4 | 0.00 | -130.61 | N/A | N/A | **Rho (spatial parameter)** | **2.59E-01** | **8.14E-02** | **9.96E-02** | **4.19E-01** | **N/A** |
| | | | | | | | | | **Maple syrup production (Yes vs. No)** | **-1.84E+00** | **8.14E-01** | **-3.43E+00** | **-2.42E-01** | **N/A** |
| | | | | | | | | | Direct effects | -1.96E+00 | 8.54E-01 | N/A | N/A | 2.18E-02 |
| | | | | | | | | | Indirect effects | -5.82E-01 | 3.29E-01 | N/A | N/A | 7.68E-02 |
| | | | | | | | | | Total effects | -2.54E+00 | 1.12E+00 | N/A | N/A | 2.37E-02 |
| | | | | | | | | | **Successional stage (Early vs. Mid)** | **2.62E+00** | **9.56E-01** | **7.50E-01** | **4.50E+00** | **N/A** |
| | | | | | | | | | Direct effects | 2.81E+00 | 1.05E+00 | N/A | N/A | 7.22E-03 |
| | | | | | | | | | Indirect effects | 8.40E-01 | 4.53E-01 | N/A | N/A | 6.35E-02 |
| | | | | | | | | | Total effects | 3.65E+00 | 1.41E+00 | N/A | N/A | 9.72E-03 |
| | | | | | | | | | Successional stage Late vs. Mid) | -3.19E-01 | 7.47E-01 | -1.78E+00 | 1.15E+00 | N/A |
| | | | | | | | | | Direct effects | -3.36E-01 | 7.67E-01 | N/A | N/A | 6.61E-01 |
| | | | | | | | | | Indirect effects | -1.06E-01 | 2.48E-01 | N/A | N/A | 6.67E-01 |
| | | | | | | | | | Total effects | -4.43E-01 | 1.00E+00 | N/A | N/A | 6.59E-01 |
| | | | | | | | | | **Dim.1[i]** | **-7.67E-01** | **2.45E-01** | **-1.25E+00** | **-2.86E-01** | **N/A** |
| | | | | | | | | | Direct effects | -7.95E-01 | 2.50E-01 | N/A | N/A | 1.50E-03 |
| | | | | | | | | | Indirect effects | -2.30E-01 | 9.94E-02 | N/A | N/A | 2.07E-02 |
| | | | | | | | | | Total effects | -1.02E+00 | 3.16E-01 | N/A | N/A | 1.21E-03 |
| | | | | | | | | | Dim.2 | -3.71E-01 | 2.79E-01 | -9.19E-01 | 1.76E-01 | N/A |
| | | | | | | | | | Direct effects | -4.02E-01 | 2.96E-01 | N/A | N/A | 1.74E-01 |
| | | | | | | | | | Indirect effects | -1.24E-01 | 1.07E-01 | N/A | N/A | 2.46E-01 |
| | | | | | | | | | Total effects | -5.26E-01 | 3.92E-01 | N/A | N/A | 1.80E-01 |
| | | | | | | | | | Dim.3 | 4.61E-01 | 3.00E-01 | -1.27E-01 | 1.05E+00 | N/A |
| | | | | | | | | | Direct effects | 4.81E-01 | 3.25E-01 | N/A | N/A | 1.38E-01 |
| | | | | | | | | | Indirect effects | 1.47E-01 | 1.20E-01 | N/A | N/A | 2.20E-01 |
| | | | | | | | | | Total effects | 6.29E-01 | 4.34E-01 | N/A | N/A | 1.47E-01 |
| *Cornus alternifolia* | Shrubs_5 | Linear | Stand | P4/A4 | 0.00 | 9.64 | 0.071 | 1,36E-01 | **Maple syrup production (Yes vs. No)** | **3.11E-02** | **1.29E-01** | **5.28E-02** | **3.83E-01** | **N/A** |
| | | | | | | | | | Successional stage (Early vs. Mid) | 2.31E-01 | 1.38E-01 | -1.51E-01 | 2.37E-01 | N/A |
| | | | | | | | | | Successional stage Late vs. Mid) | 1.12E-01 | 1.10E-01 | -1.81E-01 | 1.22E-01 | N/A |
| | | | | | | | | | Dim.1[i] | -4.81E-02 | 3.38E-02 | -5.27E-02 | 4.14E-02 | N/A |
| | | | | | | | | | Dim.2 | -5.62E-02 | 4.05E-02 | -9.62E-02 | 1.64E-02 | N/A |

| Response variable | Best models Δ $AIC_c$ < 2 | Model type | Spatial scale[a] | Temporal scale[b] | Δ $AIC_c$ | Log likelihood | Adj. $R^2$ | p-value | Explanatory variable | Estimate[j] | Std. Error[j] | Confidence intervals |  | Simulated p-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  |  |  |  |  |  |  | 2.5 % | 97.5 % |  |
|  |  |  |  |  |  |  |  |  | Dim.3 | -3.91E-02 | 4.50E-02 | -5.71E-02 | 6.48E-02 | N/A |
|  | Shrubs_3 | Linear | Stand | P2 | 0.07 | 6.98 | 0.013 | 3,27E-01 | Dim.1 | 5.26E-03 | 2.05E-02 | -3.59E-02 | 4.64E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Dim.2[i] | -1.20E-02 | 2.30E-02 | -5.81E-02 | 3.41E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Dim.3 | 3.74E-02 | 2.86E-02 | -1.98E-02 | 9.47E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Dim.4 | 5.16E-02 | 3.14E-02 | -1.14E-02 | 1.15E-01 | N/A |
| *Ilex mucronata* (4th root-transformed) | Shrubs_5[g] | Linear | Stand | P4/A4 | 0.00 | 7.22 | 0.29 | 4,11E-04 | Maple syrup production (Yes vs. No) | 1.65E-02 | 1.12E-01 | -2.09E-01 | 2.42E-01 | N/A |
|  |  |  |  |  |  |  |  |  | **Successional stage (Early vs. Mid)** | **-3.05E-01** | **1.31E-01** | **-5.68E-01** | **-4.15E-02** | **N/A** |
|  |  |  |  |  |  |  |  |  | **Successional stage Late vs. Mid)** | **-2.52E-01** | **1.22E-01** | **-4.97E-01** | **-6.87E-03** | **N/A** |
|  |  |  |  |  |  |  |  |  | **Dim.1[i]** | **-8.76E-02** | **2.69E-02** | **-1.42E-01** | **-3.36E-02** | **N/A** |
|  |  |  |  |  |  |  |  |  | **Dim.2** | **-7.50E-02** | **2.86E-02** | **-1.32E-01** | **-1.77E-02** | **N/A** |
|  |  |  |  |  |  |  |  |  | Dim.3 | 4.19E-02 | 3.44E-02 | -2.71E-02 | 1.11E-01 | N/A |
| *Parthenocissus quinquefolia* (4th root-transformed) | Shrubs_1 | Linear | Local | P4 | 0.00 | -6.58 | 0.25 | 3,95E-03 | Soil texture (Loam vs. Clay) | 5.88E-02 | 9.76E-02 | -1.37E-01 | 2.55E-01 | N/A |
|  |  |  |  |  |  |  |  |  | **Soil texture (Organic matter vs. Clay)** | **6.52E-01** | **2.04E-01** | **2.42E-01** | **1.06E+00** | **N/A** |
|  |  |  |  |  |  |  |  |  | Soil texture (Sand vs. Clay) | -3.05E-01 | 1.79E-01 | -6.65E-01 | 5.50E-02 | N/A |
|  |  |  |  |  |  |  |  |  | **Dim.1** | **-4.98E-02** | **1.95E-02** | **-8.91E-02** | **-1.06E-02** | **N/A** |
|  |  |  |  |  |  |  |  |  | Dim.2 | -1.21E-02 | 2.50E-02 | -6.24E-02 | 3.81E-02 | N/A |
|  |  |  |  |  |  |  |  |  | **Dim.3** | **-7.24E-02** | **2.93E-02** | **-1.31E-01** | **-1.35E-02** | **N/A** |
|  |  |  |  |  |  |  |  |  | Dim.4 | -3.58E-02 | 3.76E-02 | -1.11E-01 | 3.97E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Dim.5 | 1.80E-02 | 3.93E-02 | -6.10E-02 | 9.70E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Dim.6 | -3.42E-03 | 4.02E-02 | -8.41E-02 | 7.73E-02 | N/A |
|  | Shrubs_5 | Linear, spatial lag | Stand | P4/A4 | 1.06 | -10.08 | N/A | N/A | **Rho (spatial parameter)** | **2.80E-01** | **8.60E-02** | **1.11E-01** | **4.49E-01** | **N/A** |
|  |  |  |  |  |  |  |  |  | Maple syrup production (Yes vs. No) | -6.25E-02 | 1.05E-01 | -2.68E-01 | 1.43E-01 | N/A |
|  |  |  |  |  |  |  |  |  | Direct effects | -7.20E-02 | 1.04E-01 | N/A | N/A | 4.88E-01 |
|  |  |  |  |  |  |  |  |  | Indirect effects | -2.24E-02 | 3.69E-02 | N/A | N/A | 5.43E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | -9.44E-02 | 1.38E-01 | N/A | N/A | 4.95E-01 |
|  |  |  |  |  |  |  |  |  | Successional stage (Early vs. Mid) | 1.62E-01 | 1.23E-01 | -7.96E-02 | 4.04E-01 | N/A |
|  |  |  |  |  |  |  |  |  | Direct effects | 1.72E-01 | 1.35E-01 | N/A | N/A | 2.01E-01 |
|  |  |  |  |  |  |  |  |  | Indirect effects | 5.41E-02 | 4.90E-02 | N/A | N/A | 2.69E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | 2.26E-01 | 1.79E-01 | N/A | N/A | 2.06E-01 |
|  |  |  |  |  |  |  |  |  | Successional stage Late vs. Mid) | 7.98E-02 | 9.69E-02 | -1.10E-01 | 2.70E-01 | N/A |

| Response variable | Best models Δ $AIC_c$ < 2 | Model type | Spatial scale[a] | Temporal scale[b] | Δ $AIC_c$ | Log likelihood | Adj. $R^2$ | p-value | Explanatory variable | Estimate[j] | Std. Error[j] | Confidence intervals | | Simulated p-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | 2.5 % | 97.5 % | |
| | | | | | | | | | Direct effects | 8.99E-02 | 1.07E-01 | N/A | N/A | 4.00E-01 |
| | | | | | | | | | Indirect effects | 2.76E-02 | 3.61E-02 | N/A | N/A | 4.45E-01 |
| | | | | | | | | | Total effects | 1.17E-01 | 1.40E-01 | N/A | N/A | 4.03E-01 |
| | | | | | | | | | Dim.1[i] | 4.75E-03 | 3.01E-02 | -5.43E-02 | 6.38E-02 | N/A |
| | | | | | | | | | Direct effects | 4.97E-03 | 3.18E-02 | N/A | N/A | 8.76E-01 |
| | | | | | | | | | Indirect effects | 1.09E-03 | 1.10E-02 | N/A | N/A | 9.21E-01 |
| | | | | | | | | | Total effects | 6.06E-03 | 4.23E-02 | N/A | N/A | 8.86E-01 |
| | | | | | | | | | **Dim.2** | **-1.06E-01** | **3.59E-02** | **-1.76E-01** | **-3.56E-02** | **N/A** |
| | | | | | | | | | Direct effects | -1.15E-01 | 3.77E-02 | N/A | N/A | 2.33E-03 |
| | | | | | | | | | Indirect effects | -3.67E-02 | 1.94E-02 | N/A | N/A | 5.88E-02 |
| | | | | | | | | | Total effects | -1.52E-01 | 5.30E-02 | N/A | N/A | 4.22E-03 |
| | | | | | | | | | Dim.3 | -4.46E-02 | 3.88E-02 | -1.21E-01 | 3.15E-02 | N/A |
| | | | | | | | | | Direct effects | -4.50E-02 | 4.12E-02 | N/A | N/A | 2.75E-01 |
| | | | | | | | | | Indirect effects | -1.36E-02 | 1.50E-02 | N/A | N/A | 3.64E-01 |
| | | | | | | | | | Total effects | -5.86E-02 | 5.49E-02 | N/A | N/A | 2.86E-01 |
| | Shrubs_2 | Linear, spatial lag | Stand | P1 | 1.80 | -13.19 | N/A | N/A | **Rho (spatial parameter)** | **2.40E-01** | **9.14E-02** | **6.04E-02** | **4.19E-01** | **N/A** |
| | | | | | | | | | Dim.1 | 2.08E-02 | 2.74E-02 | -3.29E-02 | 7.44E-02 | N/A |
| | | | | | | | | | Direct effects | 2.35E-02 | 2.97E-02 | N/A | N/A | 4.29E-01 |
| | | | | | | | | | Indirect effects | 6.46E-03 | 9.36E-03 | N/A | N/A | 4.90E-01 |
| | | | | | | | | | Total effects | 3.00E-02 | 3.81E-02 | N/A | N/A | 4.32E-01 |
| | | | | | | | | | Dim.2[i] | 3.34E-02 | 3.14E-02 | -2.81E-02 | 9.50E-02 | N/A |
| | | | | | | | | | Direct effects | 3.37E-02 | 3.46E-02 | N/A | N/A | 3.30E-01 |
| | | | | | | | | | Indirect effects | 8.44E-03 | 1.07E-02 | N/A | N/A | 4.29E-01 |
| | | | | | | | | | Total effects | 4.22E-02 | 4.40E-02 | N/A | N/A | 3.38E-01 |
| | | | | | | | | | Dim.3 | 2.65E-02 | 3.58E-02 | -4.37E-02 | 9.66E-02 | N/A |
| | | | | | | | | | Direct effects | 2.81E-02 | 3.55E-02 | N/A | N/A | 4.28E-01 |
| | | | | | | | | | Indirect effects | 7.28E-03 | 1.06E-02 | N/A | N/A | 4.93E-01 |
| | | | | | | | | | Total effects | 3.54E-02 | 4.51E-02 | N/A | N/A | 4.32E-01 |
| | | | | | | | | | **Dim.4** | **9.82E-02** | **4.33E-02** | **1.34E-02** | **1.83E-01** | **N/A** |
| | | | | | | | | | Direct effects | 1.03E-01 | 4.54E-02 | N/A | N/A | 2.30E-02 |
| | | | | | | | | | Indirect effects | 2.76E-02 | 1.80E-02 | N/A | N/A | 1.26E-01 |
| | | | | | | | | | Total effects | 1.31E-01 | 5.95E-02 | N/A | N/A | 2.78E-02 |
| *Prunus virginiana* | Shrubs_12 | Firth penalized logistic[e] | LCC | P3/A3 | 0.00 | -13.57 | N/A | 3,84E-02 | Dim.1 | 3.78E-02 | 2.34E-01 | -4.56E-01 | 5.73E-01 | N/A |
| | | | | | | | | | Dim.2[i] | -1.44E-01 | 2.53E-01 | -6.94E-01 | 4.07E-01 | N/A |
| | | | | | | | | | Dim.3 | -2.67E-01 | 2.94E-01 | -9.86E-01 | 3.44E-01 | N/A |
| | | | | | | | | | **Dim.4** | **-1.27E+00** | **5.07E-01** | **-2.81E+00** | **-3.61E-01** | **N/A** |
| | | | | | | | | | Dim.5 | -1.94E-01 | 4.52E-01 | -1.20E+00 | 7.99E-01 | N/A |
| | Shrubs_11 | Firth penalized logistic | LCC | P2/A2 | 1.98 | -14.56 | N/A | 8,99E-02 | Dim.1 | 2.30E-01 | 2.42E-01 | -2.65E-01 | 7.89E-01 | N/A |
| | | | | | | | | | Dim.2 | 3.95E-02 | 2.41E-01 | -4.66E-01 | 5.45E-01 | N/A |
| | | | | | | | | | Dim.3 | -5.87E-01 | 3.49E-01 | -1.44E+00 | 7.73E-02 | N/A |
| | | | | | | | | | **Dim.4** | **-7.34E-01** | **3.41E-01** | **-1.56E+00** | **-7.56E-02** | **N/A** |
| | | | | | | | | | Dim.5 | -8.47E-01 | 4.40E-01 | -1.88E+00 | 1.50E-02 | N/A |

| Response variable | Best models Δ $AIC_c$ < 2 | Model type | Spatial scale[a] | Temporal scale[b] | Δ $AIC_c$ | Log likelihood | Adj. $R^2$ | p-value | Explanatory variable | Estimate[j] | Std. Error[j] | Confidence intervals | | Simulated p-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | 2.5 % | 97.5 % | |
| *Rhamnus cathartica* (4th root-transformed) | Shrubs_9[g] | Linear | LCD | P4/A4 | 0.00 | 7.86 | 0.37 | 1,47E-05 | Dim.1 | 1.78E-02 | 1.39E-02 | -1.02E-02 | 4.57E-02 | N/A |
| | | | | | | | | | **Dim.2** | **-5.60E-02** | **1.91E-02** | **-9.43E-02** | **-1.78E-02** | **N/A** |
| | | | | | | | | | **Dim.3** | **9.23E-02** | **1.55E-02** | **6.13E-02** | **1.23E-01** | **N/A** |
| | | | | | | | | | Dim.4 | -2.77E-02 | 1.98E-02 | -6.74E-02 | 1.19E-02 | N/A |
| | | | | | | | | | Dim.5 | -1.80E-02 | 3.24E-02 | -8.30E-02 | 4.69E-02 | N/A |
| *Ribes_spp.*[h] (4th root-transformed) | Shrubs_13 | Linear | LCC | P4/A4 | 0.00 | -0.57 | 0.27 | 2,55E-04 | **Dim.1** | **4.53E-02** | **2.14E-02** | **2.49E-03** | **8.81E-02** | **N/A** |
| | | | | | | | | | **Dim.2** | **-8.23E-02** | **2.21E-02** | **-1.27E-01** | **-3.80E-02** | **N/A** |
| | | | | | | | | | Dim.3 | -4.62E-02 | 2.70E-02 | -1.00E-01 | 8.06E-03 | N/A |
| | | | | | | | | | **Dim.4** | **-7.49E-02** | **3.51E-02** | **-1.45E-01** | **-4.67E-03** | **N/A** |
| *Rubus spp.*[h] (4th root-transformed) | Shrubs_7[g] | Linear, spatial lag | LCD | P2/A2 | 0.00 | -6.67 | NA | NA | **Rho (spatial parameter)** | **2.50E-01** | **9.01E-02** | **7.32E-02** | **4.26E-01** | **N/A** |
| | | | | | | | | | Dim.1 | -3.37E-03 | 1.52E-02 | -3.32E-02 | 2.65E-02 | N/A |
| | | | | | | | | | Direct effects | -3.59E-03 | 1.60E-02 | N/A | N/A | 8.22E-01 |
| | | | | | | | | | Indirect effects | -9.83E-04 | 5.06E-03 | N/A | N/A | 8.46E-01 |
| | | | | | | | | | Total effects | -4.58E-03 | 2.07E-02 | N/A | N/A | 8.25E-01 |
| | | | | | | | | | Dim.2 | 1.56E-03 | 1.35E-02 | -2.49E-02 | 2.80E-02 | N/A |
| | | | | | | | | | Direct effects | 1.42E-03 | 1.74E-02 | N/A | N/A | 9.35E-01 |
| | | | | | | | | | Indirect effects | 1.87E-04 | 5.30E-03 | N/A | N/A | 9.72E-01 |
| | | | | | | | | | Total effects | 1.61E-03 | 2.24E-02 | N/A | N/A | 9.43E-01 |
| | | | | | | | | | **Dim.3** | **8.30E-02** | **2.71E-02** | **3.00E-02** | **1.36E-01** | **N/A** |
| | | | | | | | | | Direct effects | 8.68E-02 | 2.55E-02 | N/A | N/A | 6.51E-04 |
| | | | | | | | | | Indirect effects | 2.40E-02 | 1.23E-02 | N/A | N/A | 5.00E-02 |
| | | | | | | | | | Total effects | 1.11E-01 | 3.39E-02 | N/A | N/A | 1.06E-03 |
| | | | | | | | | | Dim.4 | 2.59E-03 | 3.59E-02 | -6.78E-02 | 7.30E-02 | N/A |
| | | | | | | | | | Direct effects | 3.46E-03 | 3.55E-02 | N/A | N/A | 9.22E-01 |
| | | | | | | | | | Indirect effects | 1.63E-03 | 1.09E-02 | N/A | N/A | 8.81E-01 |
| | | | | | | | | | Total effects | 5.08E-03 | 4.58E-02 | N/A | N/A | 9.12E-01 |
| | | | | | | | | | Dim.5 | -3.57E-02 | 2.24E-02 | -7.97E-02 | 8.22E-03 | N/A |
| | | | | | | | | | Direct effects | -3.89E-02 | 3.39E-02 | N/A | N/A | 2.52E-01 |
| | | | | | | | | | Indirect effects | -1.11E-02 | 1.17E-02 | N/A | N/A | 3.44E-01 |
| | | | | | | | | | Total effects | -4.99E-02 | 4.42E-02 | N/A | N/A | 2.59E-01 |
| | Shrubs_4 | Linear, spatial error[f] | Stand | P3 | 0.29 | -9.45 | N/A | N/A | **Lamda (spatial parameter)** | **3.21E-01** | **8.86E-02** | **1.47E-01** | **4.95E-01** | **N/A** |
| | | | | | | | | | Dim.1 | -5.38E-02 | 2.97E-02 | -1.12E-01 | 4.42E-03 | N/A |
| | | | | | | | | | Dim.2[i] | -1.26E-02 | 4.04E-02 | -9.18E-02 | 6.66E-02 | N/A |
| | | | | | | | | | Dim.3 | 4.58E-02 | 3.31E-02 | -1.91E-02 | 1.11E-01 | N/A |
| | Shrubs_9 | Linear, spatial lag | LCD | P4/A4 | 0.54 | -6.94 | N/A | N/A | **Rho (spatial parameter)** | **2.79E-01** | **8.86E-02** | **1.05E-01** | **4.53E-01** | **N/A** |
| | | | | | | | | | Dim.1 | 3.00E-03 | 1.37E-02 | -2.38E-02 | 2.98E-02 | N/A |
| | | | | | | | | | Direct effects | 3.45E-03 | 1.48E-02 | N/A | N/A | 8.15E-01 |
| | | | | | | | | | Indirect effects | 1.06E-03 | 5.34E-03 | N/A | N/A | 8.42E-01 |
| | | | | | | | | | Total effects | 4.52E-03 | 1.99E-02 | N/A | N/A | 8.20E-01 |
| | | | | | | | | | Dim.2 | 2.53E-02 | 2.05E-02 | -1.48E-02 | 6.54E-02 | N/A |
| | | | | | | | | | Direct effects | 2.64E-02 | 2.25E-02 | N/A | N/A | 2.39E-01 |

| Response variable | Best models $\Delta$ AIC$_c$ < 2 | Model type | Spatial scale$^a$ | Temporal scale$^b$ | $\Delta$ AIC$_c$ | Log likelihood | Adj. R$^2$ | p-value | Explanatory variable | Estimate$^j$ | Std. Error$^j$ | Confidence intervals |  | Simulated p-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  |  |  |  |  |  |  | 2.5 % | 97.5 % |  |
|  |  |  |  |  |  |  |  |  | Indirect effects | 8.76E-03 | 8.44E-03 | N/A | N/A | 2.99E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | 3.52E-02 | 3.01E-02 | N/A | N/A | 2.42E-01 |
|  |  |  |  |  |  |  |  |  | **Dim.3** | **5.78E-02** | **2.28E-02** | **1.31E-02** | **1.02E-01** | **N/A** |
|  |  |  |  |  |  |  |  |  | Direct effects | 6.38E-02 | 2.41E-02 | N/A | N/A | 8.04E-03 |
|  |  |  |  |  |  |  |  |  | Indirect effects | 2.07E-02 | 1.10E-02 | N/A | N/A | 6.07E-02 |
|  |  |  |  |  |  |  |  |  | Total effects | 8.44E-02 | 3.25E-02 | N/A | N/A | 9.38E-03 |
|  |  |  |  |  |  |  |  |  | Dim.4 | -3.28E-03 | 2.65E-02 | -5.52E-02 | 4.86E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Direct effects | -4.61E-03 | 2.76E-02 | N/A | N/A | 8.67E-01 |
|  |  |  |  |  |  |  |  |  | Indirect effects | -1.16E-03 | 1.01E-02 | N/A | N/A | 9.09E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | -5.77E-03 | 3.73E-02 | N/A | N/A | 8.77E-01 |
|  |  |  |  |  |  |  |  |  | Dim.5 | -5.29E-02 | 3.00E-02 | -1.12E-01 | 5.99E-03 | N/A |
|  |  |  |  |  |  |  |  |  | Direct effects | -5.51E-02 | 3.38E-02 | N/A | N/A | 1.03E-01 |
|  |  |  |  |  |  |  |  |  | Indirect effects | -1.81E-02 | 1.37E-02 | N/A | N/A | 1.87E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | -7.32E-02 | 4.57E-02 | N/A | N/A | 1.09E-01 |
| *Toxicodendron radicans* (4th root-transformed) | Shrubs_9 | Linear, spatial lag | LCD | P4/A4 | 0.00 | -7.08 | N/A | N/A | **Rho (spatial parameter)** | **2.19E-01** | **9.08E-02** | **4.08E-02** | **3.97E-01** | **N/A** |
|  |  |  |  |  |  |  |  |  | Dim.1 | 7.54E-03 | 1.39E-02 | -1.97E-02 | 3.47E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Direct effects | 8.10E-03 | 1.43E-02 | N/A | N/A | 5.70E-01 |
|  |  |  |  |  |  |  |  |  | Indirect effects | 1.95E-03 | 4.01E-03 | N/A | N/A | 6.27E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | 1.01E-02 | 1.79E-02 | N/A | N/A | 5.74E-01 |
|  |  |  |  |  |  |  |  |  | Dim.2 | -3.45E-02 | 2.12E-02 | -7.61E-02 | 7.11E-03 | N/A |
|  |  |  |  |  |  |  |  |  | Direct effects | -3.64E-02 | 2.20E-02 | N/A | N/A | 9.79E-02 |
|  |  |  |  |  |  |  |  |  | Indirect effects | -8.46E-03 | 6.59E-03 | N/A | N/A | 1.99E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | -4.49E-02 | 2.72E-02 | N/A | N/A | 9.93E-02 |
|  |  |  |  |  |  |  |  |  | Dim.3 | 3.70E-02 | 2.28E-02 | -7.75E-03 | 8.18E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Direct effects | 4.03E-02 | 2.38E-02 | N/A | N/A | 9.02E-02 |
|  |  |  |  |  |  |  |  |  | Indirect effects | 9.33E-03 | 7.30E-03 | N/A | N/A | 2.02E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | 4.97E-02 | 2.94E-02 | N/A | N/A | 9.11E-02 |
|  |  |  |  |  |  |  |  |  | Dim.4 | -7.06E-03 | 2.68E-02 | -5.95E-02 | 4.54E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Direct effects | -6.93E-03 | 2.85E-02 | N/A | N/A | 8.08E-01 |
|  |  |  |  |  |  |  |  |  | Indirect effects | -1.65E-03 | 7.98E-03 | N/A | N/A | 8.36E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | -8.58E-03 | 3.59E-02 | N/A | N/A | 8.11E-01 |
|  |  |  |  |  |  |  |  |  | **Dim.5** | **-8.79E-02** | **3.06E-02** | **-1.48E-01** | **-2.80E-02** | **N/A** |
|  |  |  |  |  |  |  |  |  | Direct effects | -9.19E-02 | 3.11E-02 | N/A | N/A | 3.15E-03 |
|  |  |  |  |  |  |  |  |  | Indirect effects | -2.19E-02 | 1.29E-02 | N/A | N/A | 9.00E-02 |
|  |  |  |  |  |  |  |  |  | Total effects | -1.14E-01 | 4.00E-02 | N/A | N/A | 4.46E-03 |
|  | Shrubs_12 | Linear, spatial lag | LCC | P3/A3 | 0.29 | -7.22 | N/A | N/A | **Rho (spatial parameter)** | **2.19E-01** | **9.10E-02** | **4.08E-02** | **3.97E-01** | **N/A** |
|  |  |  |  |  |  |  |  |  | Dim.1 | 1.43E-03 | 2.37E-02 | -4.50E-02 | 4.79E-02 | N/A |
|  |  |  |  |  |  |  |  |  | Direct effects | 1.06E-03 | 2.46E-02 | N/A | N/A | 9.66E-01 |
|  |  |  |  |  |  |  |  |  | Indirect effects | -4.26E-05 | 6.71E-03 | N/A | N/A | 9.95E-01 |
|  |  |  |  |  |  |  |  |  | Total effects | 1.01E-03 | 3.08E-02 | N/A | N/A | 9.74E-01 |
|  |  |  |  |  |  |  |  |  | **Dim.2$^i$** | **-7.31E-02** | **2.48E-02** | **-1.22E-01** | **-2.44E-02** | **N/A** |
|  |  |  |  |  |  |  |  |  | Direct effects | -7.55E-02 | 2.62E-02 | N/A | N/A | 3.97E-03 |

| Response variable | Best models $\Delta$ AIC$_c$ < 2 | Model type | Spatial scale[a] | Temporal scale[b] | $\Delta$ AIC$_c$ | Log likelihood | Adj. R$^2$ | p-value | Explanatory variable | Estimate[j] | Std. Error[j] | Confidence intervals | | Simulated p-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | 2.5 % | 97.5 % | |
| | | | | | | | | | Indirect effects | -1.75E-02 | 9.99E-03 | N/A | N/A | 7.97E-02 |
| | | | | | | | | | Total effects | -9.30E-02 | 3.20E-02 | N/A | N/A | 3.65E-03 |
| | | | | | | | | | Dim.3 | -3.77E-02 | 2.83E-02 | -9.32E-02 | 1.78E-02 | N/A |
| | | | | | | | | | Direct effects | -3.70E-02 | 2.97E-02 | N/A | N/A | 2.13E-01 |
| | | | | | | | | | Indirect effects | -9.24E-03 | 9.12E-03 | N/A | N/A | 3.11E-01 |
| | | | | | | | | | Total effects | -4.62E-02 | 3.76E-02 | N/A | N/A | 2.19E-01 |
| | | | | | | | | | Dim.4 | -5.62E-02 | 3.45E-02 | -1.24E-01 | 1.14E-02 | N/A |
| | | | | | | | | | Direct effects | -5.89E-02 | 3.59E-02 | N/A | N/A | 1.01E-01 |
| | | | | | | | | | Indirect effects | -1.36E-02 | 1.13E-02 | N/A | N/A | 2.30E-01 |
| | | | | | | | | | Total effects | -7.24E-02 | 4.49E-02 | N/A | N/A | 1.06E-01 |
| | | | | | | | | | Dim.5 | -2.35E-02 | 4.05E-02 | -1.03E-01 | 5.59E-02 | N/A |
| | | | | | | | | | Direct effects | -2.10E-02 | 3.98E-02 | N/A | N/A | 5.97E-01 |
| | | | | | | | | | Indirect effects | -4.96E-03 | 1.15E-02 | N/A | N/A | 6.67E-01 |
| | | | | | | | | | Total effects | -2.60E-02 | 5.01E-02 | N/A | N/A | 6.05E-01 |
| | Shrubs_4 | Linear, spatial lag | Stand | P3 | 1.29 | -10.36 | N/A | N/A | **Rho (spatial parameter)** | **2.72E-01** | **9.07E-02** | **9.46E-02** | **4.50E-01** | **N/A** |
| | | | | | | | | | Dim.1 | -1.22E-02 | 2.56E-02 | -6.23E-02 | 3.79E-02 | N/A |
| | | | | | | | | | Direct effects | -1.09E-02 | 2.71E-02 | N/A | N/A | 6.88E-01 |
| | | | | | | | | | Indirect effects | -3.08E-03 | 8.94E-03 | N/A | N/A | 7.30E-01 |
| | | | | | | | | | Total effects | -1.40E-02 | 3.55E-02 | N/A | N/A | 6.94E-01 |
| | | | | | | | | | Dim.2[i] | 5.38E-02 | 3.12E-02 | -7.40E-03 | 1.15E-01 | N/A |
| | | | | | | | | | Direct effects | 5.66E-02 | 3.36E-02 | N/A | N/A | 9.27E-02 |
| | | | | | | | | | Indirect effects | 1.72E-02 | 1.33E-02 | N/A | N/A | 1.97E-01 |
| | | | | | | | | | Total effects | 7.37E-02 | 4.51E-02 | N/A | N/A | 1.02E-01 |
| | | | | | | | | | Dim.3 | 5.94E-02 | 3.59E-02 | -1.09E-02 | 1.30E-01 | N/A |
| | | | | | | | | | Direct effects | 6.22E-02 | 3.79E-02 | N/A | N/A | 1.00E-01 |
| | | | | | | | | | Indirect effects | 1.92E-02 | 1.52E-02 | N/A | N/A | 2.08E-01 |
| | | | | | | | | | Total effects | 8.14E-02 | 5.09E-02 | N/A | N/A | 1.10E-01 |
| | Shrubs_5 | Linear, spatial lag | Stand | P4/A4 | 1.60 | -6.48 | N/A | N/A | **Rho (spatial parameter)** | **2.29E-01** | **8.97E-02** | **5.26E-02** | **4.04E-01** | **N/A** |
| | | | | | | | | | Maple syrup production (Yes vs. No) | -1.35E-01 | 9.97E-02 | -3.31E-01 | 6.01E-02 | N/A |
| | | | | | | | | | Direct effects | -1.49E-01 | 9.88E-02 | N/A | N/A | 1.32E-01 |
| | | | | | | | | | Indirect effects | -3.91E-02 | 3.45E-02 | N/A | N/A | 2.56E-01 |
| | | | | | | | | | Total effects | -1.88E-01 | 1.29E-01 | N/A | N/A | 1.44E-01 |
| | | | | | | | | | **Successional stage (Early vs. Mid)** | **2.97E-01** | **1.17E-01** | **6.69E-02** | **5.27E-01** | **N/A** |
| | | | | | | | | | Direct effects | 3.13E-01 | 1.23E-01 | N/A | N/A | 1.08E-02 |
| | | | | | | | | | Indirect effects | 7.98E-02 | 4.78E-02 | N/A | N/A | 9.47E-02 |
| | | | | | | | | | Total effects | 3.93E-01 | 1.58E-01 | N/A | N/A | 1.29E-02 |
| | | | | | | | | | Successional stage Late vs. Mid) | 5.56E-02 | 9.17E-02 | -1.24E-01 | 2.35E-01 | N/A |

| Response variable | Best models $\Delta$ AIC$_c$ < 2 | Model type | Spatial scale[a] | Temporal scale[b] | $\Delta$ AIC$_c$ | Log likelihood | Adj. R$^2$ | p-value | Explanatory variable | Estimate[j] | Std. Error[j] | Confidence intervals | | Simulated p-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | 2.5 % | 97.5 % | |
| | | | | | | | | | Direct effects | 6.38E-02 | 9.99E-02 | N/A | N/A | 5.23E-01 |
| | | | | | | | | | Indirect effects | 1.59E-02 | 2.89E-02 | N/A | N/A | 5.82E-01 |
| | | | | | | | | | Total effects | 7.97E-02 | 1.26E-01 | N/A | N/A | 5.27E-01 |
| | | | | | | | | | Dim.1[i] | -3.12E-02 | 2.88E-02 | -8.76E-02 | 2.52E-02 | N/A |
| | | | | | | | | | Direct effects | -3.26E-02 | 2.84E-02 | N/A | N/A | 2.51E-01 |
| | | | | | | | | | Indirect effects | -8.10E-03 | 8.48E-03 | N/A | N/A | 3.39E-01 |
| | | | | | | | | | Total effects | -4.07E-02 | 3.58E-02 | N/A | N/A | 2.56E-01 |
| | | | | | | | | | Dim.2 | 1.95E-02 | 3.41E-02 | -4.73E-02 | 8.63E-02 | N/A |
| | | | | | | | | | Direct effects | 2.01E-02 | 3.69E-02 | N/A | N/A | 5.85E-01 |
| | | | | | | | | | Indirect effects | 5.17E-03 | 1.10E-02 | N/A | N/A | 6.39E-01 |
| | | | | | | | | | Total effects | 2.53E-02 | 4.71E-02 | N/A | N/A | 5.91E-01 |
| | | | | | | | | | Dim.3 | 1.86E-02 | 3.68E-02 | -5.36E-02 | 9.07E-02 | N/A |
| | | | | | | | | | Direct effects | 2.24E-02 | 3.81E-02 | N/A | N/A | 5.56E-01 |
| | | | | | | | | | Indirect effects | 5.42E-03 | 1.06E-02 | N/A | N/A | 6.08E-01 |
| | | | | | | | | | Total effects | 2.79E-02 | 4.77E-02 | N/A | N/A | 5.59E-01 |
| *Viburnum lentago* | Shrubs_10 | Firth penalized logistic | LCC | P1/A1 | 0.00 | -13.52 | N/A | 1,41E-02 | Dim.1 | 3.72E-01 | 2.13E-01 | -4.66E-02 | 8.50E-01 | N/A |
| | | | | | | | | | **Dim.2** | **6.93E-01** | **2.62E-01** | **1.98E-01** | **1.33E+00** | **N/A** |
| | | | | | | | | | Dim.3[i] | -6.60E-01 | 3.81E-01 | -1.61E+00 | 6.27E-02 | N/A |
| | | | | | | | | | Dim.4 | -3.24E-01 | 3.17E-01 | -1.04E+00 | 3.07E-01 | N/A |
| | | | | | | | | | Dim.5 | 3.79E-01 | 3.94E-01 | -4.06E-01 | 1.25E+00 | N/A |
| | Shrubs_11 | Firth penalized logistic | LCC | P2/A2 | 1.01 | -14.03 | N/A | 2,10E-02 | Dim.1 | 2.35E-01 | 1.96E-01 | -1.61E-01 | 6.47E-01 | N/A |
| | | | | | | | | | **Dim.2** | **-5.65E-01** | **2.95E-01** | **-1.29E+00** | **-6.22E-03** | **N/A** |
| | | | | | | | | | **Dim.3** | **6.83E-01** | **2.78E-01** | **1.38E-01** | **1.32E+00** | **N/A** |
| | | | | | | | | | Dim.4 | 4.11E-01 | 3.08E-01 | -1.98E-01 | 1.13E+00 | N/A |
| | | | | | | | | | Dim.5 | 3.02E-01 | 3.98E-01 | -5.17E-01 | 1.20E+00 | N/A |
| | Shrubs_8 | Firth penalized logistic | LCD | P3/A3 | 1.18 | -14.11 | N/A | 5,03E-02 | Dim.1 | -1.78E-01 | 1.61E-01 | -5.59E-01 | 1.49E-01 | N/A |
| | | | | | | | | | Dim.2 | 5.02E-01 | 2.79E-01 | -6.48E-02 | 1.19E+00 | N/A |
| | | | | | | | | | **Dim.3[i]** | **-8.63E-01** | **3.21E-01** | **-1.73E+00** | **-2.67E-01** | **N/A** |
| | | | | | | | | | Dim.4 | 2.65E-01 | 3.41E-01 | -4.39E-01 | 1.05E+00 | N/A |
| | | | | | | | | | Dim.5 | 6.18E-01 | 4.21E-01 | -2.40E-01 | 1.60E+00 | N/A |
| | Shrubs_9 | Firth penalized logistic | LCD | P4/A4 | 1.40 | -14.22 | N/A | 6,87E-02 | Dim.1 | -6.73E-02 | 1.28E-01 | -3.40E-01 | 1.96E-01 | N/A |
| | | | | | | | | | Dim.2 | -3.21E-01 | 2.10E-01 | -8.29E-01 | 8.01E-02 | N/A |
| | | | | | | | | | **Dim.3** | **7.19E-01** | **3.12E-01** | **1.57E-01** | **1.54E+00** | **N/A** |
| | | | | | | | | | Dim.4 | 4.24E-01 | 2.30E-01 | -3.50E-02 | 9.48E-01 | N/A |
| | | | | | | | | | Dim.5 | 2.29E-01 | 2.42E-01 | -2.66E-01 | 7.38E-01 | N/A |
| *Zanthoxylum americanum* (4th root-transformed) | Shrubs_6[g] | Linear | LCD | P1/A1 | 0.00 | 19.28 | 0.19 | 3,29E-03 | Dim.1 | -1.76E-02 | 9.43E-03 | -3.65E-02 | 1.30E-03 | N/A |
| | | | | | | | | | **Dim.2** | **2.02E-02** | **8.84E-03** | **2.51E-03** | **3.80E-02** | **N/A** |
| | | | | | | | | | **Dim.3** | **5.11E-02** | **2.27E-02** | **5.63E-03** | **9.65E-02** | **N/A** |
| | | | | | | | | | Dim.4 | 2.71E-02 | 1.56E-02 | -4.23E-03 | 5.84E-02 | N/A |

[a] Spatial scale: Local – 30m; Stand – 60m; LCD – Landscape composition + disturbances (600m and 2km); LCC – Landscape configuration + connectivity (600m and 2km).

[b] Temporal scale: P1 – distant past (1930-40); P2 – intermediate past (1958); P3 – recent past (1983); P4 – current (2015). For forest disturbances: A1 – distant past (before 1930-40); A2 – intermediate past (between 1930-40 and 1958); A3 – recent past (between 1958 and 1983); A4 – very recent past (between 1983 and 2015).

[c] The model Trees_5 includes the binary explanatory variable Maple syrup production Yes vs. No that represents a partial disturbance that occurred repetitively in the past, but that we cannot assign to a specific period.

[d] Spatial lag model was used to take into account spatial autocorrelation of residuals.
[e] Firth penalized logistic regression was used when the number of occurrences was too low to properly fit a linear model.
[f] Spatial error model was used to take into account spatial autocorrelation of residuals when spatial lag model failed to achieve this.
[g] Standard error and confidence intervals measured with a robust method based on a heteroscedasticity-corrected covariance matrix of the model parameters to take into account residuals heteroscedasticity.
[h] *Ribes spp.* – Currant and gooseberry species were merged for the analyses; *Rubus spp.* – *Rubus idaeus*, *R. Allegheniensis* and *R. Odoratus* were merged for the analyses.
[I] Dimension associated mostly with geographic coordinates.
[j] Simulated estimates and standard errors for the direct, indirect and total effects in spatial lag models.

Table 1.5. Best and competing regression models following model selection with the AIC$_c$ for tree diversity, richness and relative abundances. Significant explanatory variables are in bold. The direct, indirect and total effects are provided for linear spatial lag models in addition to the parameter estimates.

| Response variable | Best models $\Delta$ AIC$_c$ < 2 | Model type | Spatial scale[a] | Temporal scale[b] | $\Delta$ AIC$_c$ | Log likelihood | Adj. $R^2$ | p-value | Explanatory variable | Estimate | Std. Error | Confidence intervals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | 2.5 % | 97.5 % |
| Tree diversity | Trees_6 | Linear | LCD | P1/A1 | 0.00 | -97.29 | 0.19 | 2,31E-03 | Dim.1 | 9.98E-02 | 7.19E-02 | -4.40E-02 | 2.44E-01 |
| | | | | | | | | | Dim.2 | 8.68E-02 | 7.39E-02 | -6.12E-02 | 2.35E-01 |
| | | | | | | | | | **Dim.3** | **-3.20E-01** | **9.61E-02** | **-5.12E-01** | **-1.28E-01** |
| | | | | | | | | | **Dim.4** | **2.13E-01** | **1.01E-01** | **1.05E-02** | **4.16E-01** |
| | Trees_7 | Linear | LCD | P2/A2 | 1.11 | -96.58 | 0.19 | 3,24E-03 | Dim.1 | -1.09E-01 | 6.31E-02 | -2.36E-01 | 1.72E-02 |
| | | | | | | | | | Dim.2 | 9.81E-02 | 6.93E-02 | -4.06E-02 | 2.37E-01 |
| | | | | | | | | | **Dim.3** | **-2.87E-01** | **1.04E-01** | **-4.95E-01** | **-7.81E-02** |
| | | | | | | | | | **Dim.4** | **3.34E-01** | **1.31E-01** | **7.06E-02** | **5.97E-01** |
| | | | | | | | | | Dim.5 | 1.52E-01 | 1.38E-01 | -1.24E-01 | 4.28E-01 |
| Tree richness | Trees_5[c] | Linear | Stand | P4/A4 | 0.00 | -124.22 | 0.17 | 4,70E-03 | **Maple syrup production (Yes vs. No)** | **-1.39E+00** | **5.68E-01** | **-2.52E+00** | **-2.49E-01** |
| | | | | | | | | | Dim.1[f] | -3.85E-02 | 1.70E-01 | -3.78E-01 | 3.02E-01 |
| | | | | | | | | | **Dim.2** | **7.22E-01** | **2.08E-01** | **3.05E-01** | **1.14E+00** |
| | | | | | | | | | Dim.3 | 7.03E-02 | 2.35E-01 | -4.00E-01 | 5.40E-01 |
| | Trees_9 | Linear | LCD | P4/A4 | 0.20 | -123.06 | 0.18 | 4,43E-03 | Dim.1 | 1.63E-01 | 8.72E-02 | -1.11E-02 | 3.38E-01 |
| | | | | | | | | | **Dim.2** | **-2.82E-01** | **1.29E-01** | **-5.41E-01** | **-2.26E-02** |
| | | | | | | | | | Dim.3 | -2.33E-01 | 1.38E-01 | -5.09E-01 | 4.32E-02 |
| | | | | | | | | | **Dim.4** | **3.74E-01** | **1.69E-01** | **3.52E-02** | **7.12E-01** |
| | | | | | | | | | Dim.5 | 3.37E-01 | 1.87E-01 | -3.64E-02 | 7.11E-01 |
| | Trees_6 | Linear | LCD | P1/A1 | 0.47 | -124.46 | 0.16 | 5,71E-03 | Dim.1 | 2.09E-01 | 1.10E-01 | -1.11E-02 | 4.29E-01 |
| | | | | | | | | | Dim.2 | 1.77E-01 | 1.13E-01 | -4.89E-02 | 4.03E-01 |
| | | | | | | | | | **Dim.3** | **-3.69E-01** | **1.47E-01** | **-6.62E-01** | **-7.46E-02** |
| | | | | | | | | | Dim.4 | 3.04E-01 | 1.55E-01 | -6.14E-03 | 6.14E-01 |
| *Acer rubrum* | Trees_1[d] | Linear | Local | P4 | 0.00 | 52.46 | 0.23 | 8,76E-04 | Soil texture (Loam vs. Clay) | 3.87E-02 | 2.14E-02 | -4.23E-03 | 8.16E-02 |
| | | | | | | | | | Soil texture (Organic matter vs. Clay) | 1.23E-02 | 3.42E-02 | -5.62E-02 | 8.09E-02 |
| | | | | | | | | | Soil texture (Sand. vs. Clay) | 4.65E-02 | 6.82E-02 | -9.00E-02 | 1.83E-01 |
| | | | | | | | | | Dim.1[f] | -1.77E-02 | 1.08E-02 | -3.93E-02 | 4.04E-03 |
| | | | | | | | | | **Dim.2** | **-5.69E-02** | **1.55E-02** | **-8.80E-02** | **-2.58E-02** |
| *Acer saccharum* | Trees_5[c] | Linear | Stand | P4/A4 | 0.00 | -5.92 | 0.31 | 3,10E-05 | **Maple syrup production (Yes vs. No)** | **4.78E-01** | **8.94E-02** | **2.99E-01** | **6.57E-01** |
| | | | | | | | | | Dim.1[f] | 1.49E-02 | 2.68E-02 | -3.86E-02 | 6.85E-02 |
| | | | | | | | | | Dim.2 | 3.86E-02 | 3.28E-02 | -2.71E-02 | 1.04E-01 |
| | | | | | | | | | Dim.3 | 2.13E-02 | 3.70E-02 | -5.27E-02 | 9.54E-02 |
| *Fagus grandifolia* | Trees_8 | Firth penalized logistic | LCD | P3/A3 | 0.00 | -11.33 | N/A | 9,05E-05 | Dim.1 | 1.51E-02 | 1.52E-01 | -3.06E-01 | 3.39E-01 |
| | | | | | | | | | **Dim.2** | **-1.73E+00** | **5.03E-01** | **-3.21E+00** | **-8.39E-01** |
| | | | | | | | | | Dim.3[f] | 5.41E-01 | 2.94E-01 | -1.27E+00 | 2.94E-02 |
| | | | | | | | | | Dim.4 | 1.21E-01 | 2.73E-01 | -4.51E-01 | 7.10E-01 |
| | | | | | | | | | Dim.5 | -7.08E-01 | 5.55E-01 | -2.09E+00 | 3.71E-01 |
| *Fraxinus americana* | Trees_12 | Firth penalized logistic | LCC | P3/A3 | 0.00 | -20.49 | N/A | 8,12E-04 | Dim.1 | -6.09E-02 | 1.96E-01 | -4.65E-01 | 3.49E-01 |
| | | | | | | | | | **Dim.2** | **-6.11E-01** | **2.26E-01** | **-1.13E+00** | **-1.82E-01** |
| | | | | | | | | | **Dim.3** | **6.40E-01** | **2.49E-01** | **1.64E-01** | **1.20E+00** |
| | | | | | | | | | Dim.4 | -5.18E-01 | 2.99E-01 | -1.19E+00 | 6.96E-02 |

| Response variable | Best models $\Delta AIC_c < 2$ | Model type | Spatial scale[a] | Temporal scale[b] | $\Delta AIC_c$ | Log likelihood | Adj. $R^2$ | p-value | Explanatory variable | Estimate | Std. Error | Confidence intervals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | 2.5 % | 97.5 % |
| | | | | | | | | | **Dim.5** | **-7.96E-01** | **3.67E-01** | **-1.64E+00** | **-9.53E-02** |
| *Ostrya virginiana* | Trees_2 | Linear | Stand | P1 | 0.00 | 125.87 | 0.095 | 4,14E-02 | **Dim.1** | **-8.64E-03** | **3.12E-03** | **-1.49E-02** | **-2.40E-03** |
| | | | | | | | | | Dim.2[f] | -4.13E-03 | 3.47E-03 | -1.11E-02 | 2.82E-03 |
| | | | | | | | | | Dim.3 | 3.26E-03 | 4.11E-03 | -4.97E-03 | 1.15E-02 |
| | | | | | | | | | Dim.4 | -4.78E-03 | 4.99E-03 | -1.48E-02 | 5.21E-03 |
| *Populus spp.*[e] | Trees_10[d] | Linear | LCC | P1/A1 | 0.00 | 11.58 | 0.26 | 3,60E-04 | Dim.1 | 1.97E-03 | 2.37E-02 | -4.54E-02 | 4.94E-02 |
| | | | | | | | | | Dim.2 | 2.66E-02 | 1.86E-02 | -1.06E-02 | 6.38E-02 |
| | | | | | | | | | Dim.3[f] | -3.31E-02 | 1.75E-02 | -6.82E-02 | 1.94E-03 |
| | | | | | | | | | Dim.4 | -3.60E-02 | 2.99E-02 | -9.58E-02 | 2.38E-02 |
| | | | | | | | | | **Dim.5** | **-1.33E-01** | **3.65E-02** | **-2.06E-01** | **-5.98E-02** |
| *Thuja occidentalis* | Trees_1[d] | Linear | Local | P4 | 0.00 | -14.50 | 0.20 | 2,45E-03 | Soil texture (Loam vs. Clay) | -8.55E-02 | 1.20E-01 | -3.26E-01 | 1.55E-01 |
| | | | | | | | | | Soil texture (Organic matter vs. Clay) | 1.67E-01 | 2.31E-01 | -2.95E-01 | 6.28E-01 |
| | | | | | | | | | Soil texture (Sand. vs. Clay) | -2.92E-02 | 1.13E-01 | -2.56E-01 | 1.98E-01 |
| | | | | | | | | | **Dim.1[f]** | **7.33E-02** | **3.13E-02** | **1.06E-02** | **1.36E-01** |
| | | | | | | | | | **Dim.2** | **1.46E-01** | **4.83E-02** | **4.94E-02** | **2.43E-01** |
| *Tilia americana* | Trees_12[d] | Linear | LCC | P3/A3 | 0.00 | 85.46 | 0.42 | 4,75E-07 | Dim.1 | -1.44E-02 | 8.22E-03 | -3.09E-02 | 2.04E-03 |
| | | | | | | | | | Dim.2 | 1.66E-02 | 9.19E-03 | -1.78E-03 | 3.50E-02 |
| | | | | | | | | | **Dim.3** | **2.23E-02** | **7.97E-03** | **6.39E-03** | **3.83E-02** |
| | | | | | | | | | Dim.4 | 1.12E-02 | 1.36E-02 | -1.61E-02 | 3.85E-02 |
| | | | | | | | | | **Dim.5** | **-4.62E-02** | **1.63E-02** | **-7.88E-02** | **-1.36E-02** |
| *Tsuga canadensis* | Trees_6[d] | Linear | LCD | P1/A1 | 0.00 | 25.12 | 0.45 | 6,18E-08 | **Dim.1** | **3.25E-02** | **1.06E-02** | **1.13E-02** | **5.37E-02** |
| | | | | | | | | | **Dim.2** | **-6.01E-02** | **1.15E-02** | **-8.32E-02** | **-3.70E-02** |
| | | | | | | | | | **Dim.3** | **-5.12E-02** | **1.47E-02** | **-8.06E-02** | **-2.18E-02** |
| | | | | | | | | | Dim.4 | -2.04E-02 | 1.87E-02 | -5.79E-02 | 1.71E-02 |

[a] Spatial scale: Local – 30m; Stand – 60m; LCD – Landscape composition + disturbances (600m and 2km); LCC – Landscape configuration + connectivity (600m and 2km).

[b] Temporal scale: P1 – distant past (1930-40); P2 – intermediate past (1958); P3 – recent past (1983); P4 – current (2015). For forest disturbances: A1 – distant past (before 1930-40); A2 – intermediate past (between 1930-40 and 1958); A3 – recent past (between 1958 and 1983); A4 – very recent past (between 1983 and 2015).

[c] The model Trees_5 includes the binary explanatory variable Maple syrup production Yes vs. No that represents a partial disturbance that occurred repetitively in the past, but that we cannot assign to a specific period.

[d] Standard error and confidence intervals measured with a robust method based on a heteroscedasticity-corrected covariance matrix of the model parameters to take into account residuals heteroscedasticity.

[e] Species: *Populus spp.* – *Populus tremuloides*, *Populus grandidentata* and *Populus balsamifera* were merged for the analyses.

[f] Dimension associated mostly with geographic coordinates.

## 1.12 Annexes

Annex A. Absolute (ha) and relative (%) area of the main land-use classes in the 2km-buffer landscapes (n-64) at the four time periods.

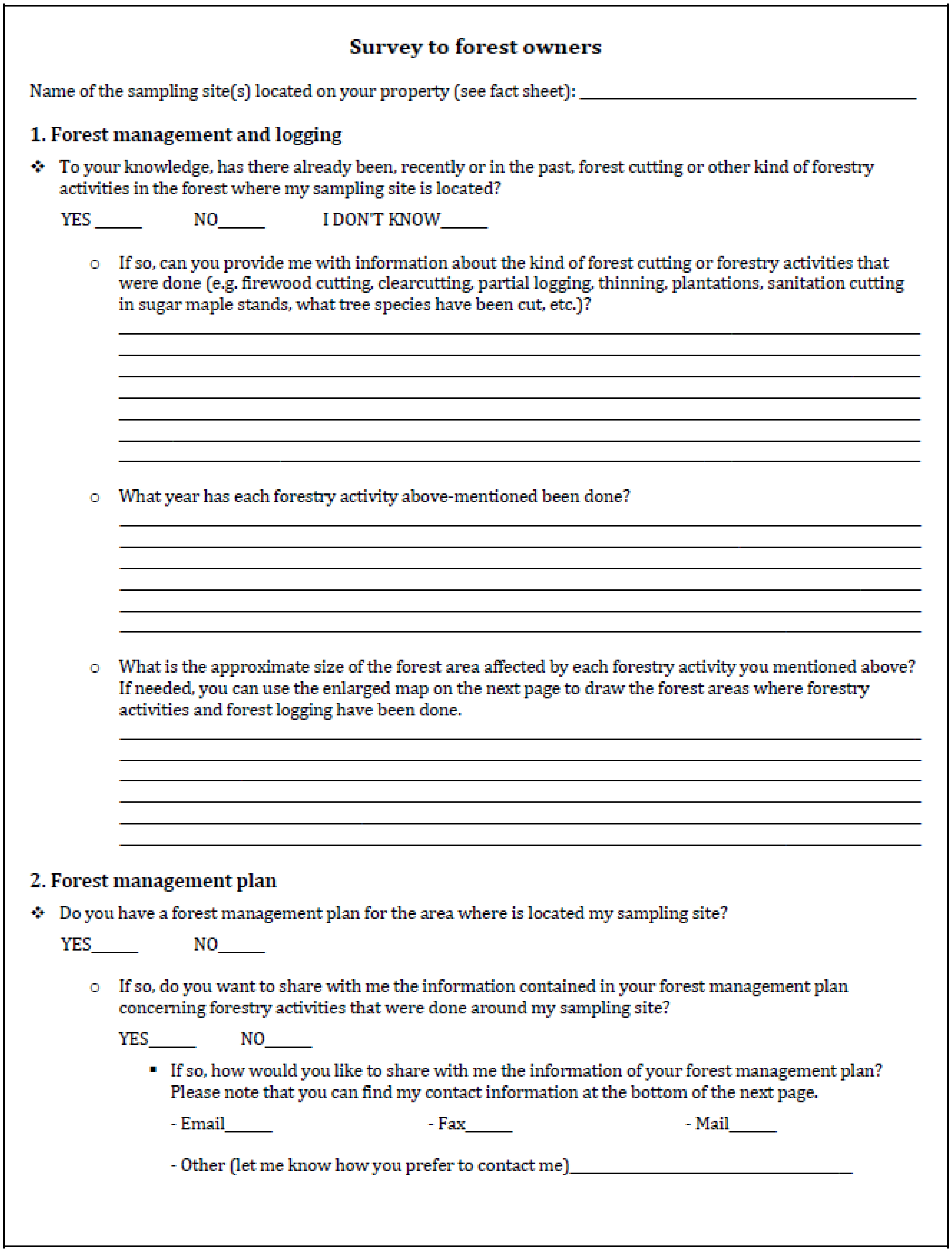
| Land use | P1 (1930-40) | | P2 (1958) | | P3 (1983) | | P4 (2015) | |
|---|---|---|---|---|---|---|---|---|
| **Agriculture** | | | | | | | | |
| Area min. | 96.1 | (7.7) | 25.6 | (2.0) | 12.1 | (1.0) | 2.4 | (0.2) |
| Area max. | 1,190.2 | (94.8) | 1,181.3 | (94.1) | 1,160.2 | (92.4) | 1,147.4 | (91.4) |
| Mean area | 669.5 | (53.3) | 638.6 | (50.9) | 586.3 | (46.7) | 470.6 | (37.5) |
| **Closed forest** | | | | | | | | |
| Area min. | 11.2 | (0.9) | 15.8 | (1.3) | 20.8 | (1.7) | 33.9 | (2.7) |
| Area max. | 691.8 | (55.1) | 894.7 | (71.3) | 954.1 | (76.0) | 1,049.8 | (83.6) |
| Mean area | 240.8 | (19.2) | 254.2 | (20.2) | 364.8 | (29.1) | 493.4 | (39.3) |
| **Sparse forest** | | | | | | | | |
| Area min. | 0 | (0.0) | 0 | (0.0) | 0 | (0.0) | 0 | (0.0) |
| Area max. | 91.9 | (7.3) | 75.3 | (6.0) | 0 | (0.0) | 55.1 | (4.4) |
| Mean area | 17.8 | (1.4) | 13.6 | (1.1) | 0 | (0.0) | 15.9 | (1.3) |
| **Open forest** | | | | | | | | |
| Area min. | 2.1 | (0.2) | 0 | (0.0) | 3.0 | (0.2) | 0 | (0.0) |
| Area max. | 214.1 | (17.1) | 215.7 | (17.2) | 221.8 | (17.7) | 160.7 | (12.8) |
| Mean area | 46.8 | (3.7) | 50.9 | (4.1) | 95.1 | (7.6) | 64.1 | (5.1) |
| **Pasture** | | | | | | | | |
| Area min. | 0 | (0.0) | 0 | (0.0) | 0 | (0.0) | 2.8 | (0.2) |
| Area max. | 519.6 | (41.4) | 451.6 | (36.0) | 338.9 | (27.0) | 382.9 | (30.5) |
| Mean area | 173.1 | (13.8) | 133.6 | (10.6) | 97.4 | (7.8) | 131.3 | (10.5) |
| **Regeneration** | | | | | | | | |
| Area min. | 0 | (0.0) | 4.5 | (0.4) | 0 | (0.0) | 0 | (0.0) |
| Area max. | 529.7 | (42.2) | 461.1 | (36.7) | 349.6 | (27.8) | 82.2 | (6.5) |
| Mean area | 52.1 | (4.1) | 116.7 | (9.3) | 51.1 | (4.1) | 23.2 | (1.8) |

Annex B. Photointerpretation of historical aerial photographs. All land uses detected on aerial photographs were drawn on acetates within a 2km-buffer zone around each sampling site (orange dot on the picture). a) Aerial photograph of one sampling site and its surrounding landscape in 1958, scale 1:30,000, b) Photointerpretation of that same region.

a)

b)

Annex C. Postal survey for forest landowners.



## Survey to forest owners

Name of the sampling site(s) located on your property (see fact sheet): ____________________________

### 1. Forest management and logging

- To your knowledge, has there already been, recently or in the past, forest cutting or other kind of forestry activities in the forest where my sampling site is located?

  YES _____ NO_____ I DON'T KNOW_____

  - If so, can you provide me with information about the kind of forest cutting or forestry activities that were done (e.g. firewood cutting, clearcutting, partial logging, thinning, plantations, sanitation cutting in sugar maple stands, what tree species have been cut, etc.)?
  - What year has each forestry activity above-mentioned been done?
  - What is the approximate size of the forest area affected by each forestry activity you mentioned above? If needed, you can use the enlarged map on the next page to draw the forest areas where forestry activities and forest logging have been done.

### 2. Forest management plan

- Do you have a forest management plan for the area where is located my sampling site?

  YES_____ NO_____

  - If so, do you want to share with me the information contained in your forest management plan concerning forestry activities that were done around my sampling site?

    YES_____ NO_____

    - If so, how would you like to share with me the information of your forest management plan? Please note that you can find my contact information at the bottom of the next page.

      - Email_____ - Fax_____ - Mail_____

      - Other (let me know how you prefer to contact me)____________________________

### 3. Agricultural activities

- To your knowledge, is there currently or has there been in the past agricultural activities in the area where is located my sampling site (e.g. cattle grazing in the wood, any kind of farming before forest regrowth, etc.)?

  YES_____ NO_____ I DON'T KNOW_____

  - If so, can you give me more information about those activities (what kind of agricultural activities, what year, etc.)?

### 4. Other uses of your forest

- To your knowledge, is there currently or has there been in the past other kind of uses in the forest where is located my sampling site?

  YES_____ NO_____ I DON'T KNOW_____

  - If so, can you describe them to me (what kind of uses, what year, etc.)?

### 5. Future collaboration

- Would you like to continue collaborating with me and other members of my research team in the coming years so that we can continue studying impacts of climate change and of other stress factors on private forests of southern Quebec?

  YES_____ NO_____

  - If so, do you want to give me your contact information (phone and email) so that we can contact you in the future? Please note that this information will be treated confidentially and will be kept for internal use only.

### 6. Other comments?

**Thank you for taking the time to complete this survey and to send it back to me by May 31 2016!**

**My contact information**
Caroline Gagné, biol. M.Sc., PhD student in biology
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Email: caroline.gagne@outlook.com
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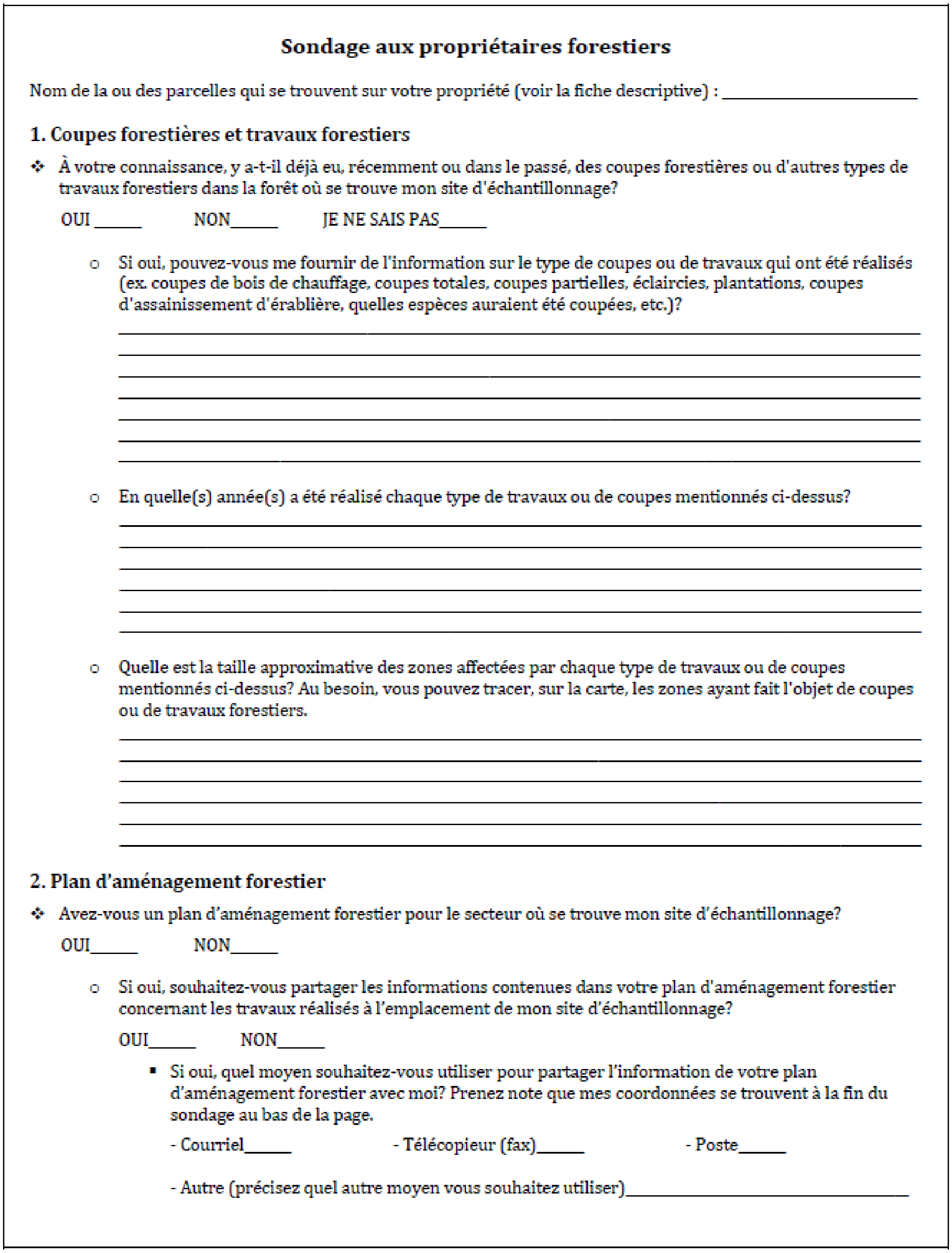

## Sondage aux propriétaires forestiers

Nom de la ou des parcelles qui se trouvent sur votre propriété (voir la fiche descriptive) : ______________________

### 1. Coupes forestières et travaux forestiers

❖ À votre connaissance, y a-t-il déjà eu, récemment ou dans le passé, des coupes forestières ou d'autres types de travaux forestiers dans la forêt où se trouve mon site d'échantillonnage?

OUI _____ NON_____ JE NE SAIS PAS_____

- Si oui, pouvez-vous me fournir de l'information sur le type de coupes ou de travaux qui ont été réalisés (ex. coupes de bois de chauffage, coupes totales, coupes partielles, éclaircies, plantations, coupes d'assainissement d'érablière, quelles espèces auraient été coupées, etc.)?

  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________

- En quelle(s) année(s) a été réalisé chaque type de travaux ou de coupes mentionnés ci-dessus?

  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________

- Quelle est la taille approximative des zones affectées par chaque type de travaux ou de coupes mentionnés ci-dessus? Au besoin, vous pouvez tracer, sur la carte, les zones ayant fait l'objet de coupes ou de travaux forestiers.

  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________
  ______________________________________________________________________

### 2. Plan d'aménagement forestier

❖ Avez-vous un plan d'aménagement forestier pour le secteur où se trouve mon site d'échantillonnage?

OUI_____ NON_____

- Si oui, souhaitez-vous partager les informations contenues dans votre plan d'aménagement forestier concernant les travaux réalisés à l'emplacement de mon site d'échantillonnage?

  OUI_____ NON_____

  - Si oui, quel moyen souhaitez-vous utiliser pour partager l'information de votre plan d'aménagement forestier avec moi? Prenez note que mes coordonnées se trouvent à la fin du sondage au bas de la page.

    - Courriel_____ - Télécopieur (fax)_____ - Poste_____

    - Autre (précisez quel autre moyen vous souhaitez utiliser)______________________________

## 3. Activités agricoles

- À votre connaissance, y a-t-il en ce moment ou y a-t-il déjà eu dans le passé des activités agricoles à l'endroit où se trouve mon site d'échantillonnage (ex. pâturage d'animaux en sous-bois, présence de cultures annuelles ou de pâturages avant de laisser la forêt repousser, etc.)?

  OUI_____ NON_____ JE NE SAIS PAS_____

  - Si oui, pouvez-vous m'informer à propos de ces activités (types d'activités, année(s), superficie, etc.)?

    ______________________________
    ______________________________
    ______________________________
    ______________________________
    ______________________________

## 4. Autres usages de votre forêt

- À votre connaissance, y a-t-il en ce moment ou y a-t-il déjà eu dans le passé des usages autres que des travaux forestiers ou des activités agricoles dans la forêt où se trouve mon site d'échantillonnage?

  OUI_____ NON_____ JE NE SAIS PAS_____

  - Si oui, pouvez-vous m'expliquer quels sont ces usages et en quelle(s) année(s) ont-ils été faits?

    ______________________________
    ______________________________
    ______________________________
    ______________________________

## 5. Collaboration future

- Seriez-vous intéressé(e) à poursuivre votre collaboration avec moi ou avec d'autres membres de mon équipe de recherche au cours des prochaines années, de manière à ce que nous puissions continuer d'étudier les impacts des changements climatiques et d'autres facteurs de stress sur les forêts privées du sud du Québec?

  OUI_____ NON_____

  - Si oui, souhaitez-vous me fournir votre adresse courriel pour que nous puissions entrer en contact avec vous plus facilement dans le futur? Prenez note que cette information sera traitée de manière confidentielle et ne sera pas divulguée à d'autres personnes.

    ______________________________

## 6. Autres commentaires?

______________________________
______________________________
______________________________
______________________________

**Merci d'avoir pris le temps de répondre à ce sondage et de me le retourner avant le 20 mai 2016!**

**Mes coordonnées**
Caroline Gagné, biol. M.Sc., candidate au doctorat en biologie
Université du Québec à Montréal et Université du Québec en Outaouais – Institut des sciences de la forêt tempérée

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Adresse postale : [redacted]
Télécopieur (fax) : [redacted]

Annex D. Original set of explanatory variables for shrub and tree analyses.

| Explanatory variable | | | Variable transformation | Shrub (S) or Tree (T) analysis |
|---|---|---|---|---|
| Factor | Spatial scale | Temporal scale[a] | | |
| **Local and stand variables** | | | | |
| % of canopy closure 0.5m above ground | 30m | P4 | | S |
| % of canopy closure 1.5m above ground | 30m | P4 | | S |
| % of ground covered by coniferous litter | 30m | P4 | | S |
| % of ground covered by deciduous litter | 30m | P4 | | S |
| % of ground covered by herbaceous plants | 30m | P4 | | S |
| % of ground covered by rocks | 30m | P4 | logit | S |
| % of ground covered by woody debris | 30m | P4 | logit | S |
| Soil pH | 30m | Long lasting | | S, T |
| Soil texture | 30m | Long lasting | | S, T |
| Tree diversity (Effective number of species) | 30m | P4 | | S |
| Tree sapling density (nb./$m^2$) | 30m | P4 | 2 root | S |
| Tree sapling diversity (Effective number of species) | 30m | P4 | | S |
| Tree seedling density (nb./$m^2$) | 30m | P4 | ln | S |
| Tree seedling diversity (Effective number of species) | 30m | P4 | | S |
| Tree total basal area ($m^2$/ha) | 30m | P4 | | S |
| Successional stage | 60m | P4 | | S |
| Agriculture area ($m^2$) | 60m | P1 | 3 root | S, T |
| Agriculture area ($m^2$) | 60m | P2 | 3 root | S, T |
| Agriculture area ($m^2$) | 60m | P3 | 3 root | S, T |
| Closed forest area ($m^2$) | 60m | P1 | | S, T |
| Closed forest area ($m^2$) | 60m | P2 | | S, T |
| Closed forest area ($m^2$) | 60m | P3 | | S, T |
| Closed forest area ($m^2$) | 60m | P4 | power 3 | S, T |
| Maple syrup production (Yes/No) | 60m | All | | S, T |
| Open forest area ($m^2$) | 60m | P3 | | S |
| Partial forest disturbance area ($m^2$) | 60m | A4 | | S, T |
| Pasture area ($m^2$) | 60m | P1 | | S, T |
| Pasture area ($m^2$) | 60m | P2 | 3 root | S, T |
| Regeneration area ($m^2$) | 60m | P1 | | S, T |
| Regeneration area ($m^2$) | 60m | P2 | | S, T |
| **Landscape composition and disturbance variables** | | | | |
| Abandoned agric. field area ($m^2$) | 2km | P3 | | S, T |
| Abandoned agric. field area ($m^2$) | 600m | P3 | | S, T |
| Agriculture area ($m^2$) | 2km | P1 | | S, T |
| Agriculture area ($m^2$) | 2km | P2 | | S, T |
| Agriculture area ($m^2$) | 2km | P3 | | S, T |
| Agriculture area ($m^2$) | 2km | P4 | | S, T |
| Agriculture area ($m^2$) | 600m | P1 | | S, T |
| Agriculture area ($m^2$) | 600m | P2 | | S, T |
| Agriculture area ($m^2$) | 600m | P3 | | S, T |
| Agriculture area ($m^2$) | 600m | P4 | | S, T |
| Closed forest area ($m^2$) | 2km | P1 | | S, T |
| Closed forest area ($m^2$) | 2km | P2 | | S, T |
| Closed forest area ($m^2$) | 2km | P3 | | S, T |
| Closed forest area ($m^2$) | 2km | P4 | | S, T |
| Closed forest area ($m^2$) | 600m | P1 | | S, T |
| Closed forest area ($m^2$) | 600m | P2 | | S, T |
| Closed forest area ($m^2$) | 600m | P3 | | S, T |
| Closed forest area ($m^2$) | 600m | P4 | | S, T |
| Open forest area ($m^2$) | 2km | P1 | | S, T |
| Open forest area ($m^2$) | 2km | P2 | | S, T |

| **Explanatory variable** | | | **Variable transformation** | **Shrub (S) or Tree (T) analysis** |
|---|---|---|---|---|
| **Factor** | **Spatial scale** | **Temporal scale[a]** | | |
| Open forest area (m$^2$) | 2km | P3 | | S, T |
| Open forest area (m$^2$) | 2km | P4 | | S, T |
| Open forest area (m$^2$) | 600m | P1 | | S, T |
| Open forest area (m$^2$) | 600m | P2 | 3 root | S, T |
| Open forest area (m$^2$) | 600m | P3 | | S, T |
| Open forest area (m$^2$) | 600m | P4 | | S, T |
| Partial forest disturbance area (m$^2$) | 2km | A1 | 3 root | S, T |
| Partial forest disturbance area (m$^2$) | 2km | A2 | 3 root | S, T |
| Partial forest disturbance area (m$^2$) | 2km | A3 | | S, T |
| Partial forest disturbance area (m$^2$) | 2km | A4 | | S, T |
| Partial forest disturbance area (m$^2$) | 600m | A2 | | S, T |
| Partial forest disturbance area (m$^2$) | 600m | A4 | | S, T |
| Pasture area (m$^2$) | 2km | P1 | | S, T |
| Pasture area (m$^2$) | 2km | P2 | | S, T |
| Pasture area (m$^2$) | 2km | P4 | | S, T |
| Pasture area (m$^2$) | 600m | P1 | | S, T |
| Pasture area (m$^2$) | 600m | P2 | | S, T |
| Pasture area (m$^2$) | 600m | P4 | | S, T |
| Regeneration area (m$^2$) | 2km | P1 | 3 root | S, T |
| Regeneration area (m$^2$) | 2km | P2 | | S, T |
| Regeneration area (m$^2$) | 2km | P3 | 3 root | S, T |
| Regeneration area (m$^2$) | 2km | P4 | | S, T |
| Regeneration area (m$^2$) | 600m | P1 | | S, T |
| Regeneration area (m$^2$) | 600m | P2 | | S, T |
| Regeneration area (m$^2$) | 600m | P3 | 3 root | S, T |
| Regeneration area (m$^2$) | 600m | P4 | | S, T |
| Severe forest disturbance area (m$^2$) | 2km | A1 | 3 root | S, T |
| Severe forest disturbance area (m$^2$) | 2km | A2 | | S, T |
| Severe forest disturbance area (m$^2$) | 2km | A3 | 3 root | S, T |
| Severe forest disturbance area (m$^2$) | 2km | A4 | | S, T |
| Severe forest disturbance area (m$^2$) | 600m | A1 | | S, T |
| Severe forest disturbance area (m$^2$) | 600m | A2 | | S, T |
| Severe forest disturbance area (m$^2$) | 600m | A3 | 3 root (shrubs), NT[b] (trees) | S, T |
| Severe forest disturbance area (m$^2$) | 600m | A4 | | S, T |
| Sparse forest area (m$^2$) | 2km | P1 | | S, T |
| Sparse forest area (m$^2$) | 2km | P2 | | S, T |
| Sparse forest area (m$^2$) | 2km | P4 | | S, T |
| Sparse forest area (m$^2$) | 600m | P1 | 3 root | S, T |
| Sparse forest area (m$^2$) | 600m | P2 | 3 root | S, T |
| Sparse forest area (m$^2$) | 600m | P4 | | S, T |
| Total % of partial forest disturbance | 2km | All | | S, T |
| Total % of severe forest disturbance | 2km | All | | S, T |
| Urban area (m$^2$) | 2km | P3 | 3 root | S, T |
| Urban area (m$^2$) | 2km | P4 | 3 root | S, T |
| Urban area (m$^2$) | 600m | P4 | 3 root | S, T |
| **Landscape configuration and connectivity variables** | | | | |
| Distance to nearest forest disturbance (m) | All | A1 | | S, T |
| Distance to nearest forest disturbance (m) | All | A2 | | S, T |
| Distance to nearest forest disturbance (m) | All | A3 | | S, T |
| Distance to nearest forest disturbance (m) | All | A4 | 3 root | S, T |
| Distance to nearest forest edge (m) | All | P1 | | S, T |
| Distance to nearest forest edge (m) | All | P2 | 3 root | S, T |
| Distance to nearest forest edge (m) | All | P3 | 3 root | S, T |
| Distance to nearest forest edge (m) | All | P4 | | S, T |
| Distance to nearest pasture (m) | All | P1 | 3 root | S, T |

| Explanatory variable |  |  | Variable transformation | Shrub (S) or Tree (T) analysis |
|---|---|---|---|---|
| Factor | Spatial scale | Temporal scale[a] |  |  |
| Distance to nearest pasture (m) | All | P2 | 3 root | S, T |
| Distance to nearest pasture (m) | All | P3 | 3 root | S, T |
| Distance to nearest pasture (m) | All | P4 |  | S, T |
| Length of forest edge (m) | 2km | P1 |  | S, T |
| Length of forest edge (m) | 2km | P2 |  | S, T |
| Length of forest edge (m) | 2km | P3 |  | S, T |
| Length of forest edge (m) | 2km | P4 |  | S, T |
| Length of roads (m) | 2km | P1 |  | S, T |
| Length of roads (m) | 2km | P2 |  | S, T |
| Length of roads (m) | 2km | P3 |  | S, T |
| Length of roads (m) | 2km | P4 | 3 root | S, T |
| Mean distance to forest disturbances (m) | All | A1 |  | S, T |
| Mean distance to forest disturbances (m) | All | A2 |  | S, T |
| Mean distance to forest disturbances (m) | All | A3 |  | S, T |
| Mean distance to forest disturbances (m) | All | A4 |  | S, T |
| Probability of connectivity | 2km | P1 | 3 root | S, T |
| Probability of connectivity | 2km | P2 | 3 root | S, T |
| Probability of connectivity | 2km | P3 |  | S, T |
| Probability of connectivity | 2km | P4 |  | S, T |

[a] Temporal scale = P1 (1930-40), P2 (1958), P3 (1983), P4 (2015), A1 (before 1930-40), A2 (between 1930-40 and 1958), A3 (between 1958 and 1983), A4 (between 1983 and 2015).

[b] NT = no transformation.

# CHAPITRE II

# EROSION OF RESPONSE DIVERSITY AND RESPONSE TRAIT FILTERING IN TREE COMMUNITIES LOCATED WITHIN HIGHLY DISTURBED LANDSCAPES

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## 2.1 Abstract

Land-use intensification over time and the resulting fragmentation of forest landscapes can play a preponderant role in determining the functional composition and structure of forest communities by altering the distribution of species based on their response traits. In this study, that was conducted in southern Quebec, Canada, we investigate whether present-day tree communities are linked to past stand and landscape conditions through their functional trait patterns. We also investigate whether more disturbed landscape trajectories over time can lead to an erosion of response diversity and a filtering of response traits in present-day local forest communities. We sampled 64 sites to assess the current tree abundance and current local explanatory variables at the sampling site scale (about 30 m radius). We also gathered information about functional response traits from the literature and trait databases and computed functional diversity indexes and the community weighted mean for each site. Aerial photographic image interpretation and analyses of forest maps were conducted to assess stand (60 m) and landscape (600 m and 2 km) historical explanatory variables for 5 time periods (1907, 1930-40, 1958, 1983 and 2015). We then identified two combinations of landscape trajectories, each combination comparing more disturbed landscapes with less disturbed landscapes over the past 85 years. We showed that forest tree communities located in fragmented landscapes carry an ecological memory in their functional structure that is related to stand and landscape conditions that date back to the years 1930-40 and 1958, but that more recent past and present-day conditions are also important. We also showed that landscape disturbance history acted as an important trait filter: more intensively disturbed landscapes showed a functional erosion of response diversity and a response trait filtering favouring species with high dispersal ability. Since response diversity is assumed to be closely related to ecosystem and community resilience, those communities located in highly disturbed landscapes over time might then have an impaired ability to adapt in the face of global change threats. Our results support the view of a need for forest restoration emphasizing an increase in response diversity to enhance forest resilience to stressors related to global changes.

Keywords: response traits, response diversity, tree communities, dispersal ability, landscape legacies, landscape disturbances, fragmentation.

## 2.2 Introduction

Response traits play an important role in determining the way species respond to disturbances and environmental changes (Garnier & Navas, 2013; Lavorel & Garnier, 2002; Naeem & Wright, 2003; Suding et al., 2008; Suding & Hobbs, 2009). They contribute to species resistance or avoidance of disturbances by providing individuals with the ability to defend themselves and survive stressful events that may reduce their biomass (Grimm & Wissel, 1997; Millar et al., 2007). For example, resistance and avoidance can occur through response traits such as wood density and rooting depth (Aubin et al., 2016) and allow individuals to survive in drought- and wind-prone habitats. Response traits also contribute to community resilience, defined as the ability of a system to recover following a stress or a disturbance and maintain the same functions, identity, and structure (Walker et al., 2004). Community resilience occurs through the species' ability to regenerate after a disturbance due to several response traits linked to plant functions such as seed production, seed dispersal, and vegetative reproduction (Larson & Funk, 2016; Suding et al., 2008). In this way, seed dispersal and vegetative reproduction traits are recognized as key to long-term population and community persistence, especially in fragmented landscapes. Seed dispersal enables population spread and benefits species recruitment through the possibility of reaching suitable germination sites and improving seed quality over the dispersal process (Ozinga et al., 2004, 2009; Rogers et al., 2021; Tackenberg et al., 2003), whereas vegetative reproduction allows species to persist over time in remnant populations and hence buffer against unfavourable periods (Eriksson, 1996; Ozinga et al., 2007).

Global changes, such as land-use intensification, can alter species distribution within a landscape based on their functional response traits (Grime, 2006). For instance, it has been shown that species with water- and fur-assisted seed dispersal were over-represented among declining species in Northwestern Europe, while species with wind- or bird-assisted seed dispersal were under-represented (Ozinga et al., 2009). On the other hand, Montoya (2008) showed that wind-dispersed species were more vulnerable to habitat loss than animal-dispersed species, provided that animal dispersers were able to persist in the fragmented landscape. Hence, highly disturbed landscapes could lead to a narrowing of dispersal strategies in plants and trigger a spatial sorting of species, advantaging those that disperse their seeds over greater distances (Dener et al., 2021). Global changes can also affect communities' functional response diversity which is the variability of responses to disturbances or stresses among species (Elmqvist et al., 2003; Suding & Hobbs, 2009; Walker, 1995). In their meta-analysis, Laliberté et al. (2010) showed that response diversity decreased with land-use intensification. For their part, Craven et al. (2016) noted that response diversity was positively correlated to functional connectivity in a highly fragmented temperate forest, implying that fragmentation may have a negative impact on response diversity. In addition, de Frutos et al. (2015) showed that in a semi-arid Mediterranean ecosystem, woody plant response diversity was negatively related to fragmentation but that response diversity of other life forms (erect annual forbs, short basal annual or perennial forbs, and grasses) was positively related to fragmentation. Pakeman (2011) noted that functional richness was reduced when disturbances increased in a diverse landscape in Scotland, but Sonnier et al. (2014) demonstrated that despite land-use intensification, functional diversity did not decrease over time because of a high level of community functional redundancy. Although in the latter two studies, functional diversity was computed with a mixture of response and effect traits, all these studies reveal that global change impacts on response diversity can vary greatly according to different factors, such as the traits and species that are considered as well as the type and severity of disturbances under investigation, thus indicating that these effects appear to be strongly context dependent.

The present study was conducted in southern Quebec, where the development of agriculture in the 1820s marked the onset of landscape transformation (Brisson & Bouchard, 2006; Domon & Bouchard, 2007). In this region, agricultural areas were at their peak around the 1890s, before starting to decline in the 1950s (Domon & Bouchard, 2007). This agricultural decline, that occurred in our study area as well as all over the world (Cramer et al., 2008; Jaworek-Jakubska et al., 2020; Lasanta et al., 2017; Tasser et al., 2007), led to major changes in landscape structure as agricultural activities intensified and forests regenerated on less productive sites. In this context, several studies have explored the impact of landscape structure at different points in time on present-day local vegetation patterns (Kolk & Naaf, 2015; Krauss et al., 2010; Lecoq et al., 2021; Lindborg, 2007; Lindborg & Eriksson, 2004; Paltto et al., 2006; van Ruremonde & Kalkhoven, 1991). However, very few studies have integrated land cover over several periods into overall landscape trajectories to investigate the relationship between temporal landscape changes and present-day biodiversity patterns in local forest stands (Davis et al., 2017).

In our study, the first goal is to determine whether present-day tree communities are linked to past stand and landscape conditions through their functional trait patterns (tree functional response diversity and response trait values). Based on the results in Gagné, Doyon et al. (2022), we hypothesize that stand and landscape conditions pertaining to the years 1930-40 and 1958 are important in explaining the current response diversity and response trait values in local tree communities, hence showing that tree communities carry internal and external ecological memories due to the persistence of legacies from the past. Ecological memory can refer to the capacity of past events or states to influence present or future community responses (Padisak, 1992; Peterson, 2002). Nonetheless, the ecological memory through functional trait patterns could be reset by more recent or present-day disturbances or habitat conditions.

The second goal is to determine whether more disturbed landscape trajectories over time can lead to an erosion of response diversity and a filtering of response traits in present-day local forest communities. Disturbed trajectories imply an alteration of landscape legacies over time due to extensive areas of open lands (e.g., agriculture, abandoned agricultural fields, pasture and shrub dominated regeneration areas) that may have decreased the availability of propagules and impeded their dispersal across the landscape. We hypothesize that highly disturbed landscape trajectories resulted in a lower response diversity and filtered species according to their response traits in local tree communities, fostering those species that reproduced mostly by seeds, had wind-dispersed seeds, and were able to disperse their seeds over greater distances to colonize distant sites. Conversely, we hypothesize that less disturbed landscape trajectory (with a greater forest area over time) resulted in a higher response diversity and fostered species reproducing vegetatively and having mammal- and bird-dispersed seeds, several bird and mammal species being sensitive to forest fragmentation and often avoiding open habitats.

## 2.3 Study area

The study area is located in the Montérégie region in southern Quebec, Canada, and covers about 983 km$^2$ (98 259 ha). It is located between 45.0 and 45.5° north, and between -74.4 and -73.8° west (Figure 2.1). The mean annual temperature ranges from 5.6 to 7.4°C and the mean total annual precipitation ranges from 896 to 1120 mm. The topography is mostly flat with a maximum elevation of 40 m, except for the Rigaud (220 m) and Covey hills (343 m). The bedrock is mostly composed of dolomite and sandstone with some areas composed of limestone or granite. Surface deposits vary across the study area and are composed of marine, moraine, sand, gravel, and glacial till. Forest stands of this region are part of the sugar maple and bitternut hickory bioclimatic zone (Robitaille & Saucier, 1998) and are dominated by a variety of species, according to their successional stages, such as sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), white ash (*Fraxinus americana*), American basswood (*Tilia americana*), eastern white cedar (*Thuja occidentalis*), grey birch (*Betula populifolia*), and large-tooth aspen (*Populus grandidentata*). In this region, agricultural areas were at their peak around the 1890s, before starting to decline in the 1950s (Domon & Bouchard, 2007). The present-day forest of this region covers about 26-36% of the territory and is highly fragmented and scattered within an agricultural matrix with few large forest remnants such as those located on the Rigaud hill (> 5 000 ha) and around the Covey hill close to the Canada-United States border (> 10 000 ha). Within the 2 km-buffer zones that we have studied, forest cover generally increased over time between 1930-40 and 2015 (Figure 2.2), and the present-day forest cover varies from less than 5% to more than 80% (Annex A).

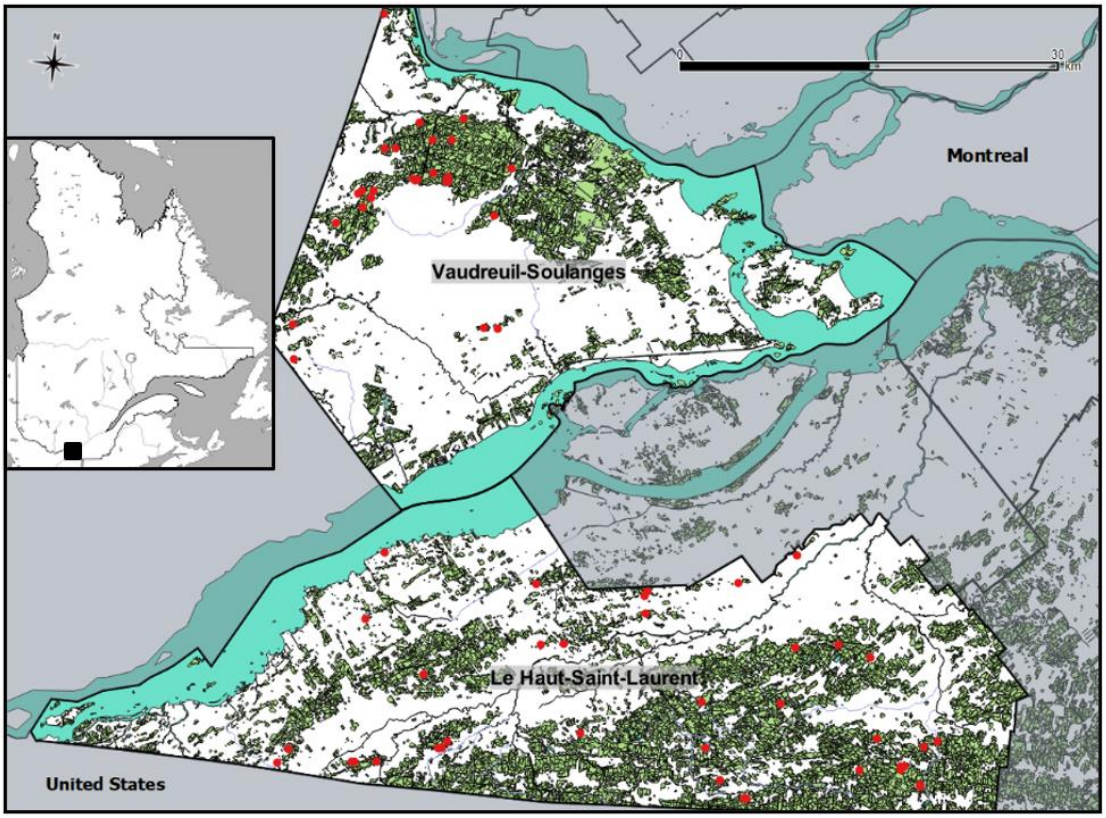


Figure 2.1. The study area and sampling sites (red dots) located in the regional county municipalities of Vaudreuil-Soulanges and Le Haut-Saint-Laurent, Quebec, Canada. Forests are represented by green patches.

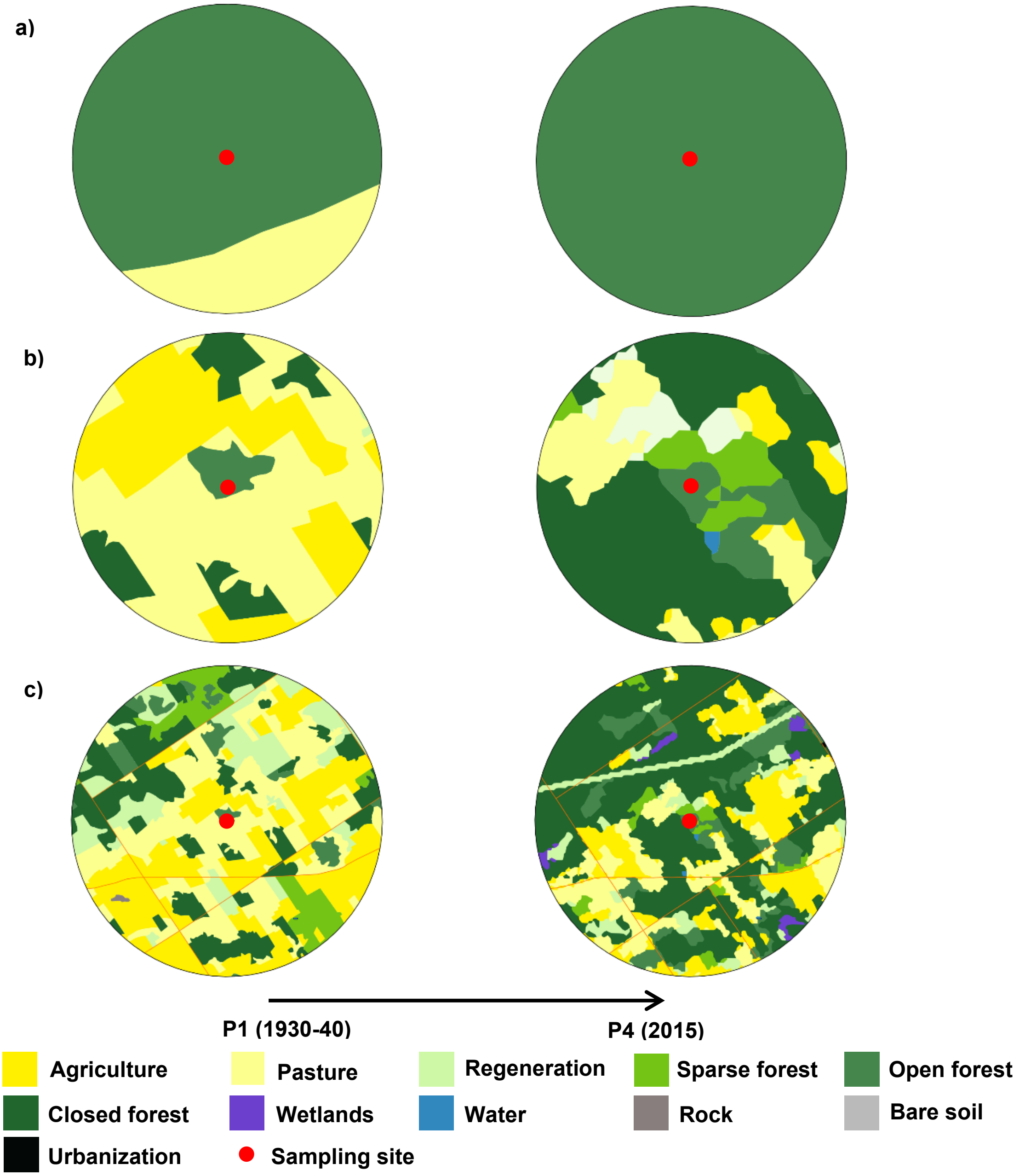


Figure 2.2. Evolution of forested areas between 1930-40 (P1) and 2015 (P4) for one of our 64 sampling sites within the 60 m-buffer zone (a), 600 m-buffer zone (b) and 2 km-buffer zone (c).

## 2.4 Methodology

Three data sources were collected for this study. First, field sampling of forest communities in the study area was done to assess the current tree abundance and biophysical variables at the local scale (30 m radius) in 64 sampling sites. Second, we gathered information about functional response traits from the literature and trait databases and computed functional diversity indexes and the community weighted mean (CWM) for each of our sites by combining species abundances and information on traits. Third, old aerial photograph interpretation and analyses of old and recent forest maps were carried out to assess stand and landscape historical explanatory variables. We investigated three spatial scales (60 m, 600 m, and 2 km radii), five periods in time, and the intervening years between each of these periods. The 60 m buffer represents the stand scale at which short-distance seed dispersal and local disturbances occur. The 600 m and 2 km buffers represent the landscape scale and encompass different scales of influence of ecosystem processes, such as long-distance seed dispersal. The use of multi-scale nested buffer zones allows us to assess the amount of habitat and other landscape characteristics in local landscapes, as recommended in Fahrig (2013) when the appropriate scale is unknown. The five periods are as follows: P0 – initial stand conditions (1907), P1 – distant past (1930-40), P2 – intermediate past (1958), P3 – recent past (1983), and P4 – current time (2015). The intervening years are as follows: A1 – distant past (before 1930-40), A2 – intermediate past (between 1930-40 and 1958), A3 – recent past (between 1958 and 1983), and A4 – very recent past (between 1983 and 2015). The choice of the five time periods was dependent on data availability, and periods about 15 to 30 years apart allowed us to witness land-use changes and forest evolution. Land use was assessed for the five time periods, whereas forest disturbances were associated with the intervening years.

### 2.4.1 Site selection

During the spring and summer 2015, 64 sites were established within mature forest patches to sample tree communities. Using ecoforestry maps (Ministère des Ressources naturelles et de la Faune [MRNF], 2009), sites having homogeneous pedological and topographic characteristics, as well as representing a diversity of historical forest disturbances and land use such as clearcutting, agriculture, and pasture, were chosen. Site selection was based on recent ecoforestry maps (MRNF, 2009), on-site physical evidence of past use (presence of recent or old cut stumps, fences, sugar shacks or signs of maple syrup production), and discussions with private landowners. Tree communities in the sampling sites had various profiles, ranging from early to late-successional assemblages.

### 2.4.2 Response variables

#### 2.4.2.1 Tree sampling

From the centre of each sampling site, trees were sampled using the prism sweep technique using a factor 1 prism. All trees with a diameter at breast height (DBH) greater than 9.1 cm were accounted for during the prism sweep and tree species were identified. The basal area was obtained by summing the number of stems that were included in the sampling site during the sweep (i.e., stems whose images saw through the prism were within the real stems), and then multiplying the number of stems by the prism factor (one in this case). A total of 27 tree species were present in the sampling sites (Table 2.1). The basal area was calculated for each tree species. Relative abundance was computed for each species based on its relative basal area in each sampling site.

#### 2.4.2.2 Selection of functional traits

Following tree sampling, a total of 17 functional response traits (Table 2.2) were selected to represent five different functions related to the life cycle of trees, and particularly to the reproductive cycle (four out of five functions). These functions are as follows: 1) reproduction, 2) seed production, 3) seed dispersal, 4) seed germination and emergence, and 5) plant protection. All selected traits are involved in avoidance, resistance or resilience of a species to different stresses or disturbances anticipated in the study area in the context of global changes, such as drought, windstorms, browsing by the white-tailed deer (*Odocoileus virginianus*), forest fragmentation, or an increase in disturbance frequency.

A review of the literature and trait databases was completed to obtain trait values for each species present in our sampling sites. The following trait databases were consulted: Traits of plants in Canada (TOPIC; Aubin et al., 2012), Fire effects information system (FEIS; Abrahamson, 2017), PLANTS database (U.S. Department of Agriculture & National Resources Conservation Service, 2017), Seed information database (SID; Royal Botanic Gardens Kew, 2017), Dispersal diaspore database (D$^3$; Hintze et al., 2013), Dryad (2017), Global wood density database (Chave et al., 2009; Zanne et al., 2009), and Stem specific density (Burton et al., 2017a, 2017b). When possible, only trait values related to site conditions similar to ours (e.g., soil texture) and to mature individuals were considered. In some cases, traits were reorganized from data found in the literature and databases. This is the case for traits related to root depth; a distinction was made between the bulk of the root system depth and the maximal depth some roots can reach. Concerning the dispersal mode, we combined both mammal endo- and exo-zoochory modes. Finally, maximal seed dispersal distance was computed for species according to their dispersal mode. Bird and mammal dispersal distances were estimated with the R function dispeRsal developed by Tamme et al. (2014), whereas wind dispersal distances were estimated following Greene & Johnson (1996).

The selected traits are quantitative, nominal, or binary multi-choice. For quantitative traits, the value for each species can be represented either by the mean of all relevant values found in literature and databases (age of sexual maturity, age of optimal seed production, seed production, interval of mast years, seed persistence, seed mass, seed viability, and wood density traits) or by the maximum relevant value (maximum plant height and tree lifespan). For some traits, the nominal type was chosen either because of a lack of quantitative information for some species (maximum root depth) or because the only information available was in this format (growth and reproduction). Binary multi-choice traits are nominal traits for which several of their levels (categories) can be true for a particular species and where each level is expressed as an independent binary variable (1/0). This type of variable is useful for representing species that can exhibit more than one trait value for a particular trait and was used here to represent the following traits: root system depth, vegetative reproduction and dispersal mode.

#### 2.4.2.3 Computation of response diversity and community weighted mean

Response diversity is represented by the functional dispersion index (FDis; Laliberté & Legendre, 2010) and was computed on all tree species in each sampling site. A global FDis index from all response traits, and two FDis indexes from plant reproduction and seed dispersal traits were computed (Table 2.2). Among traits, all but one belong to a single group. Seed mass is the exception since it is involved in seed production, dispersal and germination-emergence. The FD package (Laliberté et al., 2014; Laliberté & Legendre, 2010) in R (R Core Team, 2018) was used to compute FDis. We used the approach presented in Pavoine et al. (2009) to tackle binary multi-choice traits in the construction of the species-by-species distance matrix from functional traits, using the R package ade4 (Bougeard & Dray, 2018; Chessel et al., 2004; Dray et al., 2007; Dray & Dufour, 2007; Thioulouse et al., 2018).

The community weighted mean (CWM; Garnier et al., 2004) of each sampling site was then calculated for the nine response traits related to seed dispersal or plant reproduction. For quantitative traits, the CWM was obtained by multiplying the relative abundance of each species present in a community ($p_i$) by its respective trait value ($trait_i$) and then by summing all these $p_i$ x $trait_i$ values. For nominal and binary multi-choice traits, the CWM represents the relative abundance ($p_i$) of all species possessing each level of a particular trait. Each level of a trait is then represented as a trait in itself. The package FD (Laliberté et al., 2014; Laliberté & Legendre, 2010) in R (R Core Team, 2018) was used to compute the community weighted mean.

### 2.4.3 Local-scale explanatory variables

To characterize local soil conditions, two soil samples of the A horizon (Soil Classification Working Group, 1998) were randomly collected within a 30 m radius for each sampling site. The soil pH was measured with a digital pH meter, and the soil texture was assessed with a tactile method (Méthot et al., 2014) and classified using the Canadian system of soil classification (Soil Classification Working Group, 1998).

### 2.4.4 Explanatory variables based on historical land use and forest disturbances

#### 2.4.4.1 Classification and assessment of historical land use and forest disturbances

Land use included abandoned agricultural field, agriculture, closed forest (forest cover ≥ 60%), open forest (forest cover ≥ 25% and <60%), pasture, regeneration, sparse forest (forest cover <25%), and urbanization. Forest disturbances were divided between severe and partial disturbances where the former includes mainly forest clearcutting, while the latter includes primarily partial logging and ice storms. Forest disturbances were indicated on recent ecoforestry maps, while they were photointerpreted on older aerial photos based on the canopy opening (most trees were removed after a clear-cut, while we could detect a residual forest cover after a partial harvesting). Maple syrup production over the years is also a type of partial forest disturbance at the stand scale but was considered separately since it is a binary variable (presence/absence) for which the exact area and period were not possible to assess.

In this study, all land-use classes are related to habitat composition at the stand or landscape scale, and all but one are also related to disturbances. For example, agricultural and regeneration areas are both the result of a severe disturbance that removed all trees from a particular site, while open forests are instead associated with partial disturbances. Areas in regeneration could be the result of either a clearcut or a slow forest recovery following agricultural abandonment, while open forests could result from partial logging or from natural disturbances, such as ice storms. Closed forest is the only land-use class associated with undisturbed habitat. Moreover, landscape fragmentation in this study is a result of landscape disturbances and does not reflect natural geographical barriers.

The assessment of historical land use and forest disturbances was done through data integration from multiple sources. First, the state of the 1907 forest stands (forested vs. non-forested) was extracted from four georeferenced historical topographical maps (Department of Militia and Defence, 1909) with QGIS (QGIS Development Team, 2016).

Second, photointerpretation of 185 historical aerial photographs was conducted with a mirror stereoscope for the years 1930-40 and 1958. To achieve this, acetates were superimposed on the aerial photographs to reproduce land-use classes and forest disturbances in at least a 2 km buffer around each of the 64 sampling sites (Annex B). Drawn acetates were then scanned, georeferenced with Global Mapper (Blue Marble Geographics, 2016), and vectorized with QGIS (QGIS Development Team, 2016) to create new shapefiles. We validated the photointerpretation results during field sampling of the 64 sites and with a postal survey intended for the 52 landowners where our sampling sites were located that invited them to share their knowledge about past and current land use (Annex C). Among others, we were interested in gathering information about past logging activities. About 40% of the landowners, 21 in total, responded to the survey. This information confirmed the adequacy of the photointerpretation.

Third, georeferenced ecoforestry maps of the second forest inventory, using aerial photographs from the year 1983 (Ministère de l’Énergie et des Ressources [MER], 1984), were used to extract relevant information related to land use and forest disturbances. Since each map was a georeferenced image, it was also necessary to vectorize them to obtain new shapefiles of land use and forest disturbances.

Fourth, data originating from Landsat satellite images (30 m-resolution) that were available in a raster format for the year 2013 (Bissonnette & Lavoie, 2015) were used and converted into a vectorized polygon format with QGIS (QGIS Development Team, 2016). This layer contained information about agricultural lands, urban areas, forest areas, wetlands, and other non-forest land-use classes. In addition, very recent forest disturbances (e.g., partial logging, clearcutting) from an updated version of the 2009 ecoforestry maps (MRNF, 2015) were added to the Landsat layer. Finally, other very recent forest disturbances (in 2015 or slightly before) that occurred close to the sampling sites and that were detected during field work were also added to this layer.

#### 2.4.4.2 Stand and landscape explanatory variables

Most variables represent a combination of three components: 1) a factor related to habitat structure, connectivity or disturbance, 2) a spatial scale (30 m [local scale, field-surveyed], 60 m [stand scale], 600 m or 2 km buffers [landscape scales]), and 3) a temporal scale (one of the five time periods; Annex D). Factors related to stand composition or disturbance include the area of each land-use class and disturbance type within the 60 m radius. The initial stand condition for P0 is a binary variable related to the stand state (forested vs. non-forested) in the early 1900's. A stand was classified as forested if most of its 60 m radius was located within a forest or an open forest and was considered non-forested if most of it was outside a forest patch. Measures of landscape structure and functional connectivity include the area of each land-use class and disturbance type within the 600 m- and 2 km radii, the distance to the nearest forest disturbance, the mean distance to forest disturbances, the distance to the nearest forest edge, the distance to the nearest pasture, the length of forest edges, the length of roads, and the probability of connectivity index (PC; Saura & Pascual-Hortal, 2007). All distance variables were computed from the centre of each sampling site. The PC index was computed based on the grey squirrel's (*Sciurus carolinensis*) dispersal ability in open ground between two habitat patches (less than 500-1000 m; Fitzgibbon, 1993) and on its perceptual range in a fragmented agricultural landscape (about 300 m; Zollner, 2000). Squirrels are good seed dispersal vectors, and the lack of functional connectivity for this species and similar species is likely to impact tree seed dispersal across the landscape.

Some variables were computed at both the stand and landscape scales for the periods P1 to P4 while some others were computed only at the landscape scale (Annex D). For each sampling site, we also computed the slope of the time series showing the PC values for each of the four periods (P1 to P4) and used this slope value as the evolution of the PC index over time in each of the 64 landscapes. By doing this, we tried to consider the temporal aspect of landscape connectivity. All shapefile manipulations and spatial analyses for computing stand- and landscape-scale explanatory variables were conducted with QGIS (QGIS Development Team, 2016) and FME (Safe Software, 2016). The probability of connectivity index was obtained using Conefor (Saura & Torné, 2009).

### 2.5 Statistical analyses

We first used correlation analyses to sort out the numerous explanatory variables and kept only those displaying a higher correlation ($r \geq |0.3|$) with the following response variables: 1) a global functional dispersion index (Global FDis) computed from the 17 response traits, 2) a functional dispersion index computed from seed dispersal response traits (FDis – Seed dispersal), 3) a functional dispersion index computed from plant reproduction response traits (FDis – Reproduction), and 4) nine response traits related either to seed dispersal or plant reproduction.

We then identified the most influential landscape explanatory variables with Elastic-Net multiple linear regressions from the R packages caret and glmnet (Friedman et al., 2010; Kuhn et al., 2021). The Elastic-Net regression is a penalized regression balancing both model complexity and fit. It is not sensitive to a moderate level of collinearity between explanatory variables and is appropriate when the number of explanatory variables is high (Dormann et al., 2013; Zou & Hastie, 2005). Elastic-Net combines the strengths of Lasso and Ridge regressions, the former creating simpler models by selecting only the most meaningful explanatory variables, and the latter keeping all variables while shrinking the coefficients of the less significant variables towards zero (James et al., 2013). The caret package sorts and allows one to visualize the explanatory variables according to their relative importance, which is a scaled measure bounded between 0 and 100 based on the absolute value of the coefficients corresponding to the tuned model. Unlike other regression types, Elastic-Net does not provide information that would indicate that explanatory variables are considered statistically significant (e.g., $p \leq 0.05$).

From the Elastic-Net regression models, we then identified a set of nine variables from which landscape trajectories were subsequently drawn: regeneration area in 1958, regeneration area in 2015, pasture area in 1930-40, pasture area in 1958, abandoned agricultural field area in 1983, distance to the nearest pasture in 1930-40, distance to the nearest pasture in 1958, distance to the nearest pasture in 1983, and closed forest area in 1930-40. These variables were among the most important ones explaining the variations in the response variables.

Two pairs of landscape trajectories were identified and compared: 1) agriculture-pasture-regeneration trajectory (more disturbed) vs. agriculture-forest trajectory (less disturbed) in the 2 km landscape (Figure 2.3), and 2) agriculture trajectory (more disturbed) vs. forest trajectory (less disturbed) in the 600 m landscape (Figure 2.4). The landscapes that were characterized by an agriculture-pasture-regeneration trajectory had a larger area of agriculture, abandoned agricultural field, pasture and regeneration in 1930-40, 1958, 1983 and 2015 (15 sites), which can indicate the past abandonment of agricultural activities on part of the territory. These sites were compared to another subset of 15 sites showing smaller areas of pasture, abandoned agricultural fields and regeneration, but similar area of agriculture for each period. In the other comparison, landscapes that were characterized by a forest trajectory (less disturbed) are those with large areas of forest and small areas of agriculture in 1930-40, 1958, 1983 and 2015 (15 sites). These sites were compared to another subset of 15 sites showing small areas of forest and large areas of agriculture for each period (highly disturbed).

We used conditional inference trees with the package party (Hothorn et al., 2006; Williams, 2011) to compare both pairs of landscape trajectories and determine whether higher or lower response diversity and trait values were associated with particular trajectories. Because of our relatively small sample size, each FDis index and response trait was tested separately. With the conditional inference trees, we try to find any input variable (FDis indexes and response traits) that can be used to split a dataset (30 landscapes in a specific comparison) into two smaller datasets. The aim is to increase the homogeneity of each of the two sub-samples with respect to a specific input variable. The output of the analysis then provides information on the split value, which is the value of the input variable used to create the two most homogenous sub-samples as possible regarding the landscape trajectories. The output also provides a p-value informing us whether a particular input variable can significantly split a sample in two homogeneous sub-samples.

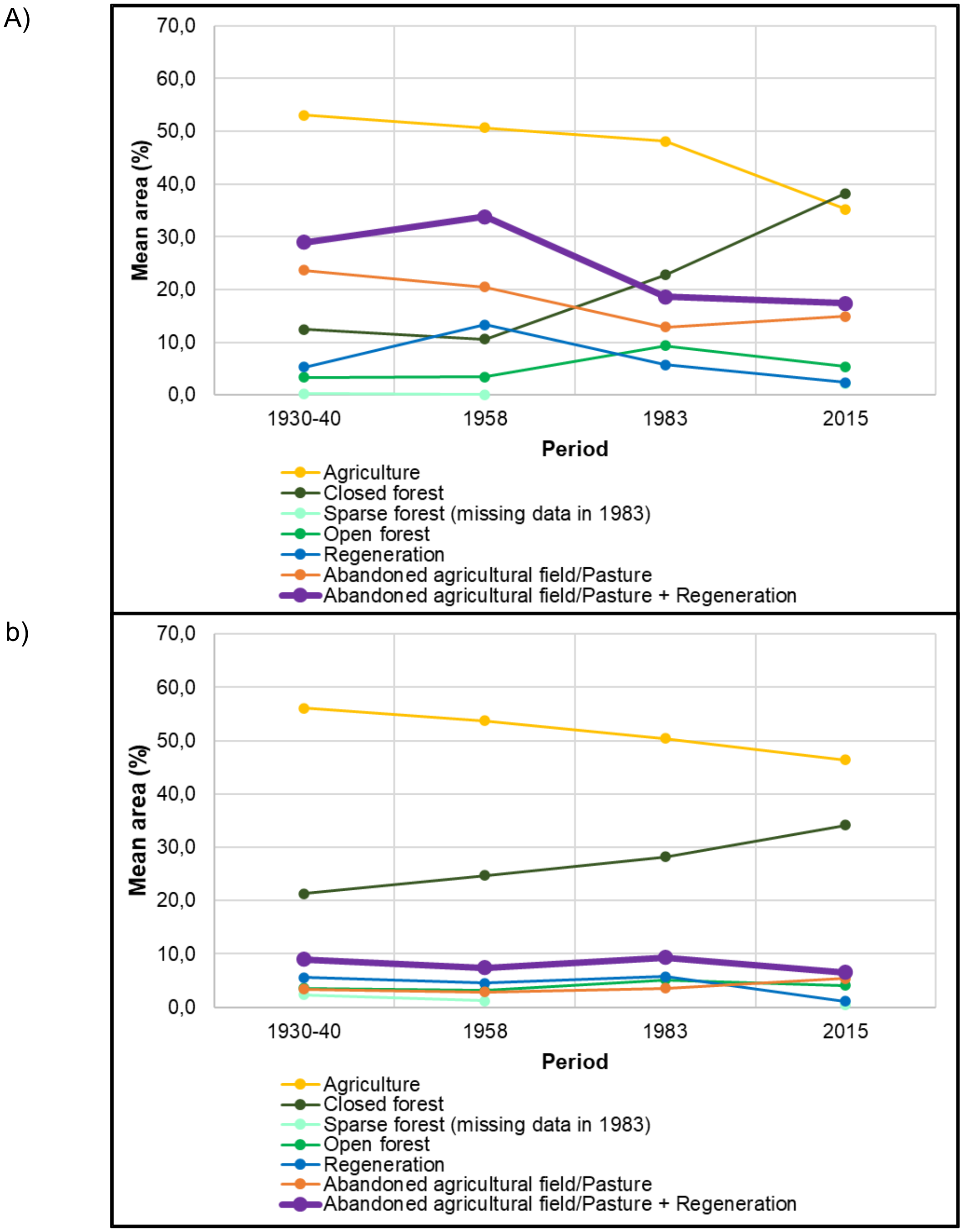


Figure 2.3. Mean area (%) of land-use classes at each period in the agriculture-pasture-regeneration (a) and agriculture-forest (b) landscape trajectories in the 2 km radius (15 sites each). In a), the area of open habitat (agriculture, abandoned agricultural field, pasture and regeneration) is greater than in b) but the amount of forest is similar. The main difference between a) and b) is driven by a change in the area of abandoned agricultural field, pasture, and regeneration (purple) in the landscape.

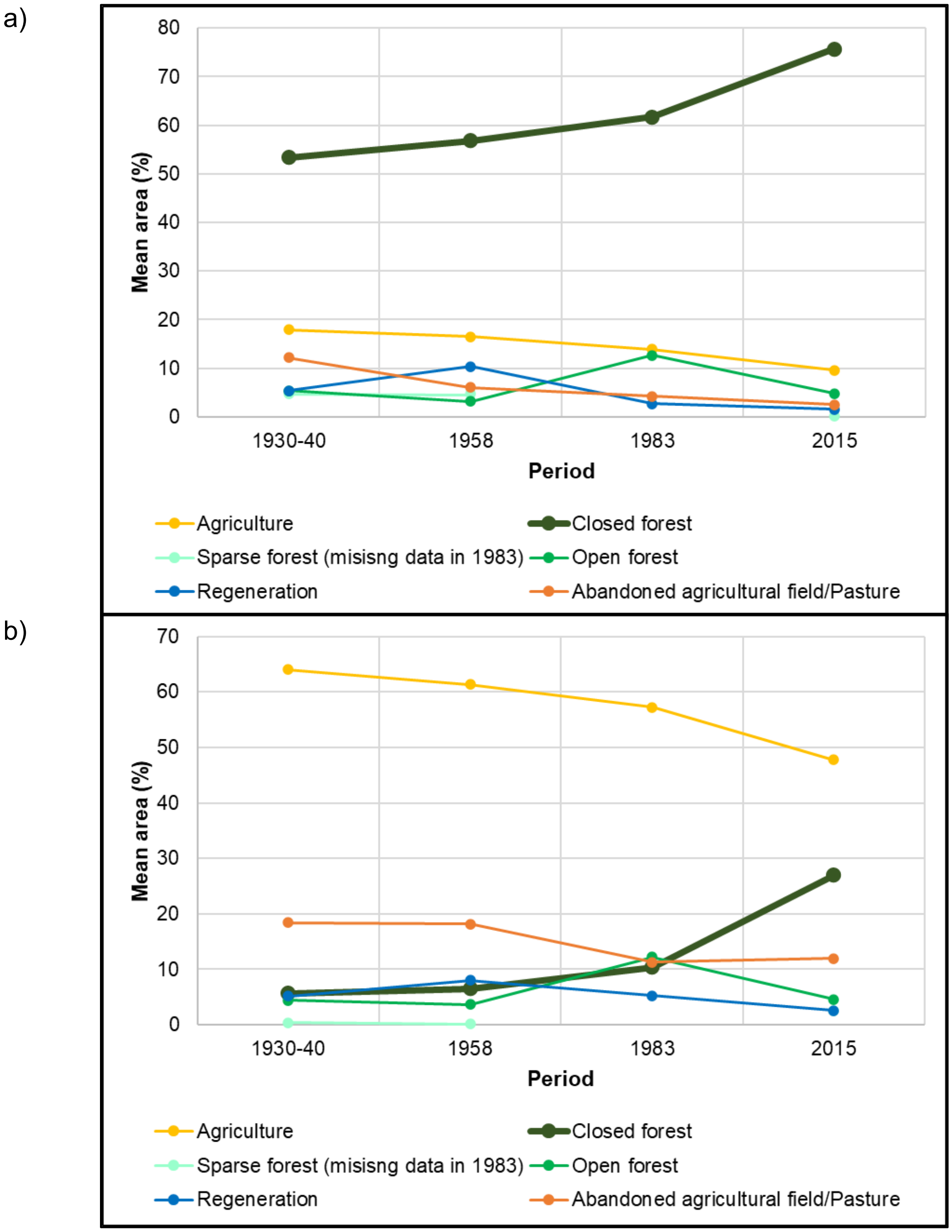


Figure 2.4. Mean area (%) of land-use classes at each period in the forest (a) and agriculture (b) landscape trajectories in the 600 m radius (15 sites each). In a), the area of open habitat (agriculture, abandoned agricultural field, pasture and regeneration) is lower than in b), and the main difference between a) and b) is driven by a change in the area of closed forest (dark green) and agriculture (yellow) in the landscape.

## 2.6 Results

### 2.6.1 Influence of past and current habitat conditions on tree response diversity

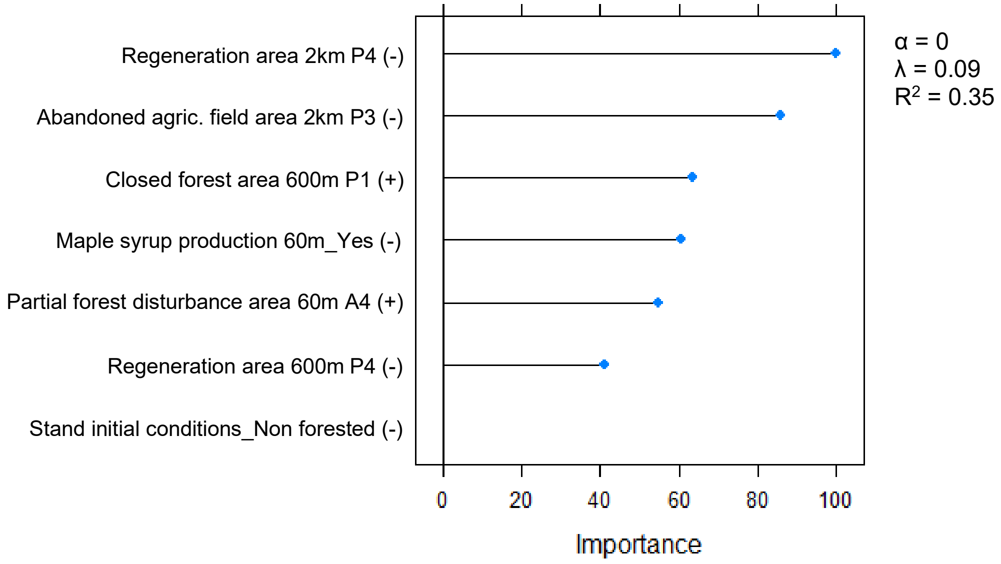
For the three FDis models, the Elastic-Net procedure resulted in a regression that is more closely related to a Ridge regression, with an alpha value of 0, for which all explanatory variables were kept into the models but where the coefficients of the less important ones were shrunk (Figure 2.5). The $R^2$ for the Global FDis, FDis – Seed dispersal and FDis – Reproduction models are 0.35, 0.39 and 0.35, respectively.

Results show that past landscape conditions are important for explaining the variation of the three FDis indexes considered here (Global FDis, FDis – Seed dispersal and FDis – Reproduction) (Figure 2.5). For instance, the area of abandoned agricultural field in the 2 km landscape in 1983 (P3) is either the most important variable or among the most important ones for explaining the variation of the three FDis indexes, and this variable is negatively associated with the three indexes. The area of partial forest disturbances (mostly partial logging) that occurred in the 2 km landscape before 1930-40 (A1; negative relationship) is also among the most important explanatory variables for both FDis – Seed dispersal and FDis – Reproduction. The area of closed forests in the 600 m landscape in 1930-40 (P1) is also always positively associated with the three FDis indexes, and is important mainly for Global FDis.

On the other hand, our results show that current landscape conditions are also important for explaining the variation of the three FDis indexes. Indeed, the area in regeneration in the 2 km landscape in 2015 (P4), which is always negatively associated with the FDis indexes, is either the most important variable or among the most important ones for explaining the variation of all indexes.

At the stand scale, maple syrup production over time, as assessed in 2015, is negatively associated with the three indexes, and is an important variable mainly for Global FDis and FDis – Reproduction.

a) Global FDis



b) FDis – Seed dispersal

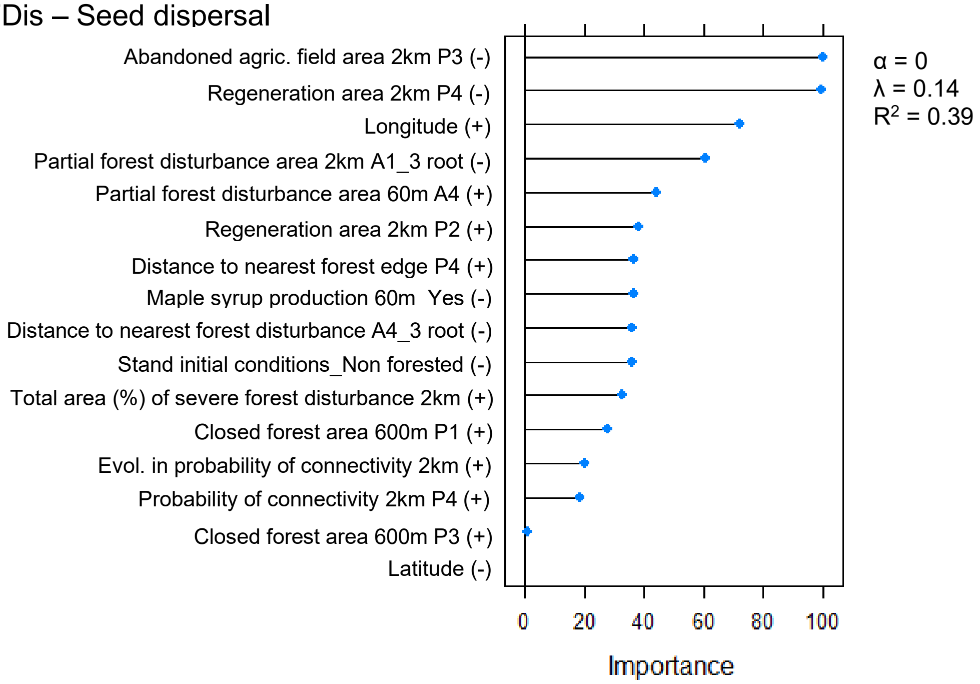


Figure 2.5. Elastic-Net regression results showing the most important explanatory variables for explaining the variation in a) Global FDis, b) FDis – Seed dispersal, and c) FDis – Reproduction.

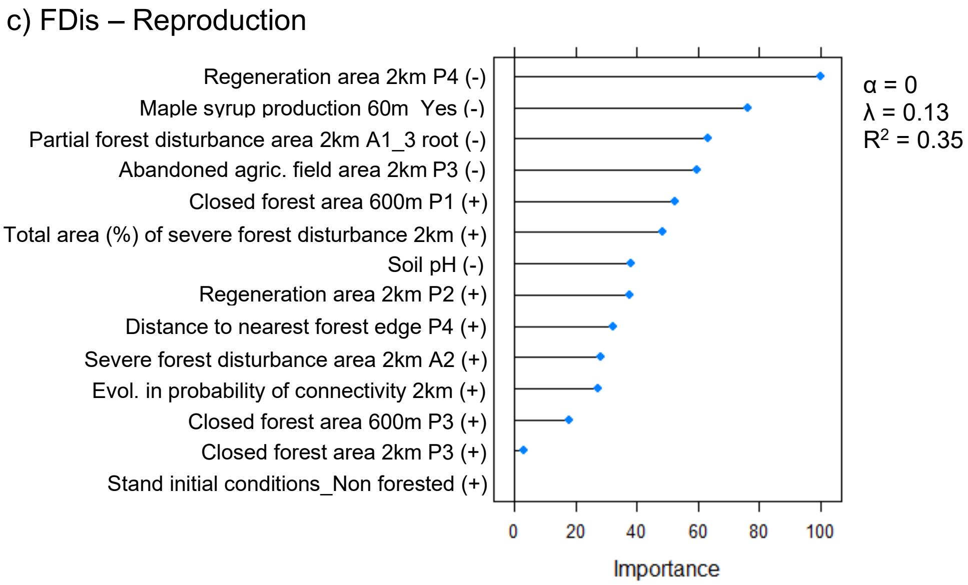


Figure 2.5. (continued) Elastic-Net regression results showing the most important explanatory variables for explaining the variation in a) Global FDis, b) FDis – Seed dispersal, and c) FDis – Reproduction.

### 2.6.2 Influence of landscape trajectories on tree response diversity

Following the conditional inference tree analyses, results show that the 2 km landscapes with a trajectory of agriculture-pasture-regeneration (highly disturbed) are characterized by a lower global response diversity (FDis; $p = 0.021$, split value = 0.18), and a lower plant reproduction response diversity (FDis – Reproduction; $p = 0.028$, split value = 0.23) at local sampling sites compared to landscapes with a less disturbed trajectory. This means that when the 30-site sample is split according to FDis and FDis – Reproduction, we obtain the most homogenous sub-sample representing highly disturbed landscapes over time (pale grey in Figure 2.6) when FDis and FDis – Reproduction are lower. No distinction arose for seed dispersal response diversity. In the same way, the second comparison shows that the 600 m landscapes with a forest trajectory (less disturbed) are characterized by a higher global response diversity ($p = 0.035$, split value = 0.25) and a higher plant reproduction response diversity ($p = 0.003$, split value = 0.29) at local sampling sites compared to landscapes with a trajectory of agriculture. When the 30-site sample is split according to FDis and FDis – Reproduction, we then obtain the most homogenous sub-sample representing less disturbed landscapes over time (pale grey in Figure 2.7) when FDis and FDis – Reproduction are higher. Again, no distinction appeared for seed dispersal response diversity.

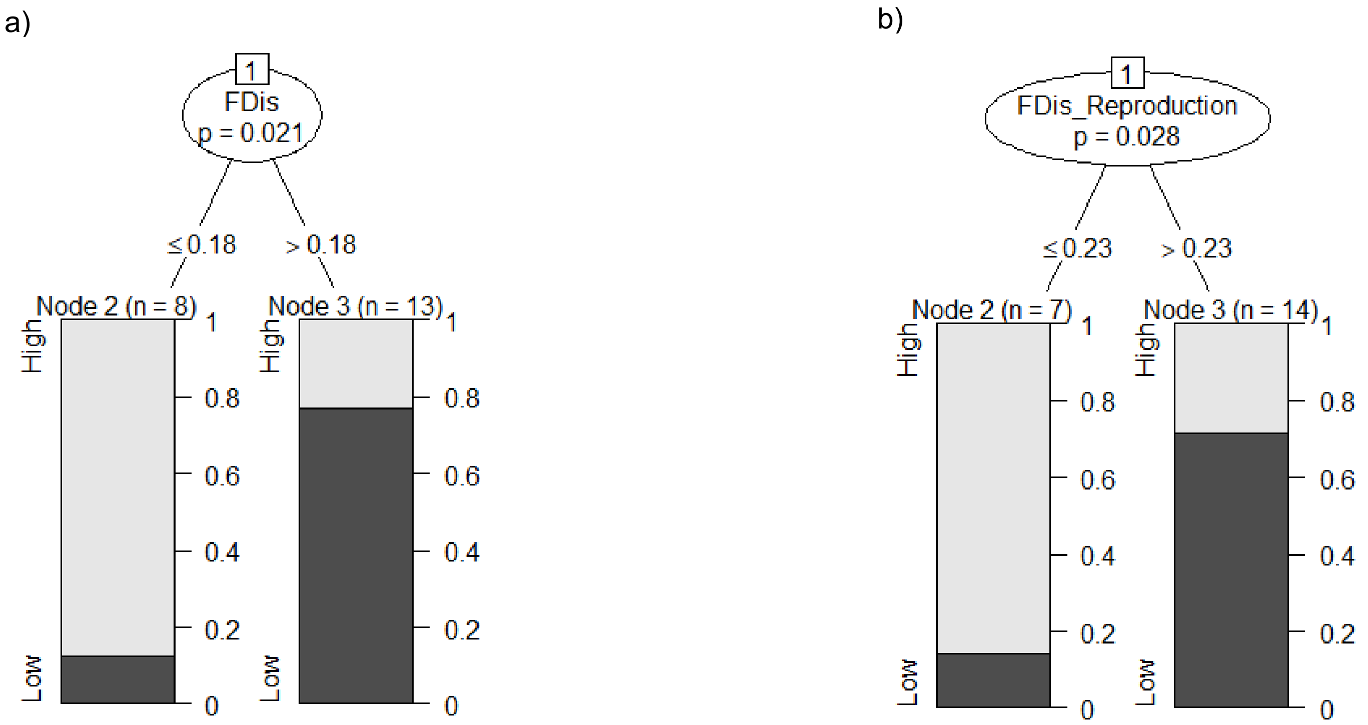


Figure 2.6. Decision trees showing that 2 km landscapes with a trajectory of agriculture-pasture-regeneration (highly disturbed, pale grey) are characterized by a lower response diversity in local sampling sites for a) all traits (FDis ≤ 0.18), and b) traits related to plant reproduction (FDis – Reproduction ≤ 0.23) compared to landscapes with a trajectory of agriculture-forest (less disturbed, black).

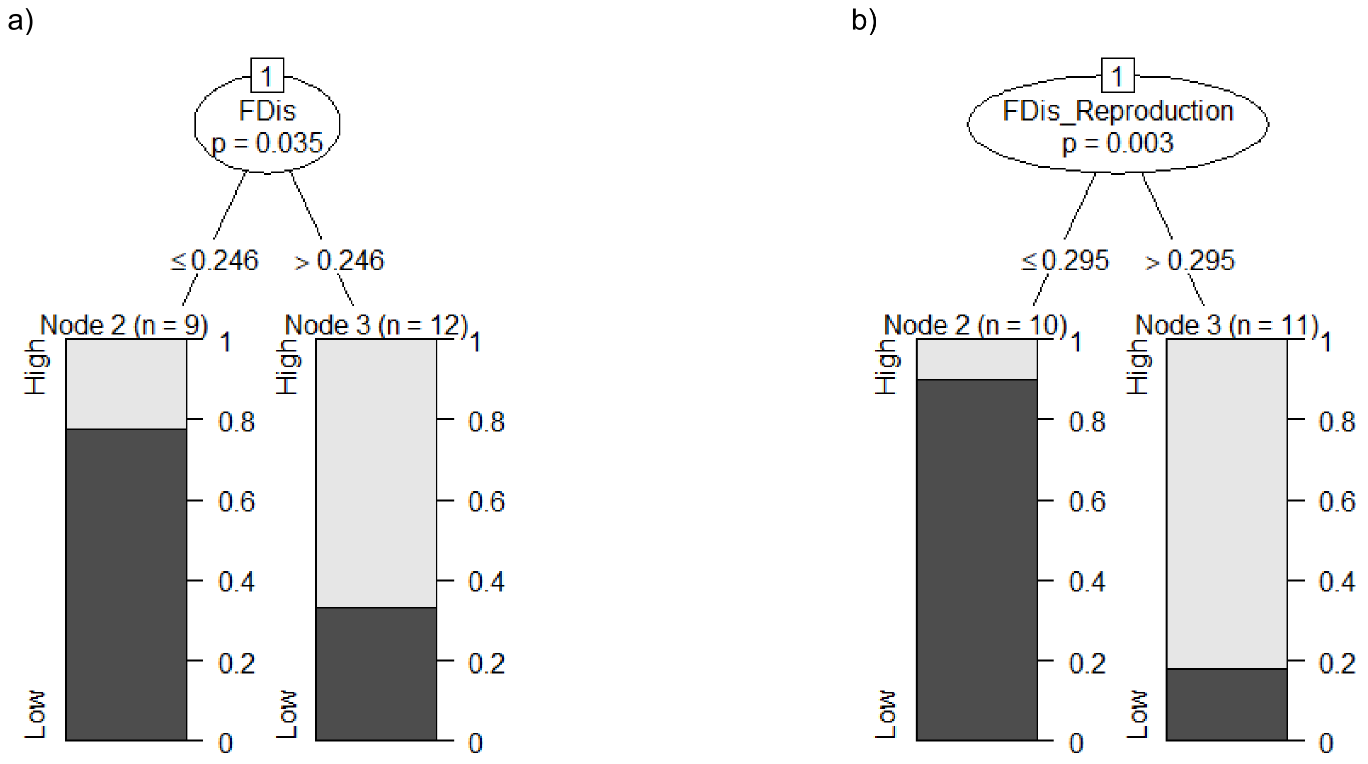


Figure 2.7. Decision trees showing that 600 m landscapes with a forest trajectory (less disturbed, pale grey) are characterized by a higher response diversity in local sampling sites for a) all traits (FDis > 0.246), and b) traits related to plant reproduction (FDis – Reproduction > 0.295) compared to landscapes with a trajectory of agriculture (highly disturbed, black).

### 2.6.3 Influence of past and current habitat conditions on tree response trait attributes

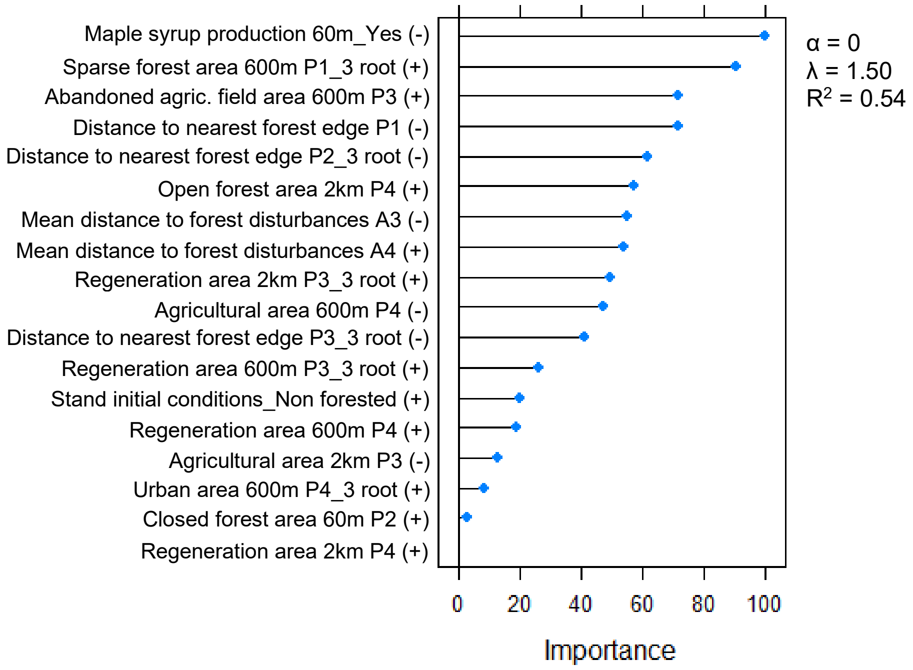
For all but two trait models, the Elastic-Net procedure resulted in a regression that is more closely related to a Ridge regression, with an α value of 0, for which all explanatory variables were kept into the models but where the coefficients of the less important ones were shrunk (Figure 2.8). For two trait models (Reproduction mostly by seeds and Root crown sprouting), the Elastic-Net procedure resulted in a regression somewhere between a Ridge and a Lasso regression with an α value of 0.3 for both models. For the model Reproduction mostly by seeds, only seven out of 25 explanatory variables were kept into the model, while nine out of 13 variables were kept into the model Root crown sprouting. The $R^2$ for the nine trait models range between 0.31 and 0.54.

Results show that distant and intermediate past landscape conditions from the years 1930-40 and 1958 are important for explaining the variation of the nine response traits considered here (Figure 2.8). For instance, the area of sparse forest in the landscape in 1930-40 (P1) is among the most important explanatory variables for several response traits. The area of pasture in the landscape in 1958 (P2) or in P1 are also among the most important variables for several traits. More precisely, an increase in pasture area in the landscape in P1 or P2 is associated with a higher maximal seed dispersal distance and a higher proportion of species reproducing mostly by seeds and with mammal-dispersed seeds in local sampling sites. On the other hand, an increase in pasture area is also associated with a lower proportion of species with stump, root and root crown sprouting capacity in local sampling sites.

More recent past conditions, such as the area of severe forest disturbances between 1983 and 2015 (A4) and the area of abandoned agricultural field in the landscape in 1983 (P3), are also among the most important explanatory variables for many response traits (Figure 2.8). A larger area of abandoned agricultural field in the landscape in P3 is associated with a smaller mean community seed mass and a lower proportion of species with bird-dispersed seeds and with stump sprouting capacity in local sampling sites.

Maple syrup production over time at the stand scale as assessed in 2015 is also important for explaining the variation of several response traits. Maple syrup production is indeed associated with a higher mean community seed mass, a lower maximal seed dispersal distance, a lower proportion of species with mammal-dispersed seeds, a higher proportion of species with stump sprouting capacity and a lower proportion of species with root crown sprouting capacity.

a) Seed mass



b) Maximal seed dispersal distance

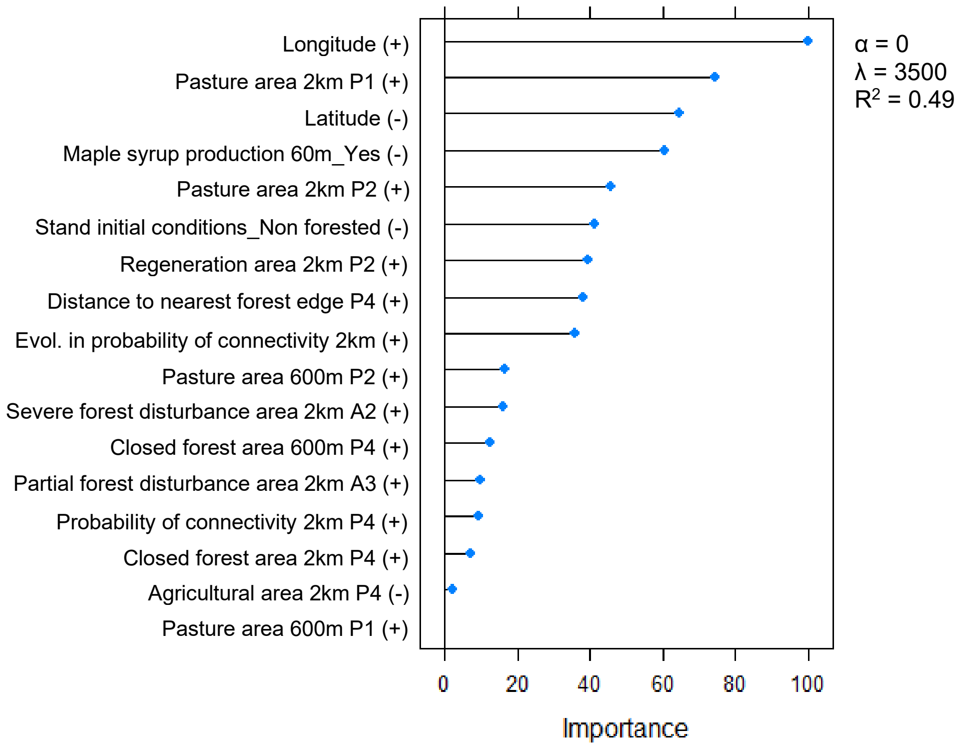
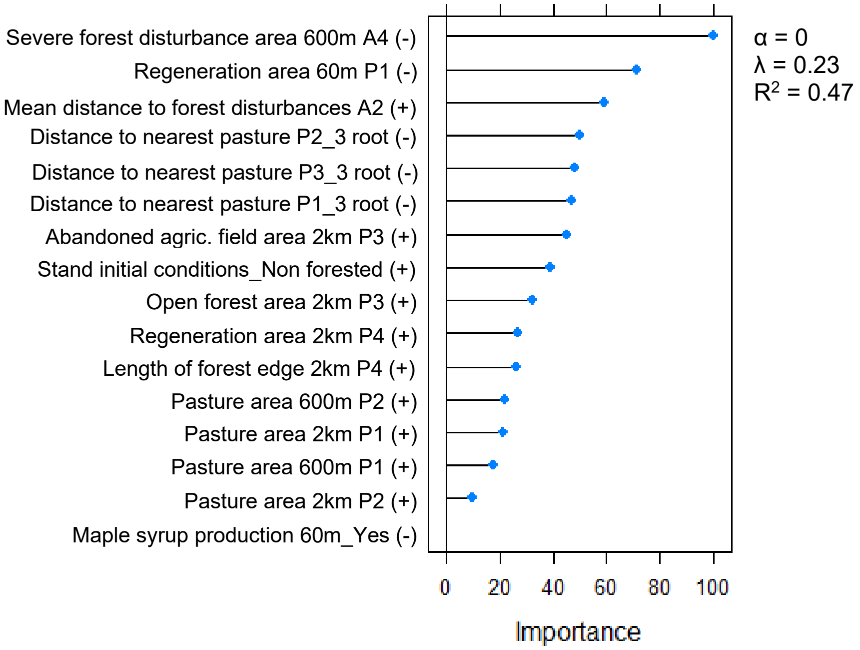


Figure 2.8. Elastic-Net regression results showing the most important explanatory variables for explaining the variation in response traits: Seed mass (a), Maximal seed dispersal distance (b), Proportion of species with wind-, mammal- and bird-dispersed seeds (c-d-e), Proportion of species reproducing mostly by seeds (f), Proportion of species with stump, root and root crown sprouting ability (g-h-i).

c) Proportion of species with wind-dispersed seeds



d) Proportion of species with mammal-dispersed seeds

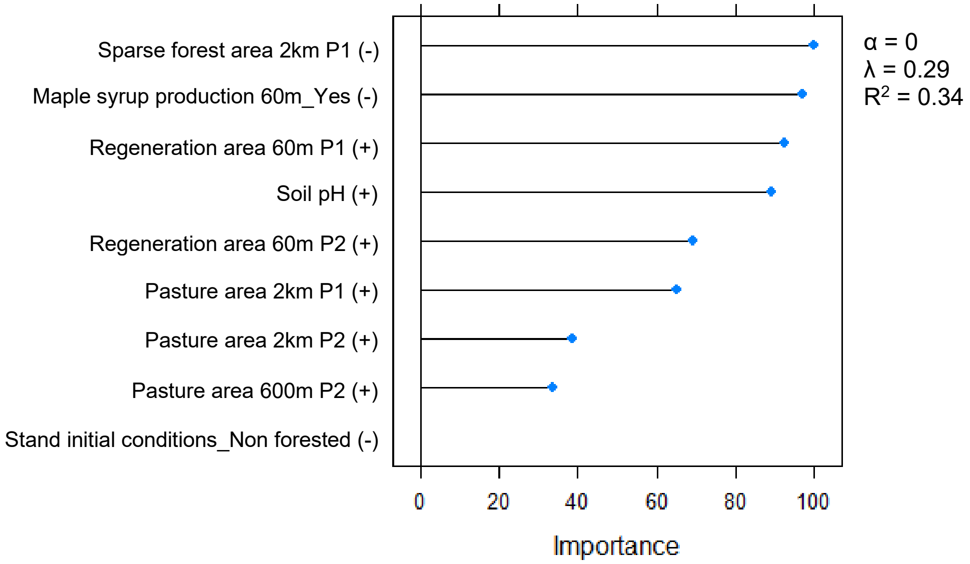


Figure 2.8. (continued) Elastic-Net regression results showing the most important explanatory variables for explaining the variation in response traits: Seed mass (a), Maximal seed dispersal distance (b), Proportion of species with wind-, mammal- and bird-dispersed seeds (c-d-e), Proportion of species reproducing mostly by seeds (f), Proportion of species with stump, root and root crown sprouting ability (g-h-i).

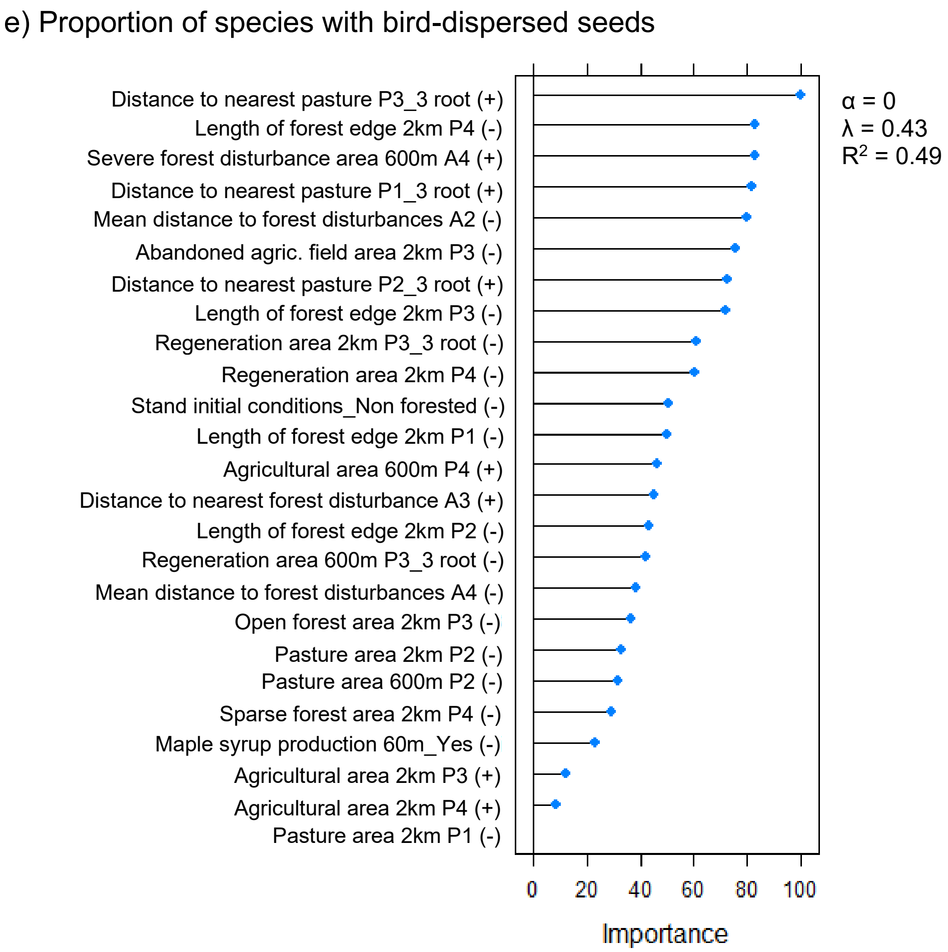

e) Proportion of species with bird-dispersed seeds

Figure 2.8. (continued) Elastic-Net regression results showing the most important explanatory variables for explaining the variation in response traits: Seed mass (a), Maximal seed dispersal distance (b), Proportion of species with wind-, mammal- and bird-dispersed seeds (c-d-e), Proportion of species reproducing mostly by seeds (f), Proportion of species with stump, root and root crown sprouting ability (g-h-i).

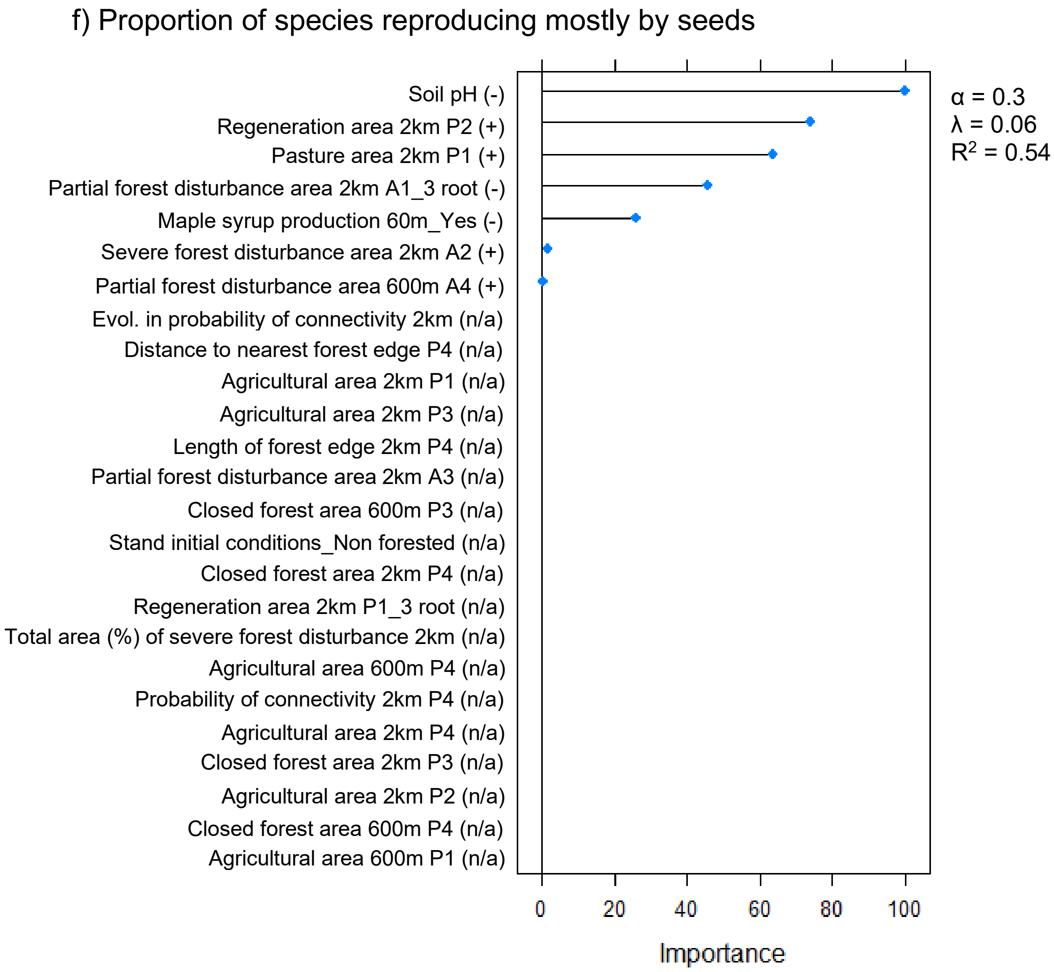
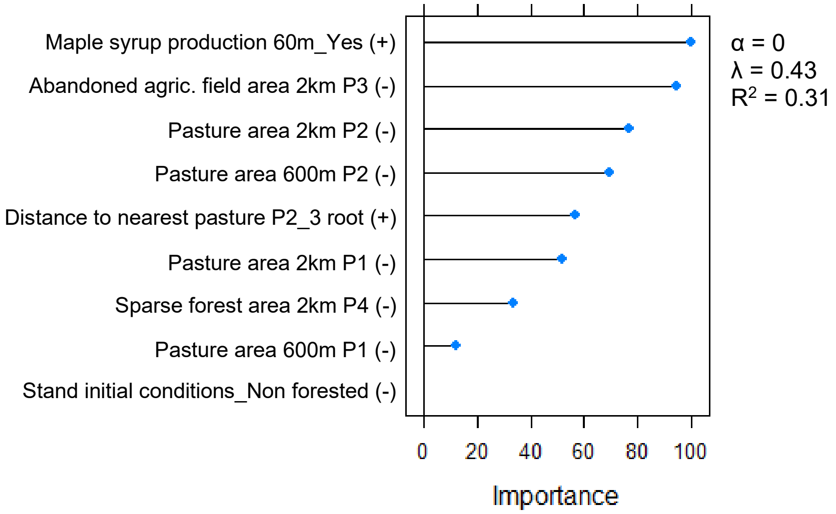


Figure 2.8. (continued) Elastic-Net regression results showing the most important explanatory variables for explaining the variation in response traits: Seed mass (a), Maximal seed dispersal distance (b), Proportion of species with wind-, mammal- and bird-dispersed seeds (c-d-e), Proportion of species reproducing mostly by seeds (f), Proportion of species with stump, root and root crown sprouting ability (g-h-i).

g) Proportion of species with stump sprouting ability



h) Proportion of species with root sprouting ability

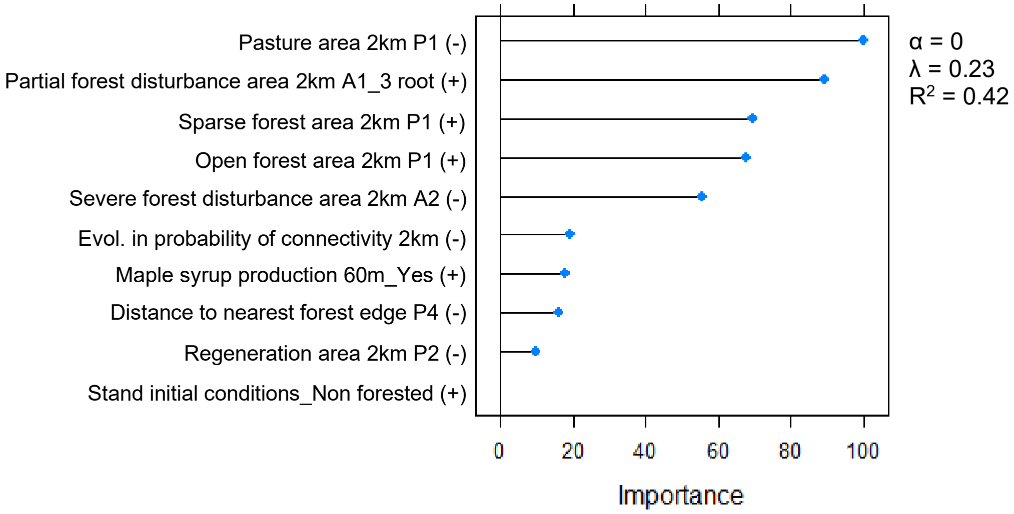


Figure 2.8. (continued) Elastic-Net regression results showing the most important explanatory variables for explaining the variation in response traits: Seed mass (a), Maximal seed dispersal distance (b), Proportion of species with wind-, mammal- and bird-dispersed seeds (c-d-e), Proportion of species reproducing mostly by seeds (f), Proportion of species with stump, root and root crown sprouting ability (g-h-i).

i) Proportion of species with root crown sprouting ability

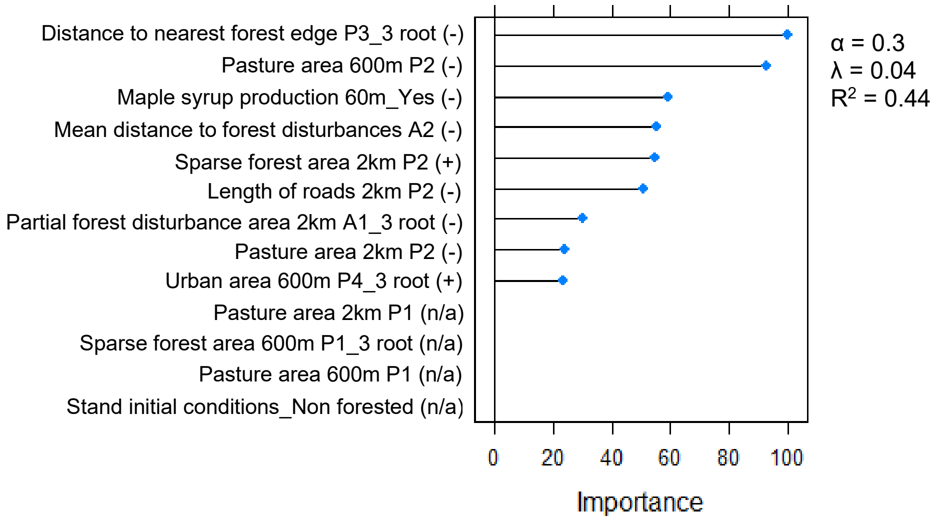


Figure 2.8. (continued) Elastic-Net regression results showing the most important explanatory variables for explaining the variation in response traits: Seed mass (a), Maximal seed dispersal distance (b), Proportion of species with wind-, mammal- and bird-dispersed seeds (c-d-e), Proportion of species reproducing mostly by seeds (f), Proportion of species with stump, root and root crown sprouting ability (g-h-i).

### 2.6.4 Influence of landscape trajectories on tree response trait attributes

Results show that forest communities within 2 km landscapes with a trajectory of agriculture-pasture-regeneration (highly disturbed) are characterized by a higher proportion of species with wind- ($p = 0.05$, split value = 0.96) and mammal-dispersed seeds ($p = 0.003$, split value = 0.28), a higher maximum seed dispersal distance ($p = 0.037$, split value = 2808), a lower proportion of species with bird-dispersed seeds ($p = 0.023$, split value = 0.03), and a lower proportion of species with stump ($p = 0.006$, split value = 0.64) and root crown sprouting capacity ($p = 0.002$, split value = 0.34) compared to those in landscapes with a trajectory of agriculture-forest (less disturbed). This means that when the 30-site sample is split according to Dispersal mode_Wind, Dispersal mode_Mammal and Maximum seed dispersal distance, we obtain the most homogenous sub-sample representing highly disturbed landscapes over time (pale grey in Figure 2.9) when these traits have higher values. On the contrary, when the 30-site sample is split according to Dispersal mode_Bird, Stump sprouting and Root crown sprouting, we obtain the most homogenous sub-sample representing highly disturbed landscapes over time (pale grey in Figure 2.9) when these

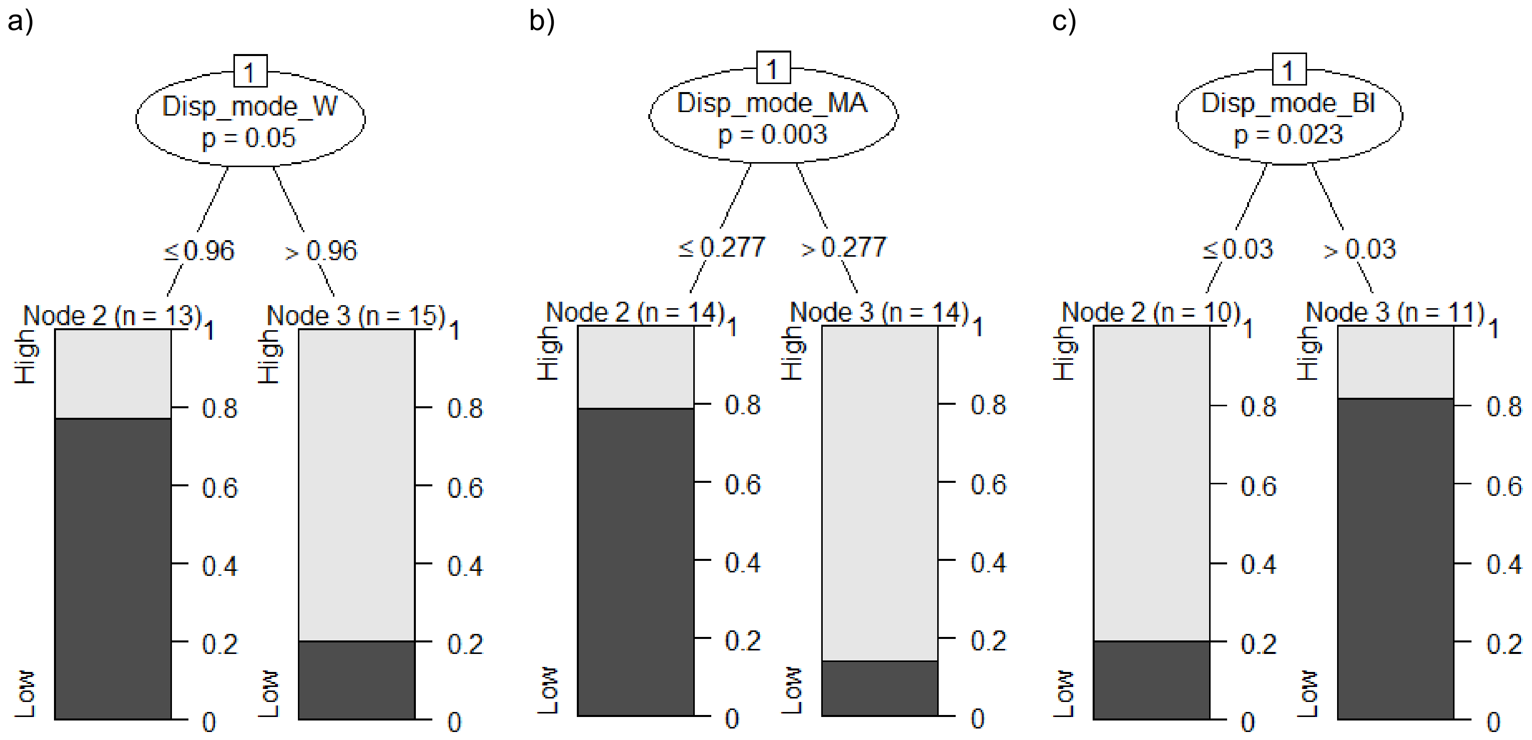


Figure 2.9. Decision trees showing that 2 km landscapes with a trajectory of agriculture-pasture-regeneration (highly disturbed, pale grey) are characterized by a higher proportion of species with wind- and mammal-dispersed seeds (a-b), a lower proportion of species with bird-dispersed seeds (c), a higher maximal seed dispersal distance (d), and a lower proportion of species with stump (SS) and root crown (RCS) sprouting capacity (e-f) in local sampling sites compared to landscapes with a trajectory of agriculture-forest (less disturbed, black).

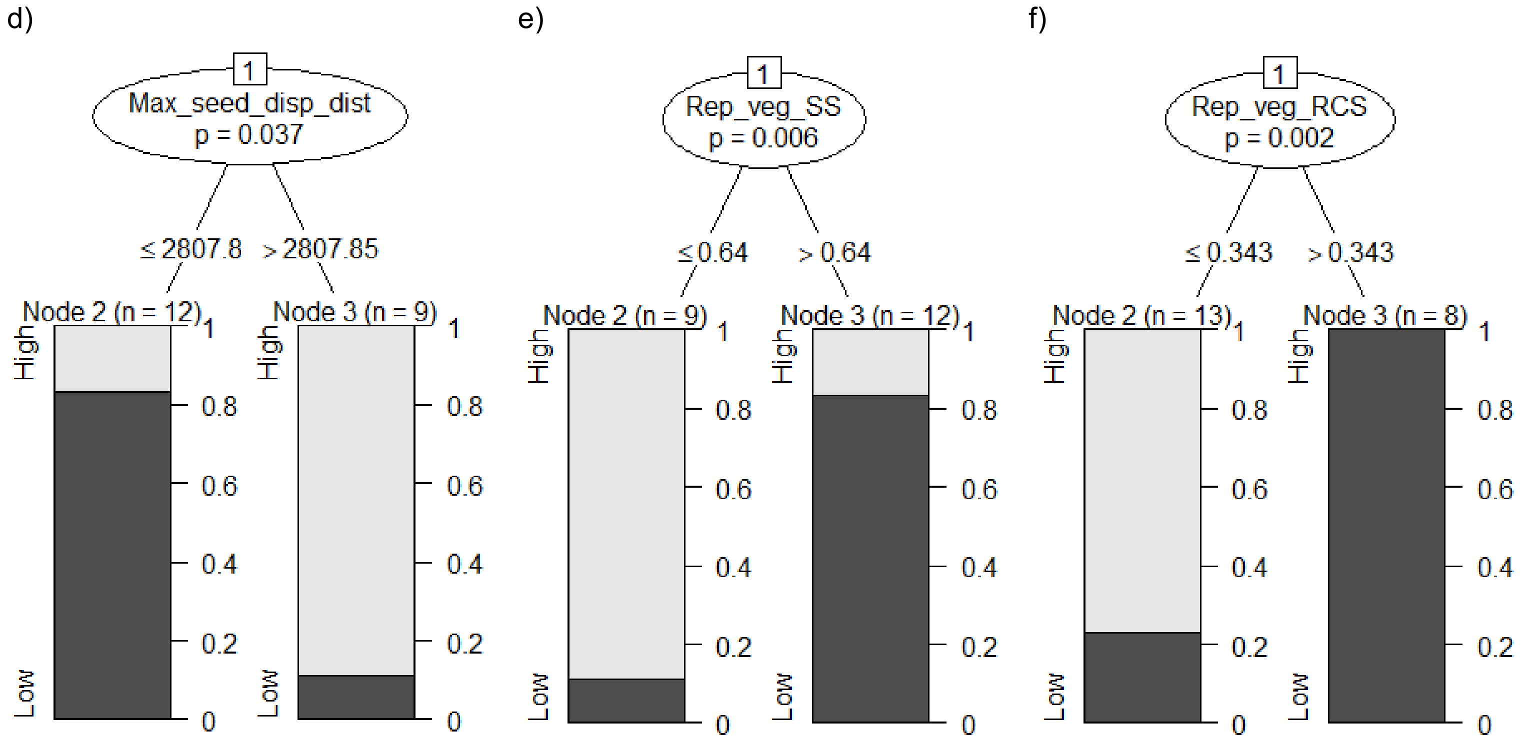


Figure 2.9. (continued) Decision trees showing that 2 km landscapes with a trajectory of agriculture-pasture-regeneration (highly disturbed, pale grey) are characterized by a higher proportion of species with wind- and mammal-dispersed seeds (a-b), a lower proportion of species with bird-dispersed seeds (c), a higher maximal seed dispersal distance (d), and a lower proportion of species with stump (SS) and root crown (RCS) sprouting capacity (e-f) in local sampling sites compared to landscapes with a trajectory of agriculture-forest (less disturbed, black).

traits have lower values. For Dispersal mode_Wind, the split value of 0.96 means that most species (> 96%) have wind-dispersed seeds in highly disturbed landscapes. For Dispersal mode_Bird, the split value of 0.03 means that very few species (≤ 3%) have bird-dispersed seeds in highly disturbed landscapes. In the same way, for Maximal seed dispersal distance, the split value of 2,808 means that tree communities with a mean very long maximal seed dispersal distance (> 2,808 m) are mainly present in highly disturbed landscapes.

For the second comparison, results show that forest communities within 600 m landscapes with a forest trajectory (less disturbed) are characterized only by a higher proportion of species reproducing mostly by seeds ($p = 0.004$, split value = 0; data not shown), which means that when the 30-site sample is split according to Reproduction – Mostly seeds, we obtain the most homogenous sub-sample representing less disturbed landscapes over time when this trait has higher values. In this particular case, the split value of 0 means that there is no species reproducing mainly by seeds in highly disturbed landscapes, and that there is a variable proportion of species reproducing mainly by seeds in less disturbed landscapes.

## 2.7 Discussion

### 2.7.1 Past and current habitat conditions influence tree functional response traits and diversity

Forest tree communities located in fragmented landscapes carry an ecological memory in their functional structure that is related to stand and landscape conditions that date back to the years 1930-40 and 1958, which is consistent with our first hypothesis. At the same time, more recent (1983) or present-day (2015) stand and landscape conditions also influence the response trait values and diversity in tree communities. Hence, recent and present-day habitat conditions can contribute to reset the ecological memory of functional response trait patterns in forest communities, although at the moment this memory is not yet completely erased. These results concur with those reported in Kimberley et al. (2016), where understorey forest community seed terminal velocity was predicted by both modern (2007) and historical (1899) patch area in fragmented forests of Great Britain. However, other studies showed that only landscape history could influence the current functional diversity and trait values in local sites. For instance, three studies that took place in semi-natural grasslands of Sweden showed the existence of historical external memory that was still affecting the current plant community functional traits or diversity. Purschke et al. (2012) indeed showed that long-distance seed dispersal potential (by wind and grazing cattle) in current communities was still positively associated with the amount of grassland in the 1835 and 1938 landscapes. Similarly, Purschke et al. (2014) showed that the current functional diversity of persistence and seed dispersal traits in present-day communities was still influenced by the amount of grassland habitat in the surrounding landscape in 1938. For its part, Lindbord (2007) showed that the proportion of long-lived clonal plants was still influenced by historical grassland connectivity and the amount of habitat within the landscape, while the proportion of species with long seed bank persistence was still influenced by historical connectivity.

Present-day landscape conditions are important for explaining tree functional response trait patterns in our study, yet they cannot directly impact mature trees in our forest communities by acting as a dispersal filter because those trees have become established in the past. This present-day dispersal filter would rather affect younger developmental stages such as tree seedlings and saplings, which were not the focus of this study. In this context, present-day landscape conditions might be a proxy for the evolution of landscape conditions over time (e.g., large areas in regeneration in the landscape in 2015 might reflect large areas of open habitat such as pasture, abandoned agricultural field and agriculture in the past). This highlights the importance of considering the evolution of landscapes over time instead of analyzing only specific periods in time.

### 2.7.2 Erosion of response diversity in local tree communities due to an alteration of legacies in surrounding landscapes over time

Our results support the hypothesis that an alteration of landscape legacies through higher landscape disturbances over time can lead to an erosion of response diversity in forest communities. Indeed, two of the three response diversity indexes were significantly lower in forest communities within landscapes with a more disturbed trajectory (greater amount of open habitats such as agricultural lands, abandoned agricultural fields, pastures and regeneration areas) compared to landscapes with a smaller amount of open habitats and a greater amount of forests. All types of open land related to extensive past and current agricultural activities can thus lead to a decrease in response diversity in forest communities. Our results agree with de Frutos et al. (2015) who showed that woody plant response diversity was negatively related to landscape fragmentation in a semi-arid Mediterranean ecosystem. Results also concur with Laliberté et al.

(2010) who showed that, in general, response diversity decreased with land-use intensification around the world. For their part, Davis et al. (2017) showed that an urbanizing landscape matrix had a negative impact on tree diversity in forest communities, which is also in line with our results and other studies showing that land-use intensification can decrease diversity in forest communities. Finally, Craven et al. (2016) also suggested that fragmentation in temperate forests could have a negative impact on response diversity in local communities.

### 2.7.3 Response trait filtering in local tree communities due to an alteration of legacies in surrounding landscapes over time

Our results suggest that the best strategy for persisting in fragmented forests embedded in an agricultural matrix is for trees to have seeds able to disperse over greater distances either by wind or mammals able to move across open habitats, the former implying smaller seed mass. In these disturbed landscapes, mammals might be able to move through open habitats by using scattered remnant trees or wooded strips (Bennett et al., 1994; Fitzgibbon, 1993; Merriam, 1988; Verboom & van Apeldoorn, 1990), which can provide feeding habitats and shelter against predation. This result may thus suggest that there is still a functional network of corridors, such as hedgerows and culverts, in these agricultural landscapes that can support active movement of the meta-communities of mammals. Our results also suggest that some vegetative reproduction types, such as stump sprouting and root crown sprouting, may not be the best strategy for tree persistence in highly disturbed landscapes. Indeed, open habitats in the highly disturbed landscape trajectories are associated with a lower vegetative reproduction capacity in local tree communities, which have been filtered toward a trait syndrome promoting high dispersal ability (Uroy et al., 2019). Our results are in accordance with Verheyen et al. (2003), who showed that low species dispersibility was the most important constraint for understorey herbaceous vascular plants recovery following agricultural abandonment in Northeastern North America and Northwestern Europe. Our results also concur with the review of Uroy et al. (2019), who illustrated that plant species less sensitive to connectivity loss were those having low clonality, producing many thin seeds, and displaying assisted dispersal (e.g., by wind or animals). However, the results reported in two other studies do not concur with ours. Indeed, Wiegmann & Waller (2006) demonstrated that understorey plant species in the Wisconsin and Michigan temperate forest that relied on animals for seed dispersal decreased in frequency in disturbed landscapes between 1950 and 2000, while those that did not rely on animals increased. For its part, Lindborg (2007) suggested that semi-natural grassland species persisting in response to landscape fragmentation relied on seed banks or vegetative spread.

In our study, we noticed that local communities having a greater maximum seed dispersal distance also have a lower proportion of species able to reproduce vegetatively and, on the contrary, have a higher proportion of species reproducing mostly by seeds (data not shown). This observation agrees with studies showing the existence of a trade-off between plant colonization ability and persistence (Cody, 2006; Ehrlén & van Groenendael, 1998; Honnay & Bossuyt, 2005; Ozinga et al., 2007; Stöcklin & Winkler, 2004), and suggests that some species with a better vegetative reproduction capacity might lack the ability to disperse their seeds over great distances across fragmented landscapes while displaying a very high local persistence. The low abundance of remnant isolated or aggregated trees within past agricultural fields might have worsened the situation, in that some tree species with high vegetative reproduction capacity might not have been able to recolonize abandoned fields from sprouting.

## 2.8 Conclusion

In this study, we showed that the present-day functional structure of tree communities located in fragmented landscapes was associated with distant, intermediate, and more recent past as well as present-day habitat conditions. An ecological memory being detected in their functional structure, these communities are thus not in equilibrium with present-day conditions. In the light of these results, we emphasize the need to consider an extended timeframe when assessing the impact of anthropogenic disturbances on tree communities, especially within landscapes where a lot of changes occurred in the past. In this context, we also studied landscape trajectories covering the past 85 years and showed that the alteration of landscape legacies through continuous landscape disturbance led to a functional erosion of response diversity and to a response trait filtering promoting species with higher colonization ability and lower persistence through vegetative spread.

It is well assumed that a decrease in response diversity can lead to a decrease in ecosystem resilience and impede their capacity to face future disturbances (Elmqvist et al., 2003; Hooper et al., 2005; Mori et al., 2013; Naeem & Wright, 2003; Walker, 1995). If this premise is also true for our forest communities, then our results suggest that communities from historically highly disturbed landscapes might have an impaired ability to adapt in the face of new disturbances. Moreover, tree species with trait values reflecting a better colonization capacity in historically highly disturbed landscapes might not be well adapted to face other stressors. For instance, species that are the best at dispersing their seeds over greater distances by wind might not be the best at resisting more severe and frequent droughts, especially during the early stages of their lives where smaller seeded species are generally less stress-tolerant (Muller-Landau, 2010). The same thinking applies when considering an increased level of white-tailed deer herbivory, where species that have been favoured by higher levels of landscape disturbance in the past might not be the most resistant to over-browsing (e.g., lower stump and root crown sprouting ability). Our results then support the view of a need for forest restoration with an emphasis on increasing response diversity to enhance forest resilience to stressors related to global changes, and allow us to identify those sites that will need to be improved in terms of their adaptive capacity.

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## 2.11 Tables

Table 2.1. List of tree species present in the 64 sampling sites and number of sites where each species occurs.

| Trees | Nb of sites where species occurs |
|---|---|
| *Abies balsamea* | 1 |
| *Acer rubrum* | 24 |
| *Acer saccharum* | 49 |
| *Betula alleghaniensis* | 10 |
| *Betula papyrifera* | 4 |
| *Betula populifolia* | 1 |
| *Carya cordiforma* | 8 |
| *Fagus grandifolia* | 15 |
| *Fraxinus americana* | 20 |
| *Fraxinus nigra* | 2 |
| *Fraxinus pennsylvanica* | 2 |
| *Ostrya virginiana* | 20 |
| *Picea glauca* | 1 |
| *Pinus strobus* | 6 |
| *Populus balsamifera* | 2 |
| *Populus grandidantata* | 9 |
| *Populus tremuloides* | 11 |
| *Prunus serotina* | 9 |
| *Quercus alba* | 1 |
| *Quercus macrocarpa* | 2 |
| *Quercus rubra* | 7 |
| *Salix nigra* | 1 |
| *Thuja occidentalis* | 14 |
| *Tilia americana* | 18 |
| *Tsuga canadensis* | 23 |
| *Ulmus americana* | 4 |
| *Ulmus rubra* | 7 |

Table 2.2. Selected functional response traits for trees.

| Response trait | Definition | Process | Tree trait | |
|---|---|---|---|---|
| | | | Type[a] | Level |
| Root system depth | Depth where bulk of roots is located. | Plant protection | B | S (1/0)[b]<br>D (1/0) |
| Maximal root depth | Maximal depth reached by roots. | Plant protection | N | S<br>I<br>D |
| Growth | Growth rate. | Plant protection | N | S[c]<br>M<br>F |
| Wood density | Stem wood density expressed as the oven-dry weight per green volume (kg/m$^3$). | Plant protection | Q | --- |
| Reproduction | Reproduction mode. | Reproduction | N | MS[d]<br>MV<br>SV<br>SO |
| Vegetative reproduction | Vegetative reproduction mode. | Reproduction | B | L (1/0) [e]<br>SS (1/0)<br>RS (1/0)<br>RCS (1/0)<br>RHS (1/0)<br>STS (1/0)<br>F (1/0) |
| Age sexual maturity | Age at first reproduction. | Seed production | Q | --- |
| Age optimal seed production | Age at which a plant begins to produce the maximum quantity of seeds per seed crop. | Seed production | Q | --- |
| Seed production | Number of seeds per individual. | Seed production | Q | --- |
| Interval mast years | Number of years between higher-than-average seed production years. | Seed production | Q | --- |
| Plant lifespan | Maximal natural plant longevity (above ground parts). | Seed production | Q | --- |
| Dispersal mode | Seed dispersal vector. | Dispersal | B | G (1/0)[f]<br>W (1/0)<br>M (1/0)<br>B (1/0) |
| Maximal seed dispersal distance | Maximal seed dispersal distance estimated for bird, mammal, or wind dispersal. | Dispersal | Q | --- |
| Maximal plant height | Species' maximal potential height (m). | Dispersal | Q | --- |
| Seed persistence | Number of years during which seeds are viable in the seed bank. | Germination / emergence | Q | --- |

| Response trait | Definition | Process | Tree trait | |
|---|---|---|---|---|
| | | | Type[a] | Level |
| Seed viability | Percentage of viable seeds per kg of seeds or germination rate (%). | Germination / emergence | Q | --- |
| Seed mass | Number of seeds per kg. | Seed production<br>Dispersal<br>Germination / emergence | Q | --- |

[a] Type of trait: N – nominal; Q – quantitative; B – binary multi-choice.

[b] Tree root system depth and maximal root depth: ≤ 1m – Shallow (S); Between 1m and 3m – Intermediate (I); ≥ 3m – Deep (D).

[c] Growth: Slow (S); Medium (M); Fast (F).

[d] Reproduction: Mostly sexual (MS); Mostly vegetative (MV); Sexual + vegetative (SV); Sexual only (SO).

[e] Vegetative reproduction: Layering (L), Stump sprouting (SS); Root sprouting (RS); Root crown sprouting (RCS); Rhizome sprouting (RHS); Stem sprouting (STS); Fragment (F).

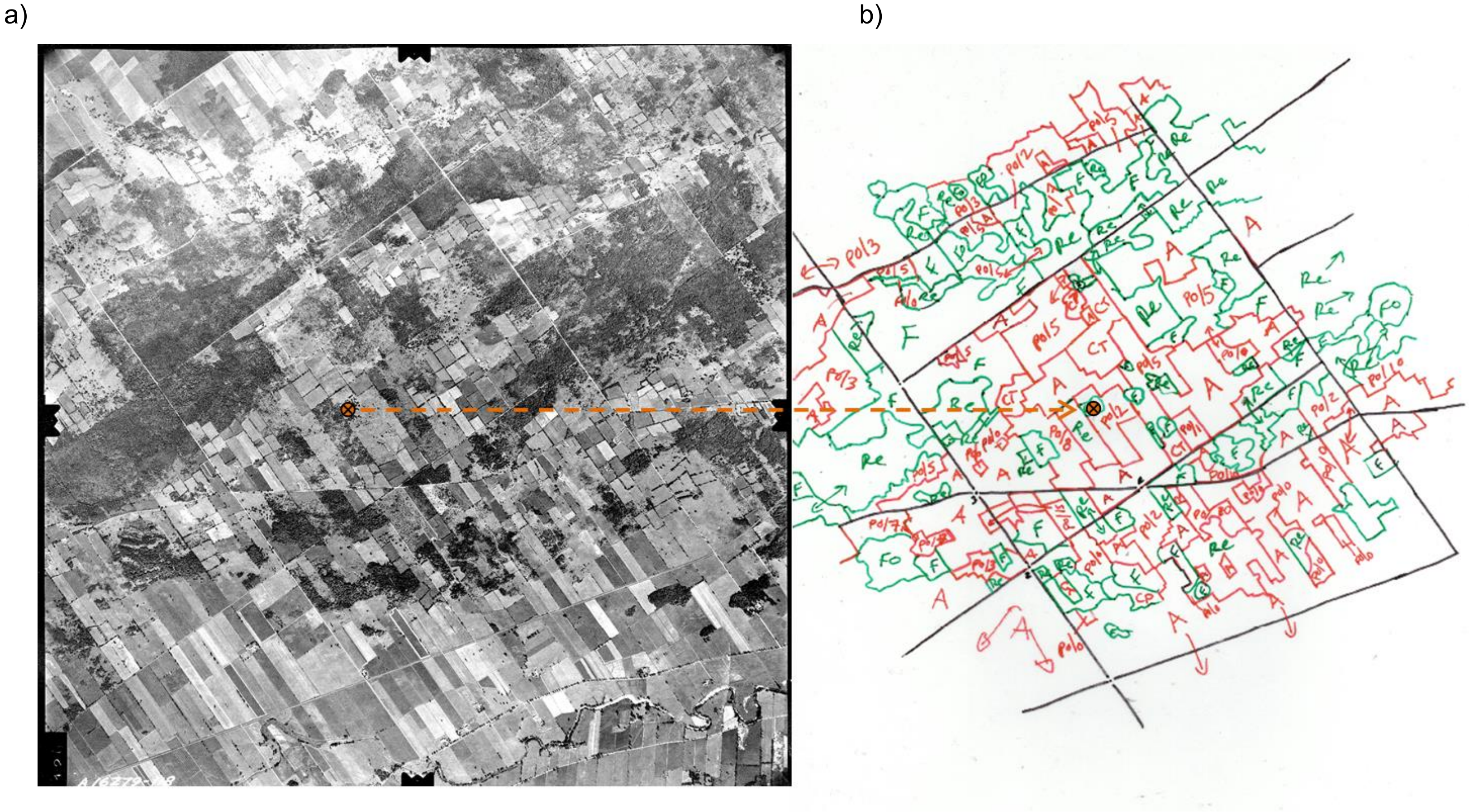
[f] Dispersal mode: Gravity (G); Wind (W); Mammals (M); Birds (B).

## 2.12 Annexes

Annex A. Absolute (ha) and relative (%) area of the main land-use classes in the 2km-buffer landscapes (n-64) at the four time periods.

| **Land use** | **P1 (1930-40)** | | **P2 (1958)** | | **P3 (1983)** | | **P4 (2015)** | |
|---|---|---|---|---|---|---|---|---|
| **Agriculture** | | | | | | | | |
| Area min. | 96.1 | (7.7) | 25.6 | (2.0) | 12.1 | (1.0) | 2.4 | (0.2) |
| Area max. | 1,190.2 | (94.8) | 1,181.3 | (94.1) | 1,160.2 | (92.4) | 1,147.4 | (91.4) |
| Mean area | 669.5 | (53.3) | 638.6 | (50.9) | 586.3 | (46.7) | 470.6 | (37.5) |
| **Closed forest** | | | | | | | | |
| Area min. | 11.2 | (0.9) | 15.8 | (1.3) | 20.8 | (1.7) | 33.9 | (2.7) |
| Area max. | 691.8 | (55.1) | 894.7 | (71.3) | 954.1 | (76.0) | 1,049.8 | (83.6) |
| Mean area | 240.8 | (19.2) | 254.2 | (20.2) | 364.8 | (29.1) | 493.4 | (39.3) |
| **Sparse forest** | | | | | | | | |
| Area min. | 0 | (0.0) | 0 | (0.0) | 0 | (0.0) | 0 | (0.0) |
| Area max. | 91.9 | (7.3) | 75.3 | (6.0) | 0 | (0.0) | 55.1 | (4.4) |
| Mean area | 17.8 | (1.4) | 13.6 | (1.1) | 0 | (0.0) | 15.9 | (1.3) |
| **Open forest** | | | | | | | | |
| Area min. | 2.1 | (0.2) | 0 | (0.0) | 3.0 | (0.2) | 0 | (0.0) |
| Area max. | 214.1 | (17.1) | 215.7 | (17.2) | 221.8 | (17.7) | 160.7 | (12.8) |
| Mean area | 46.8 | (3.7) | 50.9 | (4.1) | 95.1 | (7.6) | 64.1 | (5.1) |
| **Pasture** | | | | | | | | |
| Area min. | 0 | (0.0) | 0 | (0.0) | 0 | (0.0) | 2.8 | (0.2) |
| Area max. | 519.6 | (41.4) | 451.6 | (36.0) | 338.9 | (27.0) | 382.9 | (30.5) |
| Mean area | 173.1 | (13.8) | 133.6 | (10.6) | 97.4 | (7.8) | 131.3 | (10.5) |
| **Regeneration** | | | | | | | | |
| Area min. | 0 | (0.0) | 4.5 | (0.4) | 0 | (0.0) | 0 | (0.0) |
| Area max. | 529.7 | (42.2) | 461.1 | (36.7) | 349.6 | (27.8) | 82.2 | (6.5) |
| Mean area | 52.1 | (4.1) | 116.7 | (9.3) | 51.1 | (4.1) | 23.2 | (1.8) |

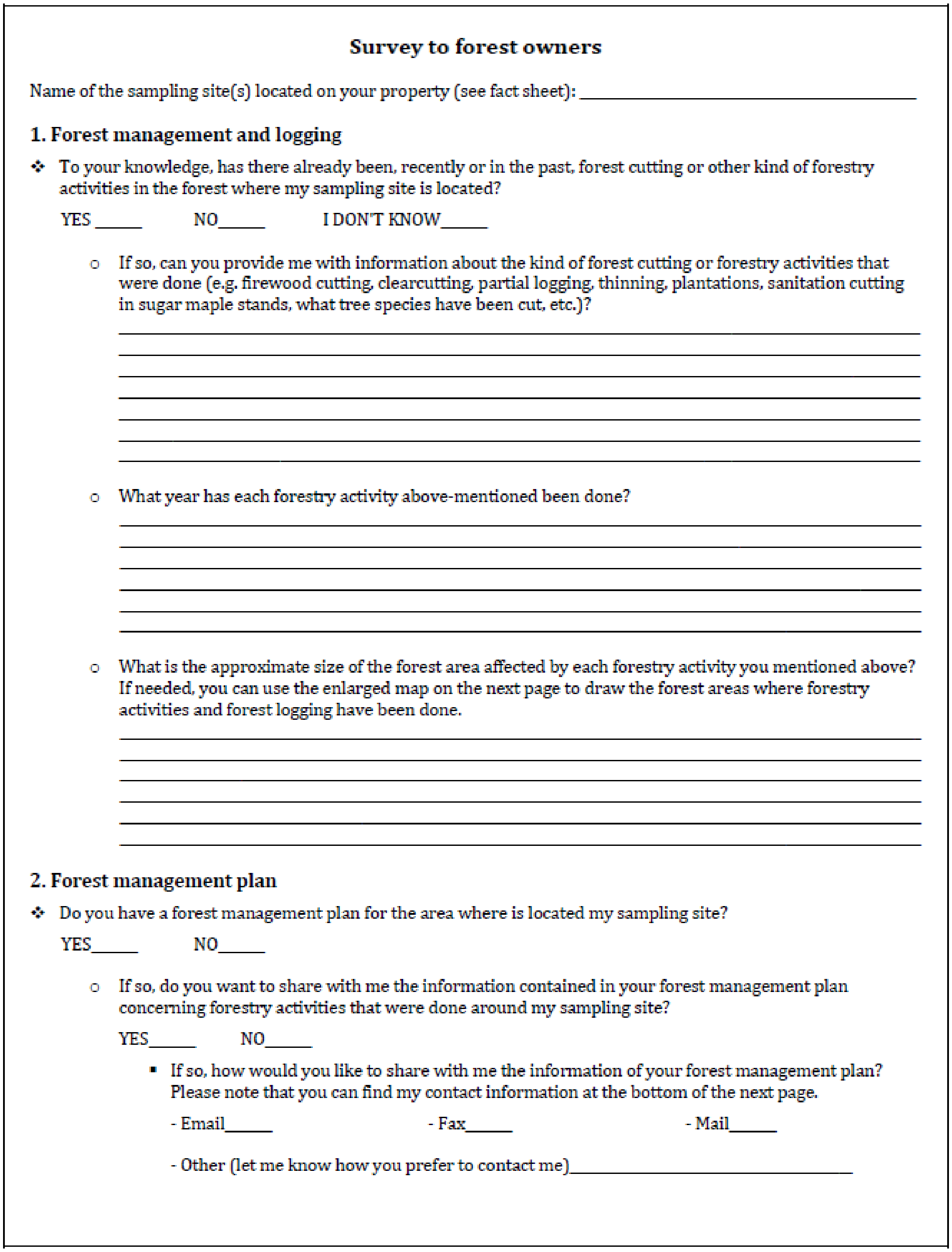
Annex B. Photointerpretation of historical aerial photographs. All land uses detected on aerial photographs were drawn on acetates within a 2km-buffer zone around each sampling site (orange dot on the picture). a) Aerial photograph of one sampling site and its surrounding landscape in 1958, scale 1:30,000, b) Photointerpretation of that same region.



a)

b)

## Annex C. Postal survey for forest landowners.



### Survey to forest owners

Name of the sampling site(s) located on your property (see fact sheet): ____________________________________

#### 1. Forest management and logging

- To your knowledge, has there already been, recently or in the past, forest cutting or other kind of forestry activities in the forest where my sampling site is located?

  YES _____ NO_____ I DON'T KNOW_____

  - If so, can you provide me with information about the kind of forest cutting or forestry activities that were done (e.g. firewood cutting, clearcutting, partial logging, thinning, plantations, sanitation cutting in sugar maple stands, what tree species have been cut, etc.)?
  - What year has each forestry activity above-mentioned been done?
  - What is the approximate size of the forest area affected by each forestry activity you mentioned above? If needed, you can use the enlarged map on the next page to draw the forest areas where forestry activities and forest logging have been done.

#### 2. Forest management plan

- Do you have a forest management plan for the area where is located my sampling site?

  YES_____ NO_____

  - If so, do you want to share with me the information contained in your forest management plan concerning forestry activities that were done around my sampling site?

    YES_____ NO_____

    - If so, how would you like to share with me the information of your forest management plan? Please note that you can find my contact information at the bottom of the next page.

      - Email_____ - Fax_____ - Mail_____

      - Other (let me know how you prefer to contact me)______________________________

### 3. Agricultural activities

- To your knowledge, is there currently or has there been in the past agricultural activities in the area where is located my sampling site (e.g. cattle grazing in the wood, any kind of farming before forest regrowth, etc.)?

  YES_____ NO_____ I DON'T KNOW_____

  - If so, can you give me more information about those activities (what kind of agricultural activities, what year, etc.)?

    ______________________________________________________________________
    ______________________________________________________________________
    ______________________________________________________________________
    ______________________________________________________________________
    ______________________________________________________________________

### 4. Other uses of your forest

- To your knowledge, is there currently or has there been in the past other kind of uses in the forest where is located my sampling site?

  YES_____ NO_____ I DON'T KNOW_____

  - If so, can you describe them to me (what kind of uses, what year, etc.)?

    ______________________________________________________________________
    ______________________________________________________________________
    ______________________________________________________________________
    ______________________________________________________________________

### 5. Future collaboration

- Would you like to continue collaborating with me and other members of my research team in the coming years so that we can continue studying impacts of climate change and of other stress factors on private forests of southern Quebec?

  YES_____ NO_____

  - If so, do you want to give me your contact information (phone and email) so that we can contact you in the future? Please note that this information will be treated confidentially and will be kept for internal use only.

    ______________________________________________________________________

### 6. Other comments?

______________________________________________________________________
______________________________________________________________________
______________________________________________________________________
______________________________________________________________________

**Thank you for taking the time to complete this survey and to send it back to me by May 31 2016!**

**My contact information**
Caroline Gagné, biol. M.Sc., PhD student in biology
Université du Québec à Montréal and Université du Québec en Outaouais – Institute of temperate forest science

Tel.: [redacted]
Email: caroline.gagne@outlook.com
Mailing address: [redacted]
Fax: [redacted]

## Sondage aux propriétaires forestiers

Nom de la ou des parcelles qui se trouvent sur votre propriété (voir la fiche descriptive) : ____________________

### 1. Coupes forestières et travaux forestiers

- ❖ À votre connaissance, y a-t-il déjà eu, récemment ou dans le passé, des coupes forestières ou d'autres types de travaux forestiers dans la forêt où se trouve mon site d'échantillonnage?

  OUI _____ NON_____ JE NE SAIS PAS_____

  - ○ Si oui, pouvez-vous me fournir de l'information sur le type de coupes ou de travaux qui ont été réalisés (ex. coupes de bois de chauffage, coupes totales, coupes partielles, éclaircies, plantations, coupes d'assainissement d'érablière, quelles espèces auraient été coupées, etc.)?

    ____________________
    ____________________
    ____________________
    ____________________
    ____________________
    ____________________
    ____________________

  - ○ En quelle(s) année(s) a été réalisé chaque type de travaux ou de coupes mentionnés ci-dessus?

    ____________________
    ____________________
    ____________________
    ____________________
    ____________________
    ____________________

  - ○ Quelle est la taille approximative des zones affectées par chaque type de travaux ou de coupes mentionnés ci-dessus? Au besoin, vous pouvez tracer, sur la carte, les zones ayant fait l'objet de coupes ou de travaux forestiers.

    ____________________
    ____________________
    ____________________
    ____________________
    ____________________
    ____________________

### 2. Plan d'aménagement forestier

- ❖ Avez-vous un plan d'aménagement forestier pour le secteur où se trouve mon site d'échantillonnage?

  OUI_____ NON_____

  - ○ Si oui, souhaitez-vous partager les informations contenues dans votre plan d'aménagement forestier concernant les travaux réalisés à l'emplacement de mon site d'échantillonnage?

    OUI_____ NON_____

    - ▪ Si oui, quel moyen souhaitez-vous utiliser pour partager l'information de votre plan d'aménagement forestier avec moi? Prenez note que mes coordonnées se trouvent à la fin du sondage au bas de la page.

      - Courriel_____ - Télécopieur (fax)_____ - Poste_____

      - Autre (précisez quel autre moyen vous souhaitez utiliser)____________________

### 3. Activités agricoles

- À votre connaissance, y a-t-il en ce moment ou y a-t-il déjà eu dans le passé des activités agricoles à l'endroit où se trouve mon site d'échantillonnage (ex. pâturage d'animaux en sous-bois, présence de cultures annuelles ou de pâturages avant de laisser la forêt repousser, etc.)?

  OUI_____ NON_____ JE NE SAIS PAS_____

  - Si oui, pouvez-vous m'informer à propos de ces activités (types d'activités, année(s), superficie, etc.)?

    ______________________________________________
    ______________________________________________
    ______________________________________________
    ______________________________________________
    ______________________________________________

### 4. Autres usages de votre forêt

- À votre connaissance, y a-t-il en ce moment ou y a-t-il déjà eu dans le passé des usages autres que des travaux forestiers ou des activités agricoles dans la forêt où se trouve mon site d'échantillonnage?

  OUI_____ NON_____ JE NE SAIS PAS_____

  - Si oui, pouvez-vous m'expliquer quels sont ces usages et en quelle(s) année(s) ont-ils été faits?

    ______________________________________________
    ______________________________________________
    ______________________________________________
    ______________________________________________

### 5. Collaboration future

- Seriez-vous intéressé(e) à poursuivre votre collaboration avec moi ou avec d'autres membres de mon équipe de recherche au cours des prochaines années, de manière à ce que nous puissions continuer d'étudier les impacts des changements climatiques et d'autres facteurs de stress sur les forêts privées du sud du Québec?

  OUI_____ NON_____

  - Si oui, souhaitez-vous me fournir votre adresse courriel pour que nous puissions entrer en contact avec vous plus facilement dans le futur? Prenez note que cette information sera traitée de manière confidentielle et ne sera pas divulguée à d'autres personnes.

    ______________________________________________

### 6. Autres commentaires?

______________________________________________
______________________________________________
______________________________________________
______________________________________________

**Merci d'avoir pris le temps de répondre à ce sondage et de me le retourner avant le 20 mai 2016!**

**Mes coordonnées**
Caroline Gagné, biol. M.Sc., candidate au doctorat en biologie
Université du Québec à Montréal et Université du Québec en Outaouais – Institut des sciences de la forêt tempérée

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Courriel : caroline.gagne@outlook.com
Adresse postale : [redacted]
Télécopieur (fax) : [redacted]

Annex D. Original set of explanatory variables.

| Explanatory variable | | | Variable transformation |
|---|---|---|---|
| Factor | Spatial scale | Temporal scale[a] | |
| **Local and stand variables** | | | |
| Soil pH | 30m | Long lasting | |
| Soil texture | 30m | Long lasting | |
| Agriculture area ($m^2$) | 60m | P1 | 3 root |
| Agriculture area ($m^2$) | 60m | P2 | 3 root |
| Agriculture area ($m^2$) | 60m | P3 | 3 root |
| Closed forest area ($m^2$) | 60m | P1 | |
| Closed forest area ($m^2$) | 60m | P2 | |
| Closed forest area ($m^2$) | 60m | P3 | |
| Closed forest area ($m^2$) | 60m | P4 | power 3 |
| Maple syrup production (Yes/No) | 60m | N/A | |
| Open forest area ($m^2$) | 60m | P3 | |
| Partial forest disturbance area ($m^2$) | 60m | A4 | |
| Pasture area ($m^2$) | 60m | P1 | |
| Pasture area ($m^2$) | 60m | P2 | 3 root |
| Regeneration area ($m^2$) | 60m | P1 | |
| Regeneration area ($m^2$) | 60m | P2 | |
| Stand initial condition (forested vs. non forested) | 60m | P0 | |
| **Landscape composition and disturbance variables** | | | |
| Abandoned agric. field area ($m^2$) | 2km | P3 | |
| Abandoned agric. field area ($m^2$) | 600m | P3 | |
| Agriculture area ($m^2$) | 2km | P1 | |
| Agriculture area ($m^2$) | 2km | P2 | |
| Agriculture area ($m^2$) | 2km | P3 | |
| Agriculture area ($m^2$) | 2km | P4 | |
| Agriculture area ($m^2$) | 600m | P1 | |
| Agriculture area ($m^2$) | 600m | P2 | |
| Agriculture area ($m^2$) | 600m | P3 | |
| Agriculture area ($m^2$) | 600m | P4 | |
| Closed forest area ($m^2$) | 2km | P1 | |
| Closed forest area ($m^2$) | 2km | P2 | |
| Closed forest area ($m^2$) | 2km | P3 | |
| Closed forest area ($m^2$) | 2km | P4 | |
| Closed forest area ($m^2$) | 600m | P1 | |
| Closed forest area ($m^2$) | 600m | P2 | |
| Closed forest area ($m^2$) | 600m | P3 | |
| Closed forest area ($m^2$) | 600m | P4 | |
| Open forest area ($m^2$) | 2km | P1 | |
| Open forest area ($m^2$) | 2km | P2 | |
| Open forest area ($m^2$) | 2km | P3 | |
| Open forest area ($m^2$) | 2km | P4 | |
| Open forest area ($m^2$) | 600m | P1 | |
| Open forest area ($m^2$) | 600m | P2 | 3 root |
| Open forest area ($m^2$) | 600m | P3 | |
| Open forest area ($m^2$) | 600m | P4 | |

| Explanatory variable | | | Variable transformation |
|---|---|---|---|
| **Factor** | **Spatial scale** | **Temporal scale[a]** | |
| Partial forest disturbance area ($m^2$) | 2km | A1 | 3 root |
| Partial forest disturbance area ($m^2$) | 2km | A2 | 3 root |
| Partial forest disturbance area ($m^2$) | 2km | A3 | |
| Partial forest disturbance area ($m^2$) | 2km | A4 | |
| Partial forest disturbance area ($m^2$) | 600m | A2 | |
| Partial forest disturbance area ($m^2$) | 600m | A4 | |
| Pasture area ($m^2$) | 2km | P1 | |
| Pasture area ($m^2$) | 2km | P2 | |
| Pasture area ($m^2$) | 2km | P4 | |
| Pasture area ($m^2$) | 600m | P1 | |
| Pasture area ($m^2$) | 600m | P2 | |
| Pasture area ($m^2$) | 600m | P4 | |
| Regeneration area ($m^2$) | 2km | P1 | 3 root |
| Regeneration area ($m^2$) | 2km | P2 | |
| Regeneration area ($m^2$) | 2km | P3 | 3 root |
| Regeneration area ($m^2$) | 2km | P4 | |
| Regeneration area ($m^2$) | 600m | P1 | |
| Regeneration area ($m^2$) | 600m | P2 | |
| Regeneration area ($m^2$) | 600m | P3 | 3 root |
| Regeneration area ($m^2$) | 600m | P4 | |
| Severe forest disturbance area ($m^2$) | 2km | A1 | 3 root |
| Severe forest disturbance area ($m^2$) | 2km | A2 | |
| Severe forest disturbance area ($m^2$) | 2km | A3 | 3 root |
| Severe forest disturbance area ($m^2$) | 2km | A4 | |
| Severe forest disturbance area ($m^2$) | 600m | A1 | |
| Severe forest disturbance area ($m^2$) | 600m | A2 | |
| Severe forest disturbance area ($m^2$) | 600m | A3 | |
| Severe forest disturbance area ($m^2$) | 600m | A4 | |
| Sparse forest area ($m^2$) | 2km | P1 | |
| Sparse forest area ($m^2$) | 2km | P2 | |
| Sparse forest area ($m^2$) | 2km | P4 | |
| Sparse forest area ($m^2$) | 600m | P1 | 3 root |
| Sparse forest area ($m^2$) | 600m | P2 | 3 root |
| Sparse forest area ($m^2$) | 600m | P4 | |
| Total % of partial forest disturbance | 2km | All | |
| Total % of severe forest disturbance | 2km | All | |
| Urban area ($m^2$) | 2km | P3 | 3 root |
| Urban area ($m^2$) | 2km | P4 | 3 root |
| Urban area ($m^2$) | 600m | P4 | 3 root |
| **Landscape configuration and connectivity variables** | | | |
| Distance to nearest forest disturbance (m) | N/A | A1 | |
| Distance to nearest forest disturbance (m) | N/A | A2 | |
| Distance to nearest forest disturbance (m) | N/A | A3 | |
| Distance to nearest forest disturbance (m) | N/A | A4 | 3 root |
| Distance to nearest forest edge (m) | N/A | P1 | |
| Distance to nearest forest edge (m) | N/A | P2 | 3 root |
| Distance to nearest forest edge (m) | N/A | P3 | 3 root |

| Explanatory variable | | | Variable transformation |
|---|---|---|---|
| Factor | Spatial scale | Temporal scale[a] | |
| Distance to nearest forest edge (m) | N/A | P4 | |
| Distance to nearest pasture (m) | N/A | P1 | 3 root |
| Distance to nearest pasture (m) | N/A | P2 | 3 root |
| Distance to nearest pasture (m) | N/A | P3 | 3 root |
| Distance to nearest pasture (m) | N/A | P4 | |
| Length of forest edge (m) | 2km | P1 | |
| Length of forest edge (m) | 2km | P2 | |
| Length of forest edge (m) | 2km | P3 | |
| Length of forest edge (m) | 2km | P4 | |
| Length of roads (m) | 2km | P1 | |
| Length of roads (m) | 2km | P2 | |
| Length of roads (m) | 2km | P3 | |
| Length of roads (m) | 2km | P4 | 3 root |
| Mean distance to forest disturbances (m) | N/A | A1 | |
| Mean distance to forest disturbances (m) | N/A | A2 | |
| Mean distance to forest disturbances (m) | N/A | A3 | |
| Mean distance to forest disturbances (m) | N/A | A4 | |
| Probability of connectivity | 2km | P1 | 3 root |
| Probability of connectivity | 2km | P2 | 3 root |
| Probability of connectivity | 2km | P3 | |
| Probability of connectivity | 2km | P4 | |
| Probability of connectivity | 2km | P1-P4 (slope) | |

[a] Temporal scale = P0 (1907), P1 (1930-40), P2 (1958), P3 (1983), P4 (2015), A1 (before 1930-40), A2 (between 1930-40 and 1958), A3 (between 1958 and 1983), A4 (between 1983 and 2015).

# CHAPITRE III

# THE RELATIONSHIP BETWEEN REMNANT TREES IN AGRICULTURAL LANDSCAPES AND LOCAL TREE AND SHRUB COMMUNITIES IN THE SURROUNDING FORESTS

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## 3.1 Abstract

Remnant trees in fragmented landscapes are often considered keystone structures for maintaining biodiversity. However, they are frequently overlooked in conservation efforts, even in agricultural areas where the conservation or restoration of larger forest patches can be conflicting with other land uses. In this study, that was conducted in southern Quebec, Canada, we mapped and included these remnant trees in the landscape as part of the forest cover to determine if they could be related to local shrub and tree community composition and structure at the specific and functional levels. We hypothesized that remnant trees in the landscape are associated with local forest communities by fostering the movement of seed dispersers and acting as sources of propagules. We also hypothesized that remnant trees that have persisted for a longer period (older trees) are more important than non-persistent ones (younger trees) for explaining community patterns in the nearby forests. We sampled 27 sites (forest communities) to assess the current tree and shrub abundance. We also gathered information about functional response traits from the literature and trait databases and computed functional diversity indexes and the community weighted mean for each site. The forest cover and remnant trees present in 2015 were then mapped within a 600 m radius around sampling sites. These remnant trees were also characterized as persistent (present in 2015 and 1983) or non-persistent (present only in 2015) using georeferenced aerial photographs from the year 1983. We then calculated landscape explanatory variables based on forest area, remnant tree density, and functional connectivity indexes computed from network analyses with and without remnant trees. We show that remnant trees spread throughout the agricultural matrix are important interconnecting features that contribute to increasing the number of possible paths and the presence of stepping stones for maintaining landscape connectivity when forest cover is below 60%. We also show that remnant trees, regardless of their persistence over time, are related to local shrub and tree communities in the surrounding forests. This relationship could stem from their role as sources of propagules and their capacity to foster the movement of seed dispersers in open land.

Keywords: remnant trees, landscape functional connectivity, network analyses, stepping stones, fragmentation, shrub and tree communities, response and specific diversity, community weighted mean.

## 3.2 Introduction

Over the last decades, landscape attributes have been widely recognized as important drivers impacting forest dynamics. Whether forest dynamics was tackled from the angle of landscape structure, land-use legacies, or external ecological memory, studies have shown that forest community assemblages were influenced by past or present-day landscape disturbances, land use, and permeability (Bellemare et al., 2002; Douda, 2010; Jamoneau et al., 2011; Jules & Shahani, 2003; Kimberley et al., 2016; Lloren et al., 2020; Takkis et al., 2018). On the other hand, some authors have focused their research on smaller landscape attributes such as remnant trees in agricultural land and their role in preserving biodiversity in fragmented landscapes. These remnant trees encompass isolated trees, also referred to as scattered or paddock trees in the literature (Fischer et al., 2010; Fischer & Lindenmayer, 2002a, 2002b; Gibbons & Boak, 2002; Manning et al., 2006; Prevedello et al., 2017), as well as trees organized in linear features, such as fencerows, hedgerows, riparian strips and windbreaks, and small islets, such as remnant woodlands on farmlands.

Remnant trees in agricultural landscapes are often considered keystone structures for maintaining biodiversity (Bodin et al., 2006; Gibbons et al., 2008; Manning et al., 2006, 2009; Moga et al., 2016). Indeed, they can act as seed dispersal hotspots by attracting many seed-dispersing animals (Harvey, 2000; Herrera & García, 2009; Lindenmayer & Laurance, 2017), sources of propagules for the surrounding area (Chazdon, 2003; Laborde et al., 2008; Lindenmayer & Laurance, 2017; Turner & Corlett, 1996), and habitat for a wide variety of plants and animals (Corbit et al., 1999; de Blois et al., 2002; Dunn, 2000; Fischer & Lindenmayer, 2002c; Lumsden & Bennett, 2005; McCollin et al., 2000; Prevedello et al., 2017). Moreover, by acting as stepping stones (i.e., habitat patches that facilitate species movement between other patches) or corridors (Fischer & Lindenmayer, 2002b; Harvey, 2000; Lindenmayer & Laurance, 2017; Manning et al., 2006), remnant trees can increase the level of connectivity in fragmented landscapes, hence fostering movement of seed dispersers across open lands (Cole et al., 2010; de Carvalho Vergne et al., 2016; Benayas et al., 2008), and connecting distant, isolated habitat patches.

Given the disproportionate importance remnant trees can have in fragmented landscapes (Fischer et al., 2010), it is puzzling that they are often overlooked in conservation efforts, especially in agricultural areas where the conservation or restoration of larger forest patches can be conflicting with other land uses. Similarly, ecological studies rarely consider remnant trees as small-size habitat patches and include them as part of the forest cover. As landscape attributes, these remnant trees could be part of the external ecological memory of nearby forest communities and affect how they reorganize after disturbances or throughout their development (Bengtsson et al., 2003; Johnstone et al., 2016; Perry, 1995).

This study builds on the work in chapters 1 and 2 of this thesis, that demonstrated the influence of past and current land use on present-day shrub and tree forest community patterns located in fragmented agricultural landscapes in southern Quebec, Canada. The forests in those studies were mapped using a conventional approach, and considered only forest patches larger than about 2 ha (Ministère des Forêts de la Faune et des Parcs [MFFP], 2015). This approach hence excluded all remnant trees in agricultural areas. In the present study, we mapped and included these remnant trees in the landscape as part of the forest cover to determine if they could be related to local shrub and tree community composition and structure at the specific and functional levels.

We hypothesize that remnant trees in the landscape are associated with local forest communities (species relative abundance, diversity and richness, and response diversity and trait values) by fostering the movement of seed dispersers and acting as sources of propagules. The scientific literature is scarce regarding the relationship between remnant trees in the landscape and tree and shrub community patterns in the nearby forest. However, in his review, Levin (1995) provided support for the proposition that outlying plants, which we call remnant trees in the present study, could be an important source of extraneous pollen and seeds for local populations. Aldrich & Hamrick (1998) also showed that spatially isolated trees in tropical forest pasture could dominate reproduction in nearby forest patches and lead to a genetic bottleneck. In light of this information, the effects of remnant trees on local communities could translate into a higher specific and functional response trait diversity for both shrubs and trees due to long-distance animal seed dispersal that could be fostered by remnant trees, though it could also translate into a lower specific and functional diversity through a bottleneck effect. We also hypothesize that remnant trees that have persisted for a longer period (older trees) are more important than non-persistent ones (younger trees) for explaining community patterns in the nearby forests.

## 3.3 Study area

The study area is located in the Montérégie region in southern Quebec, Canada, and covers about 983 km$^2$ (98 259 ha). It is located between 45.0 and 45.5° north, and between -74.4 and -73.8°

west (Figure 3.1). The mean annual temperature ranges from 5.6 to 7.4°C and the mean total annual precipitation ranges from 896 to 1120 mm. The topography is mostly flat with a maximum elevation of 40 m, except for the Rigaud (220 m) and Covey hills (343 m). The bedrock is mostly composed of dolomite and sandstone with some areas composed of limestone or granite. Surface deposits vary across the study area and are composed of marine, moraine, sand, gravel, and glacial till. Forest stands of this region are part of the sugar maple and bitternut hickory bioclimatic zone (Robitaille & Saucier, 1998) and are dominated by a variety of species, according to their successional stages, such as sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), white ash (*Fraxinus americana*), American basswood (*Tilia americana*), eastern white cedar (*Thuja occidentalis*), grey birch (*Betula populifolia*), and large-tooth aspen (*Populus grandidentata*). In this region, agricultural areas were at their peak around the 1890s, before starting to decline in the 1950s (Domon & Bouchard, 2007). The present-day forest of this region covers about 26-36% of the territory and is highly fragmented and scattered within an agricultural matrix with few large forest remnants such as those located on the Rigaud hill (> 5 000 ha) and around the Covey hill close to the Canada-United States border (> 10 000 ha).

## 3.4 Methodology

Three data sources were collected for this study. First, field sampling of forest communities in the study area was carried out to assess the current tree and shrub abundance at the local scale (30 m radius) in 64 sampling sites. Second, we gathered information about functional response traits from the literature and trait databases and computed functional diversity indexes and the community weighted mean (CWM) for each of our sites by combining species abundance and information on traits. Third, we assessed forest cover and remnant trees within a 600 m radius around the sampling sites in 2015 using ecoforestry maps and satellite imagery. The 600 m radius was chosen based on results from Gagné, Doyon, et al. (2022) and Gagné, Messier, et al. (2022), which indicated that forest cover was the most influential on tree and shrub community patterns at this spatial scale.

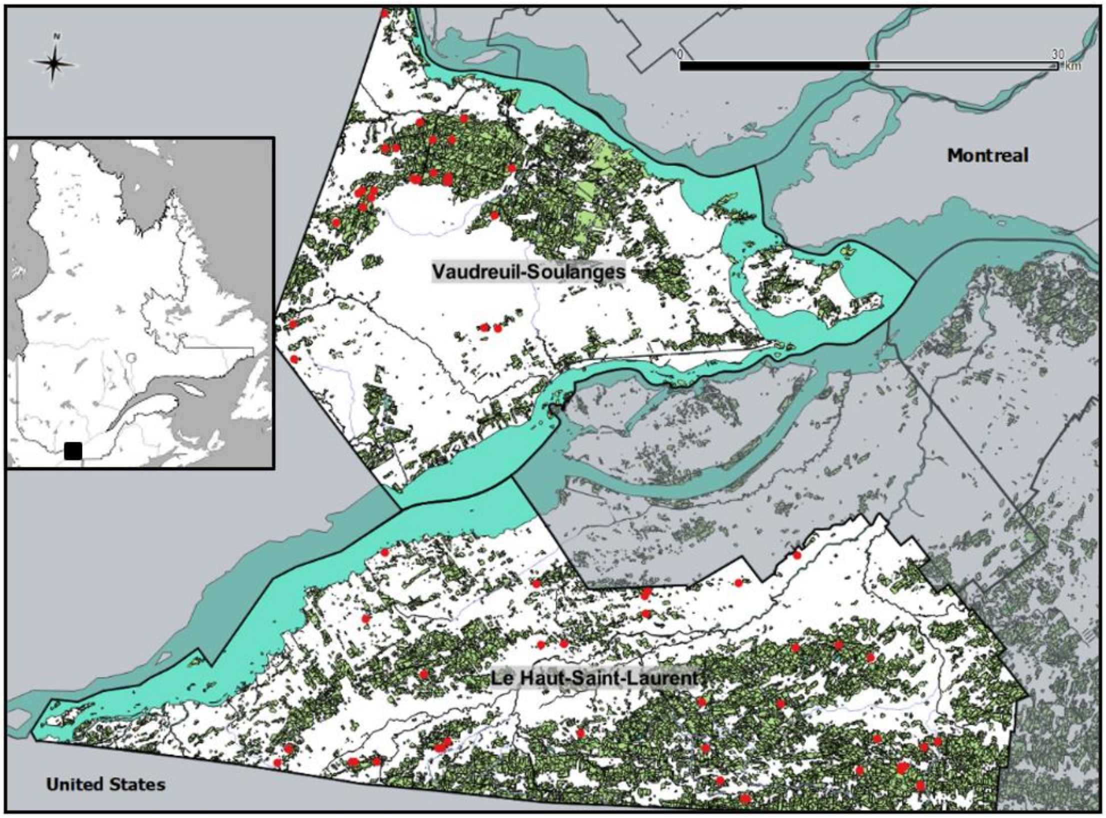


Figure 3.1. The study area and sampling sites (red dots) located in the regional county municipalities of Vaudreuil-Soulanges and Le Haut-Saint-Laurent, Quebec, Canada. Forests are represented by green patches.

### 3.4.1 Site selection

During the spring and summer 2015, 64 sites were established within mature forest patches to sample tree and shrub communities. Using ecoforestry maps (Ministère des Ressources naturelles et de la Faune [MRNF], 2009), sites having homogeneous pedological and topographic characteristics, as well as representing a diversity of historical forest disturbances and land uses such as clearcutting, agriculture, and pasture, were chosen. Site selection was based on recent ecoforestry maps (MRNF, 2009), on-site physical evidence of past use (presence of recent or old cut stumps, fences, sugar shacks or signs of maple syrup production), and discussions with private landowners. Tree communities in the sampling sites had various profiles, ranging from early to late-successional assemblages.

In the present study, we excluded sites that were embedded within landscapes with more than 60% of forest cover because we anticipated that connectivity would not be an issue in these landscapes. We thus kept a subset of 27 sites where forest covered between 1 and 60% of the territory within the 600 m radius in 2015 for subsequent analyses. However, since one of these sampling sites had no shrub species, we removed this site for shrub analyses and kept the other 26 sites.

### 3.4.2 Response variables based on tree and shrub sampling

From the centre of each sampling site, trees were sampled using the prism sweep technique using a factor 1 prism. All trees with a diameter at breast height (DBH) greater than 9.1 cm were accounted for during the prism sweep and tree species were identified. The basal area was obtained by summing the number of stems that were included in the sampling site during the sweep (i.e., stems whose images saw through the prism were within the real stems), and then multiplying the number of stems by the prism factor (one in this case). A total of 21 tree species were present in the 27 sampling sites kept for analyses (Table 3.1). The basal area was calculated for each tree species. Information on shrubs was collected within four circular subplots with a 2.5 m radius (total area of 78.5 $m^2$) located 20 m from the central point of the sampling sites in four directions (north, south, east and west). Within these subplots, shrubs were counted, and species were identified. A total of 29 shrub species were present in the 26 sampling sites kept for analyses (Table 3.1). In this study, shrubs include all woody species of shrubs, subshrubs, and vines as defined in the PLANTS Database (U.S. Department of Agriculture & National Resources Conservation Service, 2017).

Tree and shrub relative abundance was then computed for each species in each site based on the relative basal area and relative density, respectively. Tree and shrub richness and diversity were also calculated, where the diversity index corresponded to the effective number of species (Jost, 2006) and was based on the Shannon-Wiener index using the relative basal area and the relative frequency for all trees and shrubs, respectively.

### 3.4.3 Response variables based on functional response traits

#### 3.4.3.1 Selection of functional traits

Following shrub and tree sampling, a total of 14 functional response traits for shrubs and 17 for trees (Table 3.2) were selected to represent 5 different functions related to life cycle of plants, and particularly to their reproductive cycle (four out of five functions). These functions are 1) reproduction, 2) seed production, 3) seed dispersal, 4) seed germination and emergence, and 5) plant protection. All selected traits are involved in the avoidance, resistance, or resilience of species to different stresses or disturbances anticipated in the study area in the context of global changes, such as drought, windstorms, browsing by the white-tailed deer (*Odocoileus virginianus*), forest fragmentation, or an increase in disturbance frequency.

A search of the literature and trait databases was completed to obtain trait values for each species present in our sampling sites. The main trait databases consulted are the following: Traits of plants in Canada (TOPIC; Aubin et al., 2012), Fire effects information system (FEIS; Abrahamson, 2017), PLANTS database (U.S. Department of Agriculture & National Resources Conservation Service, 2017), Seed information database (SID; Royal Botanic Gardens Kew, 2017), Dispersal diaspore database ($D^3$; Hintze et al., 2013), Dryad (2017), Global wood density database (Chave et al., 2009; Zanne et al., 2009) and Stem specific density (Burton et al., 2017a, 2017b). When possible, only trait values related to site conditions similar to ours (e.g., soil texture) and to mature individuals were considered. In some cases, traits were reorganized from data found in the literature and databases. This is the case for traits related to root depth, for which a distinction was made between the bulk of the root system depth and the maximum depth some roots can reach. Concerning the dispersal mode, we combined both mammal endo- and exo-zoochory modes. Finally, maximum seed dispersal distance was computed for species according to their dispersal mode. Bird and mammal dispersal distances were estimated with the R function dispeRsal developed by Tamme et al. (2014) whereas wind dispersal distances were estimated following Greene & Johnson (1996).

The selected traits are quantitative, nominal, or binary multi-choice. For quantitative traits, the value for each species can be represented either by the mean of all relevant values found in the literature and databases (age of sexual maturity, age of optimal seed production, seed production, interval of mast years, seed persistence, seed mass, seed viability, and wood density traits) or by the maximum relevant value (maximum plant height and tree lifespan). For some traits, the nominal type was chosen either because of a lack of quantitative information for some species (maximum root depth) or because the only information available was in this format (growth and reproduction). Binary multi-choice traits are nominal traits where several of their levels (categories) can be true for a particular species and where each level is expressed as an independent binary variable (1/0). This type of variable is useful for representing species that can exhibit more than one trait value for a particular trait and was used here to represent the following traits: root system depth, vegetative reproduction and dispersal mode.

#### 3.4.3.2 Computation of response diversity and community weighted mean

Response diversity is represented by the functional dispersion index (FDis; Laliberté & Legendre, 2010) and was computed for each sampling site on all tree and shrub species, separately. A global FDis index from all response traits, and two FDis indexes for plant reproduction and seed dispersal traits were computed (Table 3.2). Among traits, all but one belong to a single group. Seed mass is the exception, since it is involved in seed production, dispersal as well as germination-emergence. The FD package (Laliberté et al., 2014; Laliberté & Legendre, 2010) in R (R Core Team, 2018) was used to compute FDis. We used the approach presented in Pavoine et al. (2009) to tackle binary multi-choice traits in the construction of the species-by-species distance matrix from functional traits, using the R package ade4 (Bougeard & Dray, 2018; Chessel et al., 2004; Dray et al., 2007; Dray & Dufour, 2007; Thioulouse et al., 2018).

The community weighted mean (CWM; Garnier et al., 2004) of each sampling site was then calculated for the nine response traits related to seed dispersal and plant reproduction. For quantitative traits, CWM was obtained by multiplying the relative abundance of each species present in a community ($p_i$) by its respective trait value ($trait_i$) and then summing all these $p_i$ x $trait_i$ values. For nominal and binary multi-choice traits, the CWM represents the relative abundance ($p_i$) of all species possessing each level of a particular trait. Each level of a trait is then represented as a trait in itself. The package FD (Laliberté et al., 2014; Laliberté & Legendre, 2010) in R (R Core Team, 2018) was used to compute the community weighted mean.

### 3.4.4 Explanatory variables at the landscape scale

#### 3.4.4.1 Analyses of aerial photographs and satellite imagery

The forest cover in 2015 was mapped within a 600 m radius around sampling sites using an updated version of the 2009 ecoforestry maps (MRNF, 2015). We then confirmed and adjusted the contour of forest patches using 2015 satellite images available through the Esri Wayback – Living Atlas platform (Esri, 2021b) so that forest patches on ecoforestry maps and satellite images were perfectly aligned. We also mapped remnant trees for 2015 within the 600 m radius landscapes with the same set of satellite images (Esri, 2021b). When some images were not available for 2015, we used images between 2016 and 2018 depending on their availability. In some cases, we also used images from the years 2011 to 2013 to validate the forest patch contour and identify remnant trees. The resolution of all satellite images ranged from 0.3 to 0.5 m, and their precision ranged from 4 to 10 m.

Three types of remnant trees were identified (Figure 3.2). First, isolated trees (IT) consisted of individual trees located outside standard forest patches, regardless of their distance to the forest edge, that had a treetop width larger than or equal to 5 m. Shrubs and immature trees were thus excluded. To consider two isolated trees as separate entities, their treetops had to be at least 5 m apart. If several trees were adjacent to one another, they were aggregated in either a linear feature (LF) or a wooded islet (WI). Linear features consisted of tree aggregations with an elongated shape, with trees arranged in a single or a few rows. Wooded islets consisted of tree aggregations that could take any other shape and that were either too small or too narrow to be included on ecoforestry maps. Linear features and wooded islets were either located away from a standard forest patch or extended from a forest patch into an open area. Trees with treetop widths larger than or equal to 5 m formed the backbone of linear features and wooded islets, though smaller trees and shrubs could also occur between mature trees.

Remnant trees were also characterized as either persistent (older) or non-persistent (younger) (Figure 3.2). Persistent remnant trees are those that were present in 2015 and 1983, while non-persistent remnant trees are those that were present in 2015 but absent in 1983. The georeferenced aerial photographs for 1983 (scale 1:15000) allowed us to distinguish between persistent and non-persistent remnant trees detected in 2015. All spatial analyses were conducted with ArcGIS Pro (Esri, 2021a).

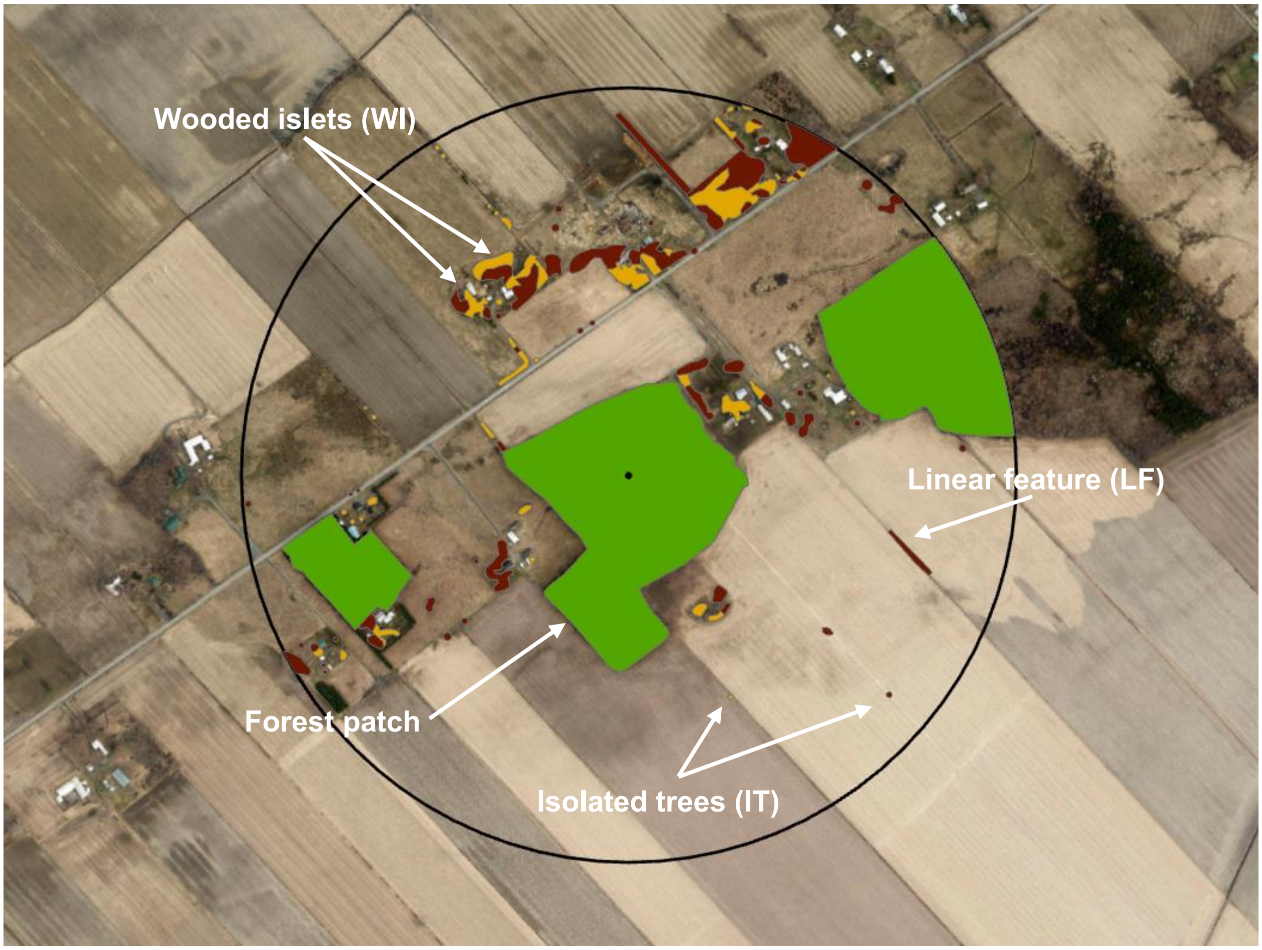


Figure 3.2. Difference between forest patches (green) and remnant trees (yellow and red) in a 600 m buffer around a sampling site. Remnant trees in red are persistent (older; present in 2015 and in 1983). Remnant trees in yellow are non-persistent (younger; present only in 2015).

#### 3.4.4.2 Computation of forest area, remnant tree density and functional connectivity indexes

In each 600 m landscape, we first calculated the forest area distributed within forest patches only (usual approach) for 2015. We then calculated explanatory variables that were based on both structural connectivity measures (density of remnant trees in the landscape) and functional connectivity indexes computed from spatial network analyses. In a spatial network, all forest patches are represented by nodes that can be connected with each other by edges, or connections (Figure 3.3). Two nodes are connected if the distance between them is smaller than a personalized potential dispersal distance (Minor & Urban, 2007). We used structural and functional connectivity measures in a complementary way, as functional connectivity indexes are specifically parameterized for animal-dispersed species, while structural connectivity variables are more general and might be better suited for wind-dispersed species.

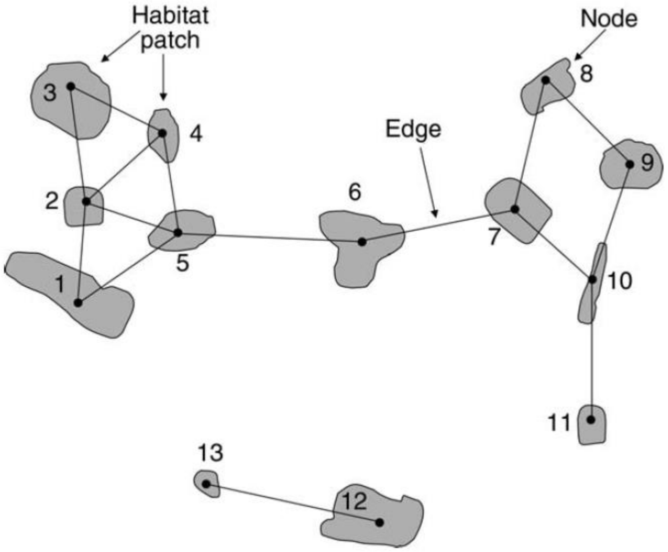


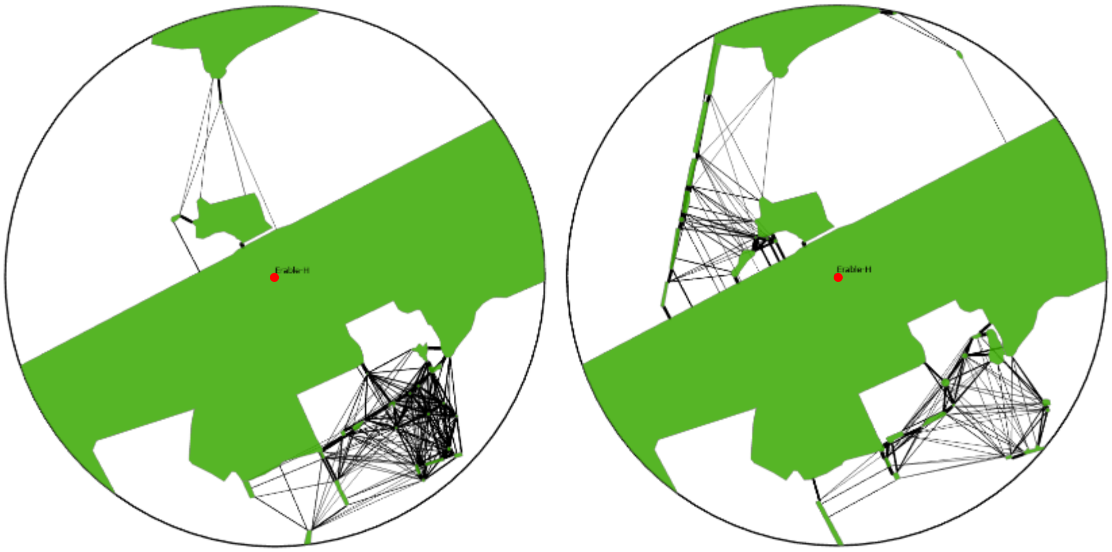
Figure 3.3. Schematic representation of a spatial network and basic terminology, in which nodes are forest patches and edges represent the connectivity between two nodes. Nodes that are not connected are farther apart than the dispersal distance used to parameterize the network. Figure from Minor & Urban (2007).

For structural connectivity, we calculated the density (ha/600 m buffer zone) of the different types of remnant trees (isolated trees, linear features, wooded islets, and all three types together) for each temporal persistence status (persistent, non-persistent, and both persistent and non-persistent together) based on the treetop (for isolated trees) or canopy (for linear features and wooded islets) area. This gave us a total of 12 explanatory variables related to remnant tree density.

For functional connectivity, we built 12 different spatial networks according to four node scenarios and three dispersal distances characterizing connections between nodes (Figure 3.4). The node scenarios are as follows: 1) nodes include forest patches only (usual approach), 2) nodes include forest patches and all remnant trees, 3) nodes include forest patches and persistent remnant trees, and 4) nodes include forest patches and non-persistent remnant trees. The nodes were characterized by their forest area.

Node scenario: Forest patches only

Node scenario: Forest patches + all RT



Node scenario: Forest patches + non-persistent RT

Node scenario: Forest patches + persistent RT

Figure 3.4. Examples of networks built in the 600 m radius landscape surrounding one sampling site showing the four node scenarios and one of the three dispersal distances characterizing connections between nodes (50 m). Remnant trees and forest patches that are connected according to this dispersal distance have a black line between them. Larger lines represent connections with higher direct dispersal probabilities. Connections for which the direct dispersal probability is at least 1% are shown. The red dot is the sampling site. RT = Remnant trees.

To characterize the symmetric connections between all pairs of nodes of the networks, we used the probabilistic approach (Saura & Pascual-Hortal, 2007), for which the probability of dispersal of a species between two nodes is a function of distance. We used the three distances (50 m, 100 m and 175 m) to establish negative exponential kernels. The distances were measured between the borders of the nodes (forest patches). These median dispersal distances cover the dispersal abilities of several small forest birds, such as Black-capped Chickadees (*Poecile atricapillus*) and White-breasted Nuthatches (*Sitta carolinensis*), larger birds such as Blue Jays (*Cyanocitta cristata*), and small mammals such as Eastern Chipmunks (*Tamias striatus*) and Grey Squirrels (*Sciurus carolinensis*). All these species can contribute to seed dispersal across fragmented landscapes and have shown varying gap-crossing abilities and perceptual ranges (Bélisle & Desrochers, 2002; Bowman & Fahrig, 2002; Desrochers & Hannon, 1997; Fitzgibbon, 1993; Grubb & Doherty, 1999; Rail et al., 1997; St. Clair et al., 1998; Stevenson et al., 2013; Zollner, 2000).

From these 12 networks, we calculated five network-based functional connectivity indexes (60 indexes in total) derived from the Probability of connectivity index (PC) with Conefor Sensinode 2.6 (Saura et al., 2011; Saura & Pascual-Hortal, 2007; Saura & Rubio, 2010; Saura & Torné, 2009). The Probability of connectivity is based on the concept of habitat availability and defined as the probability that two animals randomly placed within the landscape fall into habitat patches that are reachable from each other (Saura & Pascual-Hortal, 2007). The five indexes that were calculated are 1) ECA (equivalent connected area, a measure of the overall landscape connectivity), 2) $\sum$ dPC (sum of the relative importance of all elements in the landscape to maintain the overall connectivity), 3) $\theta$ $dPC_{intra}$ (relative contribution of intrapatch connectivity to maintain landscape connectivity), 4) $\theta$ $dPC_{flux}$ (relative contribution of interpatch connectivity to maintain landscape connectivity), and 5) $\theta$ $dPC_{connector}$ (relative contribution of patches acting as stepping stones to maintain landscape connectivity; Table 3.3).

Since several of these 60 functional connectivity indexes were correlated with each other (Baranyi et al., 2011), we performed one Principal Component Analysis (PCA) for each of the four node scenarios to reduce the collinearity and the number of explanatory variables. We kept the first three dimensions for each node scenario, that summarized about 98% of the variance, which resulted in a total of 12 dimensions related to functional connectivity indexes (Table 3.4).

## 3.5 Statistical analyses

To test whether remnant trees in the landscape are related to local forest communities, we first need to determine if they can increase landscape connectivity, and to what extent, by acting as stepping stones or by increasing interpatch connectivity compared to the forest cover that does not include remnant trees. To do so, we used a variant of the paired t-test based on the trimmed mean, where the lowest and largest values of a response variable are excluded before calculating the mean on the remaining values. This approach is a robust alternative to the classic paired t-test and allows for the presence of unequal variances (Mair & Wilcox, 2020). For each of the five functional connectivity indexes, we compared the trimmed mean value in the 27 landscapes surrounding the sampling sites according to two node scenarios: 1) forest patches and all remnant trees in the 600 m radius landscape were included as part of the forest cover when calculating the indexes, and 2) only forest patches were included. The approach used also provides a standardized effect size (explanatory measure of effect size), that can be useful for quantifying the differences between the trimmed means of both groups and inform us whether considering remnant trees has a large or negligeable impact on the landscape functional connectivity indexes. Values of effect size of 0.10, 0.30, and 0.50 correspond to small, medium, and large effect sizes, respectively (Mair & Wilcox, 2020; Wilcox & Tian, 2011).

We then constructed 17 multiple linear regression models aiming to explain each of the following response variables: tree species relative abundance, tree richness and diversity, shrub species relative abundance, shrub richness and diversity, three functional diversity indexes based on all traits (FDis), dispersal traits (FDis – Dispersal) and reproduction traits (FDis – Reproduction) for shrubs and trees separately, and the community weighted mean of traits related to dispersal and reproduction for shrubs and trees separately. Each of these 17 models represents a different combination of explanatory variables characterizing the forest area and landscape connectivity in the 600 m radius around the sampling sites (Table 3.5). We compared these models with the Akaike's information criterion ($AIC_c$) to identify those with the highest strength of evidence (Burnham & Anderson, 2002). Among these models, two included solely explanatory variables computed from the landscape forest patches only, without considering remnant trees (models M1 and M2), while all other models included explanatory variables computed from forest patches and remnant trees in the surrounding landscape. When either of the models M1 or M2 were included among the best and competing models ($\Delta\ AIC_c \leq 2$), we concluded that taking remnant trees into account did not significantly increase the model fit compared to models based on forest patches alone.

For all models, the following multiple linear regression assumptions were tested: residual normality, homoscedasticity and collinearity, outliers, relationship linearity, and spatial autocorrelation. When necessary, some response variables were transformed (e.g., ln and square root transformations) to improve the linearity of the relationships. We also occasionally removed some sampling sites that were shown to be influential outliers according to the residuals vs. leverage plot (sites that were outside the 0.5 level of the Cook's distance). For both shrubs and trees, only response variables showing a sufficient gradient across sampling sites were modeled and, among them, only those meeting the regression assumptions and for which at least one model happened to be statistically significant are reported in the results. All statistical analyses were completed with R (R Core Team, 2021) with the following packages: WRS2 (Mair & Wilcox, 2020), Hmisc (Harrell & Dupont, 2017), stats (R Core Team, 2021), car (Fox & Weisberg, 2011), ape (Paradis & Schliep, 2019), FactoMineR (Lê et al., 2008), and AICcmodavg (Mazerolle, 2017).

## 3.6 Results

The forest cover distributed within forest patches in the 27 landscapes ranges between 1% and 60% with a mean of 37% (Table 3.6). The forest cover is lower than 20% in eight landscapes, ranges from 20% to 40% in five landscapes, and from 40% to 60% in 14 landscapes. The total area of all remnant trees in these landscapes ranges from about 0.02% to 10% with a mean of 2% (Table 3.6). More precisely, the total area of persistent remnant trees ranges from 0% to 9,1% with a mean of 1.3%, and the total area of non-persistent remnant trees ranges from 0.02% to 3.5% with a mean of 0.7% (Table 3.6).

### 3.6.1 The role of remnant trees in increasing landscape connectivity

The results from the paired t-tests based on the trimmed means show that four of the five functional connectivity indexes increase when remnant trees are included as part of the forest cover in the 600 m landscapes compared to the same indexes calculated from forest patches alone. These results are consistent over the three dispersal distance thresholds used to build the networks (50 m, 100 m, and 175 m), though the effect of remnant trees is higher for indexes calculated from networks built at the smallest (50 m) dispersal distance threshold (e.g., effect size of 0.72, 0.68, and 0.63 for θ $dPC_{connector}$ computed with the 50 m, 100 m and 175 m distances, respectively; Table 3.7). The overall landscape connectivity (ECA) is significantly higher when remnant trees are considered (test statistic: -3.5 to -4.1, p-value: 0.0008 to 0.00), with an effect size between 0.06 and 0.07 (Table 3.7, Figure 3.5). This is also true for the sum of the relative importance of all elements in the landscape for maintaining the overall connectivity (∑ dPC), that is significantly higher when calculated from both forest patches and remnant trees compared to the same index calculated only from forest patches (test statistic: -3.6 to -3.8, p-value: 0.002, effect size: 0.29 to 0.44; Table 3.7, Figure 3.6). Moreover, the relative contribution of interpatch connectivity (θ $dPC_{flux}$) is significantly higher when remnant trees are added to the forest cover (test statistic: -2.6 to -3.5, p-value: 0.003 to 0.02), with an effect size between 0.19 and 0.28 (Table 3.7, Figure 3.7), which is also the case for the relative contribution of patches acting as stepping stones for maintaining landscape connectivity (θ $dPC_{connector}$; test statistic: -3.1 to -3.4, p-value: 0.003 to 0.006, effect size: 0.63 to 0.72; Table 3.7, Figure 3.8). The only index that is significantly higher when calculated from forest patches alone is the relative contribution of intrapatch connectivity (θ $dPC_{intra}$; test statistic: 3.3 to 4.4, p-value: 0.0004 to 0.005), with an effect size between 0.24 and 0.37 (Table 3.7, Figure 3.9).

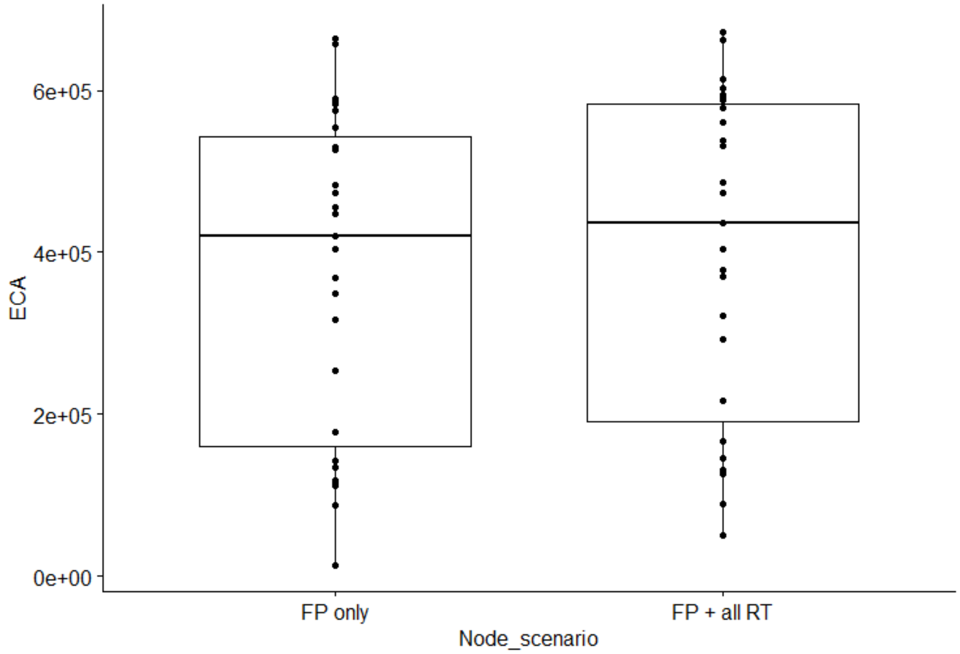


Figure 3.5. Overall landscape connectivity (ECA) based on the 50 m dispersal distance networks with and without remnant trees in the 600 m radius landscapes (n-27). FP only = forest patches only. FP + all RT = forest patches and all remnant trees. Effect size: 0.07.

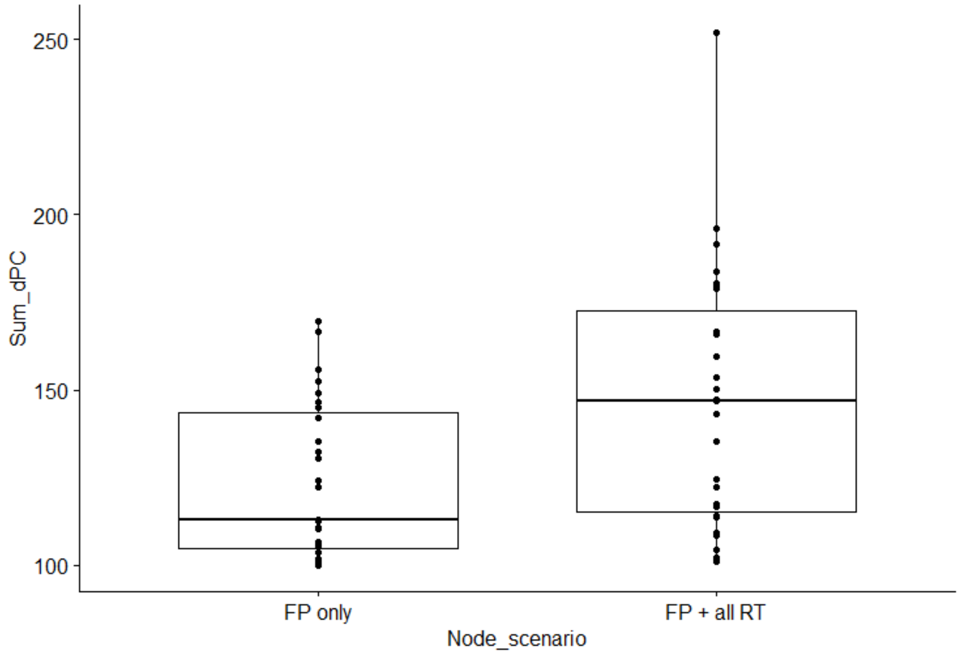


Figure 3.6. Sum of the relative importance of all elements in the landscape for maintaining the overall connectivity (∑ dPC) based on the 50 m dispersal distance networks with and without remnant trees in the 600 m radius landscapes (n-27). FP only = forest patches only. FP + all RT = forest patches and all remnant trees. Effect size: 0.44.

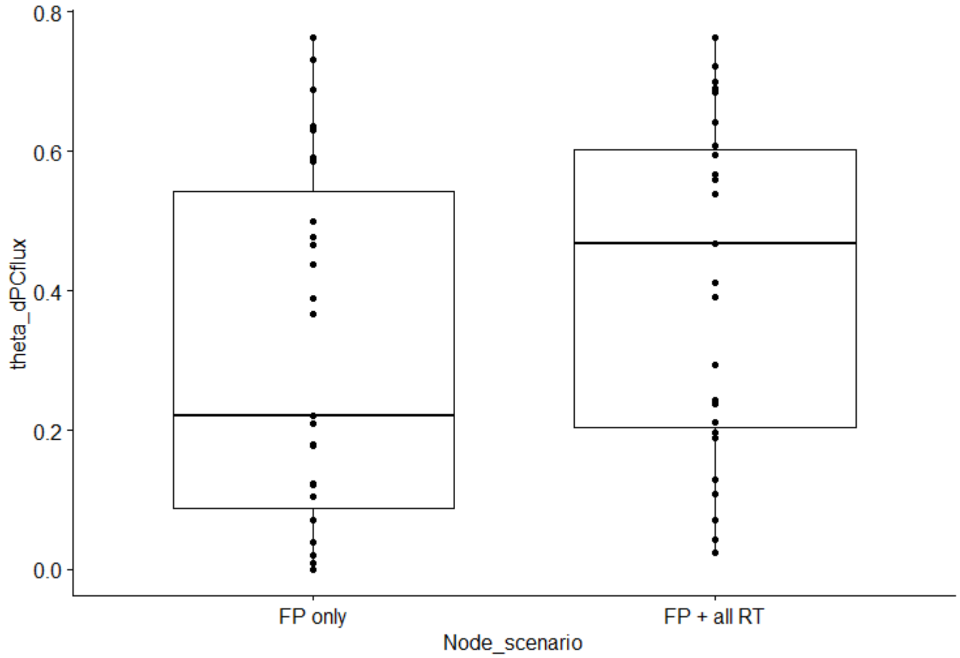


Figure 3.7. Relative contribution of interpatch connectivity for maintaining landscape connectivity (θ $dPC_{flux}$) based on the 50 m dispersal distance networks with and without remnant trees in the 600 m radius landscapes (n-27). FP only = forest patches only. FP + all RT = forest patches and all remnant trees. Effect size: 0.28.

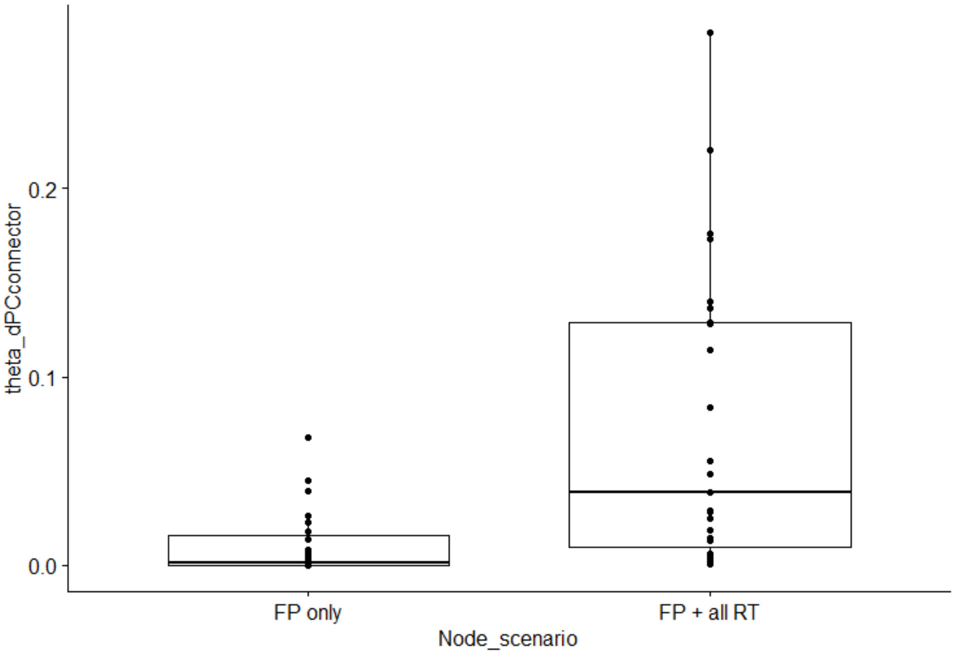


Figure 3.8. Relative contribution of patches acting as stepping stones for maintaining landscape connectivity (θ dPC$_{connector}$) based on the 50 m radius dispersal distance networks with and without remnant trees in the 600 m radius landscapes (n-27). FP only = forest patches only. FP + all RT = forest patches and all remnant trees. Effect size: 0.72.

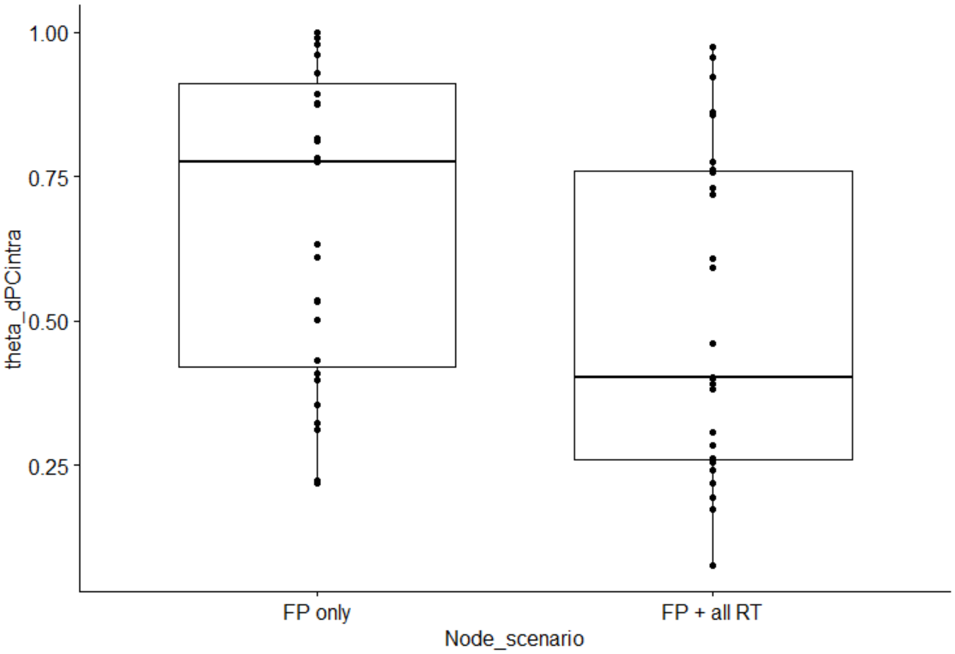


Figure 3.9. Relative contribution of intrapatch connectivity for maintaining landscape connectivity (θ dPC$_{intra}$) based on the 50 m dispersal distance networks with and without remnant trees in the 600 m radius landscapes (n-27). FP only = forest patches only. FP + all RT = forest patches and all remnant trees. Effect size: 0.37.

### 3.6.2 The relationship between remnant trees and local shrub and tree communities

For shrubs, from 21 response variables in total, we were able to model properly three of them (FDis – Seed dispersal, FDis – Reproduction and Shrub diversity; Table 3.8). Indeed, 10 response variables are not shown because none of their 17 models (groups of explanatory variables) had a good fit prior to the model selection. Another six response variables had an insufficient gradient that prevented us from building linear regression models. For two other response variables, the regression assumptions were not met. The adjusted $R^2$ of best and competing models for shrubs range from 0.0025 to 0.51. The low adjusted $R^2$ for Shrub diversity models (between 0.0025 and 0.17) remind us to be cautious when interpreting these results.

For trees, from 22 response variables in total, we were able to model properly six of them (Root crown sprouting, Dispersal mode – birds, Dispersal mode – wind, Reproduction – mostly seeds, Root sprouting, and *Tilia americana*; Table 3.8). For five response variables that were not modeled, none of their 17 models (groups of explanatory variables) had a good fit prior to the model selection. For another five response variables, the models selected by the $AIC_c$ had a very poor fit (none was significant), while six variables had an insufficient gradient that prevented us from building linear regression models. The adjusted $R^2$ of best and competing models for trees range from 0.16 to 0.47. In this study, our small sub-sample size (27 sampling sites for trees and 26 for shrubs) is an important limitation. Indeed, several shrub and tree species could not be modeled because their abundance was too low or they were absent from most of the selected sites.

#### 3.6.2.1 Strength of evidence of models with vs. without remnant trees

For shrubs, the set of best and competing models for FDis – Seed dispersal, FDis – Reproduction and Shrub diversity all include explanatory variables computed from both forest patches and remnant trees, while none include solely explanatory variables computed from forest patches alone (Table 3.8). Hence, remnant trees contribute to increasing the strength of evidence of the models for these three response variables. The two response diversity indexes and shrub diversity are all negatively associated with the functional landscape connectivity index related to stepping stones ($\theta\ dPC_{connector}$), which is summarized into the dimension 3 of the Principal Component Analysis (Table 3.4 and 3.8).

For trees, the sets of best and competing models for Root crown sprouting, Reproduction – Mostly seeds, Dispersal mode – Birds, and Dispersal mode – Wind also all include explanatory variables computed from both forest patches and remnant trees (Table 3.8), which means that remnant trees contribute to increasing the strength of evidence of models for these response variables. Remnant trees are positively associated with Root crown sprouting, Reproduction – Mostly seeds, and Dispersal mode – Wind, and negatively associated with Dispersal mode – Birds (Table 3.8).

For the set of best and competing models for *Tilia americana* and Root sprouting, the presence of the "forest patches only" models (M1 and M2) among the best models show that remnant trees fail to increase the strength of evidence of models beyond the threshold we had set ($\Delta$ $AIC_c > 2$).

#### 3.6.2.2 Strength of evidence of models with persistent vs. non-persistent remnant trees

For shrubs, the sets of best and competing models for FDis – Seed dispersal and FDis – Reproduction both include explanatory variables related to non-persistent remnant trees, while variables related to the persistent remnant trees are not among the best models (Table 3.8). For Shrub diversity, the best models mainly include explanatory variables related to non-persistent remnant trees, but one model includes an explanatory variable related to both persistent and non-persistent remnant trees. Hence, for Shrub diversity, all remnant trees might be of equal importance, regardless of their persistence over time. Here, it is worth noting that persistent and non-persistent remnant tree densities have a weak correlation coefficient ($r = 0.42$), indicating that they are independent of each other.

For trees, the set of best and competing models for Root crown sprouting and Dispersal mode – Birds include explanatory variables related to non-persistent remnant trees, while variables related to the persistent remnant trees are not among the best models (Table 3.8). For Reproduction – Mostly seeds and Dispersal mode – Wind, both persistent and non-persistent remnant trees are included among the best models, hence showing that all remnant trees are important regardless of their persistence.

## 3.7 Discussion

Our results first show that remnant trees had a positive effect on landscape connectivity which added to the effect of forest area. Their positive effect was mainly due to their important role as stepping stones based on their location within the network, as measured by the index $\theta$ $dPC_{connector}$, though their addition to the forest cover also added more habitat patches that increased the number of possible paths for maintaining landscape connectivity (interpatch connectivity; $\theta$ $dPC_{flux}$). Indeed, the effect size suggests a large positive effect of remnant trees on connectivity related to stepping stones and a small to moderate positive effect on interpatch connectivity. For all dispersal distances (50 m, 100 m and 175 m), remnant trees in the landscape were then generally close enough to each other and to other forest patches to be considered as connected in the networks, otherwise they would have contributed only to intrapatch connectivity. Consequently, despite the small area they occupy on the territory (mean of 2 % of the landscape area), we find that remnant trees are important features for maintaining landscape connectivity when forest cover is below 60%. Our results concur with Gibbons & Boak (2002) who showed that the loss of remnant trees led to a decrease in landscape connectivity.

However, the question now is whether there exists a threshold of forest area in the landscape below which remnant trees would play a preponderant role in maintaining connectivity. In this regard, we explored our data a little deeper and did another set of paired t-tests based on the trimmed means with the 18 landscapes with a forest cover below 50% (a subset of the 27 landscapes; unpublished data). These additional tests showed similar results to those with the 27 landscapes with a forest cover equal to or below 60%, but systematically showed a higher explanatory measure of effect size for all functional connectivity indexes. This result confirms that landscapes with a lower forest cover would benefit more from the presence of remnant trees to maintain connectivity. In this regard, Figure 3.10 shows that landscapes with a forest cover below 30% to 40% are those where remnant trees have the largest contribution as stepping stones to increasing landscape connectivity. This percentage of forest cover corresponds to the threshold below which the effects of fragmentation are more preponderant (Andrén, 1994). However, these results show a certain level of variability, where some landscapes do not benefit from the addition of remnant trees, independently of their forest cover. It is possible that remnant trees in those particular landscapes are too far from each other and from forest patches or too few to impact landscape connectivity.

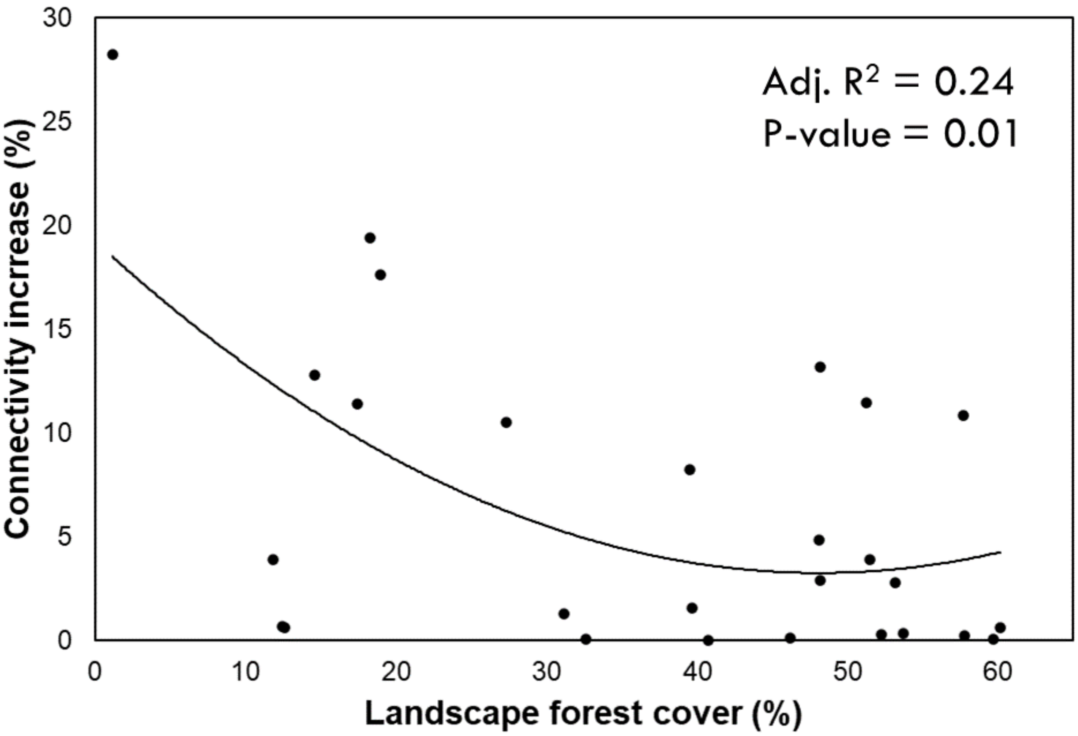


Figure 3.10. Gain in connectivity in landscapes where the forest cover is less than or equal to 60% when remnant trees and forest patches are included in the calculation of θ $dPC_{connector}$ compared to when the index is calculated from forest patches alone. θ $dPC_{connector}$ is calculated from networks parameterized with the 50 m dispersal distance.

### 3.7.1 Remnant trees are important landscape features that are linked to local forest community patterns

In our study, several models including remnant trees in the nearby landscape explain local shrub and tree community patterns. Indeed, for shrubs, the two response diversity indexes and specific diversity are negatively related to remnant trees acting as stepping stones within the landscape (Table 3.8). For trees, four community weighted mean traits out of six response variables are also related to both forest patches and remnant trees in the landscape (Table 3.8). The association between community patterns and connectivity variables computed with remnant trees suggests that remnant trees may act as sources of propagules dispersing in surrounding forest communities as proposed by Levin (1995) and demonstrated by Aldrich & Hamrick (1998). This association also suggests that remnant trees may foster the movement of seed dispersers in open lands (Fischer & Lindenmayer, 2002b; Harvey, 2000; Lindenmayer & Laurance, 2017; Manning et al., 2006), as anticipated from the network analyses where they acted as stepping stones for the three dispersal distances tested. However, the association between remnant trees and local forest community patterns could also indicate that the dispersal process is ongoing throughout the landscape. In other words, remnant trees could be the result of successful seed dispersal from the surrounding forests rather than be hotspots fostering dispersal, though both options may be true and occurring at the same time and cannot be distinguished in this study. Nonetheless, no matter the direction of the relationship, remnant trees in the landscape may represent low-density assemblages interconnected with forest communities through seed and pollen dispersal (Levin, 1995) and contribute to the external ecological memory of nearby forest communities (Johnstone et al., 2016). In this context, the role of remnant trees is not to be neglected.

Our results show that remnant trees are important landscape features and add to the growing scientific literature on the subject (Aldrich & Hamrick, 1998; Bodin et al., 2006; Fischer et al., 2010; Gibbons et al., 2008; Levin, 1995; Manning et al., 2006, 2009; Moga et al., 2016). Moreover, our results concur with other studies showing that landscape features, such as broad land-use classes, forest disturbances, and landscape configuration, are important drivers of forest community assemblages in local sites (Bellemare et al., 2002; de Blois et al., 2001; Douda, 2010; Gagné, Doyon, et al., 2022; Gagné, Messier, et al., 2022; Jamoneau et al., 2011; Jules & Shahani, 2003; Kimberley et al., 2016; Lloren et al., 2020; Takkis et al., 2018). Thus, the landscape influence on local communities may not be restricted to the more extensive events or features, but may also include smaller features such as isolated trees or small fragments (Bodin et al., 2006).

### 3.7.2 Persistent and non-persistent remnant trees are important

Contrary to what we expected, persistent remnant trees do not stand out as being more important in explaining shrub and tree community structure in local sites compared to non-persistent remnant trees. In fact, in some models, non-persistent remnant trees were found to be the most important, while in other models, both types were important (Table 3.8). This could partly be explained by the fact that despite the younger age of non-persistent remnant trees, many of them have established before 1983, but were not considered as persistent because the diameter of their crown on the 1983 aerial photos was smaller than the mapping threshold (5 m). This methodological choice could then have blurred the temporal aspect of the results. Moreover, in this study, only remnant trees present in 2015 (non-persistent), as well as those present in 2015 and 1983 (persistent), were considered. It is then plausible that more ancient remnant trees from the years 1930-40 and 1958 that died before 2015, as well as those that were present in 1983, but that were not considered because they died before 2015, would also have influenced local forest assemblages (Gagné, Doyon, et al., 2022; Gagné, Messier, et al., 2022). Hence, as expected, it is possible that historical remnant trees had provided a better explanatory power for the response variables for which no significant relationships were found with present-day remnant trees. Although interesting, the effect of historical remnant trees was outside the scope of this study and was not investigated.

The notion of persistence refers here to the length of time a tree has been living and can thus also refer to its age (or the stand age) and size. The fact that non-persistent remnant trees, mostly represented by smaller trees, were shown to be important in agricultural landscapes leads us to wonder whether remnant shrubs could influence local forest dynamics in the same way as remnant trees. The importance of shrubs in agricultural land for providing sources of propagules, wildlife habitat and fostering movement across open land has been recognized since the 1940s (Davison, 1940; de Carvalho Vergne et al., 2016; Gallé et al., 2017), though most studies have emphasized the role of trees rather than shrubs. It is then possible that remnant shrubs, organized in fencerows, riparian strips and other linear or non-linear features, act as dispersal hotspots fostering seed dispersal and are sources of propagules similar to remnant trees. Future studies are however needed to confirm this hypothesis.

## 3.8 Conclusion

In this study, we showed that remnant trees in the landscape, regardless of their persistence over time, were interrelated to shrub and tree community patterns in the surrounding forests and that this relationship could stem from their role as sources of propagules and stepping stones increasing landscape connectivity for seed dispersers. Those trees may then be part of the external ecological memory of forest communities and contribute to their development (Bengtsson et al., 2003). In this context, we agree with Manning et al. (2006) that remnant trees are keystone features that need to be preserved in fragmented landscapes.

By providing a continuous tree cover across landscapes that facilitates species movement (Manning et al., 2009), remnant trees in agricultural land could contribute to increasing forest resilience to climate change. In the same way, remnant trees with complementary functional traits could be introduced in fragmented landscapes to increase the overall functional diversity and connectivity, and thus the overall resilience (Messier et al., 2019). Further studies are however needed to determine to what extent remnant trees with complementary traits would be able to disperse their seeds into adjacent forests and whether dispersal would be limited to the forest edge or extend deeper into the forest.

Benayas et al. (2008) consider remnant trees a promising, less-conflicting, more flexible, and cost-effective way for restoring biodiversity and landscape connectivity in agricultural land compared to approaches aimed only at restoring larger forest patches. We agree with these authors and can easily see their idea extended to agroforestry, where the establishment of windbreaks, buffer strips and other woody structures could help restore connectivity between larger forest patches (Jose, 2012). Of course, remnant trees and agroforestry systems cannot support the same level of biodiversity as larger forests but can nevertheless represent an interesting complementary approach that should not be overlooked (Fischer et al., 2010; Fischer & Lindenmayer, 2002c; Manning et al., 2009; Schwartz, 1999; Shafer, 1995; Turner & Corlett, 1996).

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## 3.11 Tables

Table 3.1. List of tree and shrub species present in the sampling sites.

| **Trees (n-27 sampling sites)** | **Shrubs (n-26 sampling sites)** |
|---|---|
| *Acer rubrum* | *Acer pensylvanicum* |
| *Acer saccharum* | *Amelanchier spp.* |
| *Betula alleghaniensis* | *Cornus alternifolia* |
| *Betula papyrifera* | *Cornus stolonifera* |
| *Carya cordiforma* | *Corylus cornuta* |
| *Fagus grandifolia* | *Crataegus spp*. |
| *Fraxinus americana* | *Diervilla lonicera* |
| *Fraxinus pennsylvanica* | *Dirca palustris* |
| *Ostrya virginiana* | *Frangula alnus* |
| *Pinus strobus* | *Ilex mucronata* |
| *Populus balsamifera* | *Lonicera canadensis* |
| *Populus grandidantata* | *Menispermum canadense* |
| *Populus tremuloides* | *Parthenocissus quinquefolia* |
| *Prunus serotina* | *Prunus virginiana* |
| *Quercus alba* | *Rhamnus cathartica* |
| *Quercus macrocarpa* | *Ribes spp.* |
| *Salix spp*. | *Rubus allegheniensis* |
| *Thuja occidentalis* | *Rubus idaeus* |
| *Tilia americana* | *Rubus odoratus* |
| *Tsuga canadensis* | *Rubus pubescens* |
| *Ulmus rubra* | *Sambucus pubens* |
|  | *Taxus canadensis* |
|  | *Toxicodendron radicans* |
|  | *Vaccinium myrtilloides* |
|  | *Viburnum lantanoides* |
|  | *Viburnum nudum var. cassinoides* |
|  | *Viburnum lentago* |
|  | *Vitis riparia* |
|  | *Zanthoxylum americanum* |

Table 3.2. Selected functional response traits for shrubs and trees.

| Response trait | Definition | Process | Tree trait | | Shrub trait | |
|---|---|---|---|---|---|---|
| | | | Type[a] | Level | Type | Level |
| **Root system depth** | Depth where bulk of roots is located. | Plant protection | B | S (1/0)[b]<br>D (1/0) | --- | --- |
| **Maximal root depth** | Maximal depth reached by roots. | Plant protection | N | S<br>I<br>D | --- | --- |
| **Growth** | Growth rate. | Plant protection | N | S[c]<br>M<br>F | N | S<br>M<br>F |
| **Physical defence** | Presence of spinescence or urticant oil. | Plant protection | --- | --- | D | Yes (1)<br>No (0) |
| **Wood density** | Stem wood density expressed as the oven dry weight per green volume (kg/m$^3$). | Plant protection | Q | --- | Q | --- |
| **Reproduction** | Reproduction mode. | Reproduction | N | MS[d]<br>MV<br>SV<br>SO | N | MS<br>MV<br>SV<br>SO |
| **Vegetative reproduction** | Vegetative reproduction mode. | Reproduction | B | N (1/0)[e]<br>L (1/0)<br>SS (1/0)<br>RS (1/0)<br>RCS (1/0)<br>RHS (1/0)<br>STS (1/0)<br>F (1/0) | B | N (1/0)<br>A (1/0)<br>USS (1/0)<br>L (1/0)<br>SS (1/0)<br>RS (1/0)<br>RCS (1/0)<br>RHS (1/0)<br>SLS (1/0) |
| **Age sexual maturity** | Age at first reproduction. | Seed production | Q | --- | Q | --- |
| **Age optimal seed production** | Age at which a plant begins to produce the maximum number of seeds per seed crop. | Seed production | Q | --- | --- | --- |
| **Seed production** | Number of seeds per individual. | Seed production | Q | --- | --- | --- |
| **Interval mast years** | Number of years between higher-than-average seed production years. | Seed production | Q | --- | Q | --- |
| **Plant lifespan** | Maximal natural plant longevity (above ground parts). | Seed production | Q | --- | B | S (0/1)[f]<br>M (0/1)<br>L (0/1) |

| Response trait | Definition | Process | Tree trait | | Shrub trait | |
|---|---|---|---|---|---|---|
| | | | Type[a] | Level | Type | Level |
| **Dispersal mode** | Seed dispersal vector. | Dispersal | B | G (1/0)[g]<br>W (1/0)<br>M (1/0)<br>B (1/0) | B | G (1/0)<br>W (1/0)<br>M (1/0)<br>B (1/0) |
| **Maximal seed dispersal distance** | Maximal seed dispersal distance estimated for bird, mammal or wind dispersal. | Dispersal | Q | --- | Q | --- |
| **Maximal plant height** | Species' maximal potential height (m). | Dispersal | Q | --- | Q | --- |
| **Seed persistence** | Number of years during which seeds are viable in the seed bank. | Germination / emergence | Q | --- | Q | --- |
| **Seed viability** | Percentage of viable seeds per kg of seeds or germination rate (%). | Germination / emergence | Q | --- | Q | --- |
| **Seed mass** | Number of seeds per kg. | Seed production<br>Dispersal<br>Germination / emergence | Q | --- | Q | --- |

[a] Type of trait: N – nominal; Q – quantitative; B – binary multi-choice; D – dichotomous.

[b] Tree root system depth and maximal root depth: ≤ 1m – Shallow (S); Between 1m and 3m – Intermediate (I); ≥ 3m – Deep (D).

[c] Growth: Slow (S); Medium (M); Fast (F).

[d] Reproduction: Mostly sexual (MS); Mostly vegetative (MV); Sexual + vegetative (SV); Sexual only (SO).

[e] Vegetative reproduction: None (N); Layering (L), Stump sprouting (SS); Root sprouting (RS); Root crown sprouting (RCS); Rhizome sprouting (RHS); Stem sprouting (STS); Fragment (F); Apomixis (A); Underground stem sprouting (USS); Stolon sprouting (SLS).

[f] Shrub lifespan: < 20 years – Short (S); Between 20 and 50 years – Moderate (M); > 50 years – Long (L).

[g] Dispersal mode: Gravity (G); Wind (W); Mammals (M); Birds (B).

Table 3.3. The five functional connectivity indexes based on the Probability of connectivity used in this study.

| **Index** | **Description** | **Interpretation** | **Reference** |
|---|---|---|---|
| ECA | Equivalent connected area. A measure of the overall landscape connectivity based on the Probability of connectivity index (PC). | Larger values of ECA in landscapes where connectivity is higher. | Saura et al. (2011) |
| $\sum$ dPC | Sum of the relative importance of all elements in the landscape for maintaining the overall connectivity. | Larger values in landscapes where there are several possible paths (important habitat patches) to maintain habitat connectivity. $\sum$ dPC is lower in landscapes where there are only one or a few alternative paths (important habitat patches) to maintain connectivity. | Saura and Rubio (2010) |
| $\theta$ $dPC_{intra}$ | Relative contribution of intrapatch connectivity for maintaining landscape connectivity. | Higher values when landscape connectivity is mainly achieved through habitat availability within patches (e.g., when there are one or a few larger habitat patches accounting for most habitat area). Lower values when landscape connectivity is mainly achieved through interpatch connectivity (e.g., when most habitat is spread within several smaller interconnected patches). | Saura and Rubio (2010) |
| $\theta$ $dPC_{flux}$ | Relative contribution of interpatch connectivity for maintaining landscape connectivity. | Higher values when habitat is spread within several interconnected patches throughout the landscape. Lower values when habitat is concentrated in one or a few larger patches in the landscape and when patches are not interconnected. | Saura and Rubio (2010) |
| $\theta$ $dPC_{connector}$ | Relative contribution of patches acting as stepping stones for maintaining landscape connectivity. | Higher values in landscapes where more patches act as connecting element between other patches. Lower values in landscapes where no or fewer patches act as connecting element between other patches. | Saura and Rubio (2010) |

Table 3.4. Functional connectivity indexes and total forest area summarized in the first three PCA dimensions for each of the four network node scenarios.

| **Functional connectivity indexes**[a] | **Dim.1**[b] | **Dim.2** | **Dim.3** |
|---|---|---|---|
| Total forest area | | +++[c] | |
| ECA_50 m | | +++ | |
| ∑ dPC_50 m | +++ | | |
| θ $dPC_{intra}$_50 m | - - - | | |
| θ $dPC_{flux}$_50 m | +++ | | |
| θ $dPC_{connector}$_50 m | ++ | | ++ |
| ECA_100 m | | +++ | |
| ∑ dPC_100 m | +++ | | |
| θ $dPC_{intra}$_100 m | - - - | | |
| θ $dPC_{flux}$_100 m | +++ | | |
| θ $dPC_{connector}$_100 m | ++ | | ++ |
| ECA_175 m | | +++ | |
| ∑ dPC_175 m | +++ | | |
| θ $dPC_{intra}$_175 m | - - - | | |
| θ $dPC_{flux}$_175 m | +++ | | |
| θ $dPC_{connector}$_175 m | ++ | | ++ |

[a] Node scenarios: 1) nodes include forest patches only, 2) nodes include forest patches and all remnant trees, 3) nodes include forest patches and persistent remnant trees, and 4) nodes include forest patches and non-persistent remnant trees.

[b] For the four node scenarios, the first PCA dimension summarizes between 62.7 and 69.5% of the variance, the second dimension summarizes between 21.0 and 25.8% of the variance, and the third dimension summarizes between 7.8 and 12.1% of the variance.

[c] The + and - signs indicate the strength and direction of the relationship between the indexes and dimensions, +++/- - - summarizing a correlation coefficient ranging from 0.800-0.999 and ++/- - a correlation coefficient ranging from 0.600-0.799. Lower coefficients are not reported in this table.

Table 3.5. Set of 17 multiple linear regression models compared for each response variable.

| Model | Explanatory variable | Description of explanatory variable |
|---|---|---|
| **Usual approach – Forest patches only** | | |
| M1 | Total forest area_Patch only | Total forest area in the 600m-landscape when considering only forest patches, without considering any remnant tree (usual approach). |
| M2 | Patch only_Dim.1 + Patch only_Dim.2 + Patch only_Dim.3 | Three PCA dimensions based on functional connectivity indexes and total forest area in the 600m-landscape calculated from forest patches only, without considering any remnant tree (usual approach). |
| **Forest patches and persistent and non-persistent remnant trees** | | |
| M3 | PNP_Dim.1 + PNP_Dim.2 + PNP_Dim.3 | Three PCA dimensions based on functional connectivity indexes and total forest area in the 600m-landscape calculated from forest patches and persistent and non-persistent remnant trees (PNP; persistent and non-persistent). The three remnant tree types are considered altogether (isolated trees, linear features and wooded islets). |
| M4 | M1 + PNP_IT | Total forest area in forest patches in the 600m-landscape and density of persistent and non-persistent isolated trees. |
| M5 | M1 + PNP_LF | Total forest area in forest patches in the 600m-landscape and density of persistent and non-persistent linear features. |
| M6 | M1 + PNP_WI | Total forest area in forest patches in the 600m-landscape and density of persistent and non-persistent wooded islets. |
| M7 | M1 + PNP_3 types | Total forest area in forest patches in the 600m-landscape and density of persistent and non-persistent isolated trees, linear features and wooded islets. |
| **Forest patches and persistent remnant trees** | | |
| M8 | PO_Dim.1 + PO_Dim.2 + PO_Dim.3 | Three PCA dimensions based on functional connectivity indexes and total forest area in the 600m-landscape calculated from forest patches and persistent remnant trees (PO; persistent only). The three remnant tree types are considered altogether (isolated trees, linear features and wooded islets). |
| M9 | M1 + PO_IT | Total forest area in forest patches in the 600m-landscape and density of persistent isolated trees. |
| M10 | M1 + PO_LF | Total forest area in forest patches in the 600m-landscape and density of persistent linear features. |
| M11 | M1 + PO_WI | Total forest area in forest patches in the 600m-landscape and density of persistent wooded islets. |
| M12 | M1 + PO_3 types | Total forest area in forest patches in the 600m-landscape and density of persistent isolated trees, linear features and wooded islets. |
| **Forest patches and non-persistent remnant trees** | | |
| M13 | NP_Dim.1 + NP_Dim.2 + NP_Dim.3 | Three PCA dimensions based on functional connectivity indexes and total forest area in the 600m-landscape calculated from forest patches and non-persistent remnant trees (NP; non-persistent only). The three remnant tree types are considered altogether (isolated trees, linear features and wooded islets). |
| M14 | M1 + NP_IT | Total forest area in forest patches in the 600m-landscape and density of non-persistent isolated trees. |

| | | |
|---|---|---|
| M15 | M1 + NP_LF | Total forest area in forest patches in the 600m-landscape and density of non-persistent linear features. |
| M16 | M1 + NP_WI | Total forest area in forest patches in the 600m-landscape and density of non-persistent wooded islets. |
| M17 | M1 + NP_3 types | Total forest area in forest patches in the 600m-landscape and density of non-persistent isolated trees, linear features and wooded islets. |

Table 3.6. Mean area of forest cover in the 600 m radius landscapes (n-27) distributed within forest patches, non-persistent remnant trees (RT), persistent remnant trees, and all remnant trees together.

| | Mean | Min. | Max. | SD |
|---|---|---|---|---|
| **Forest area – patches only** | | | | |
| **m$^2$** | 421,051 | 13,132 | 679,530 | 203,109 |
| **(%)** | (37.27) | (1.16) | (60.15) | (17.98) |
| **Forest area – non-persistent RT** | | | | |
| **m$^2$** | 7,867 | 237 | 39,260 | 7,848 |
| **(%)** | (0.70) | (0.02) | (3.47) | (0.69) |
| **Forest area – persistent RT** | | | | |
| **m$^2$** | 14,740 | 0 | 103,305 | 20,995 |
| **(%)** | (1.30) | (0.00) | (9.14) | (1.86) |
| **Forest area – all RT** | | | | |
| **m$^2$** | 22,606 | 237 | 111,948 | 25,316 |
| **(%)** | (2.00) | (0.02) | (9.91) | (2.24) |

Table 3.7. Results from the paired t-tests on the trimmed means comparing each functional connectivity index in the 600 m radius landscapes (n-27) with and without remnant trees. For this test, the scenario with remnant trees includes all remnant trees (persistent and non-persistent). All indexes were calculated from networks built with the three dispersal distances (50 m, 100 m, and 175 m).

| **Functional connectivity index** | **Dispersal distance** | | |
|---|---|---|---|
| | **50 m** | **100 m** | **175 m** |
| **ECA** | | | |
| Test statistic | -3.5 | -3.8 | -4.1 |
| p-value[a] | (**) | (**) | (***) |
| Explanatory measure of effect size | 0.07 | 0.07 | 0.06 |
| **∑ dPC** | | | |
| Test statistic | -3.8 | -3.7 | -3.6 |
| p-value | (**) | (**) | (**) |
| Explanatory measure of effect size | 0.44 | 0.34 | 0.29 |
| **θ dPC$_{flux}$** | | | |
| Test statistic | -3.5 | -2.8 | -2.6 |
| p-value | (**) | (*) | (*) |
| Explanatory measure of effect size | 0.28 | 0.21 | 0.19 |
| **θ dPC$_{connector}$** | | | |
| Test statistic | -3.1 | -3.3 | -3.4 |
| p-value | (**) | (**) | (**) |
| Explanatory measure of effect size | 0.72 | 0.68 | 0.63 |
| **θ dPC$_{intra}$** | | | |
| Test statistic | 4.4 | 3.6 | 3.3 |
| p-value | (***) | (**) | (**) |
| Explanatory measure of effect size | 0.37 | 0.29 | 0.24 |

[a] p-values: (***) $p \leq 0.001$; (**) $0.001 < p \leq 0.01$; (*) $0.01 < p \leq 0.05$; (.) $0.05 < p \leq 0.1$; ( ) $p > 0.1$.

Table 3.8. Best and competing models for response variables related to shrubs and trees.

| # | Best and competing models | $\Delta$ AIC$_c$ | Model adj. $R^2$ (p-value)[a] | Response variable description |
|---|---|---|---|---|
| **Shrubs** | | | | |
| **FDis – Seed dispersal** | | | | Functional dispersion of seed dispersal traits |
| M13 | + NP_Dim.1 ( ) + NP_Dim.2 ( ) - NP_Dim.3 (**) | 0.00 | 0.2898 (*) | |
| **FDis – Reproduction** | | | | Functional dispersion of plant reproduction traits |
| M13 | - NP_Dim.1 ( ) + NP_Dim.2 (.) - NP_Dim.3 (***) | 0.00 | 0.5057 (***) | |
| **Shrub diversity** | | | | Shrub specific diversity |
| M14 | + M1 ( ) - NP_IT (*) | 0.00 | 0.1715 (*) | |
| M15 | + M1 ( ) + NP_LF ( ) | 0.76 | 0.002465 ( ) | |
| M4 | - M1 ( ) - PNP_IT (*) | 1.74 | 0.1142 (.) | |
| M13 | - NP_Dim.1 ( ) + NP_Dim.2 ( ) - NP_Dim.3 (*) | 1.98 | 0.1701 (.) | |
| **Trees** | | | | |
| ***Tilia americana*** | | | | Relative abundance of *Tilia americana* |
| M1 | - Total forest area_Patch only (***) | 0.00 | 0.3628 (***) | |
| M12 | - M1 (***) + PO_3_types ( ) | 1.47 | 0.3686 (**) | |
| M11 | - M1 (***) + PO_WI ( ) | 1.47 | 0.3686 (**) | |
| M10 | - M1 (***) + PO_LF ( ) | 1.66 | 0.364 (**) | |
| M14 | - M1 (***) + NP_IT ( ) | 1.73 | 0.3621 (**) | |
| M6 | - M1 (***) + PNP_WI ( ) | 1.78 | 0.3609 (**) | |
| M7 | - M1 (***) + PNP_3_types ( ) | 1.88 | 0.3586 (**) | |
| **Root crown sprouting** | | | | Proportion of species reproducing by root crown sprouting |
| M14 | - M1 ( ) + NP_IT (***) | 0.00 | 0.4668 (***) | |
| **Root sprouting** | | | | Proportion of species reproducing by root sprouting |
| M2 | + Patch only _Dim.1 ( ) + Patch only _Dim.2 (*) + Patch only _Dim.3 ( ) | 0.00 | 0.1607 (.) | |
| M5 | + M1 (*) - PNP_LF ( ) | 1.55 | 0.2312 (*) | |
| M7 | + M1 (*) - PNP_3 types ( ) | 1.61 | 0.2294 (*) | |
| M6 | + M1 (*) - PNP_WI ( ) | 1.84 | 0.2226 (*) | |
| M11 | + M1 (*) - PO_WI ( ) | 1.94 | 0.2197 (*) | |
| **Reproduction – Mostly seeds** | | | | Proportion of species reproducing mainly by seeds[b] |
| M7 | + M1 (*) + PNP_3 types (**) | 0.00 | 0.2712 (*) | |
| M6 | + M1 (*) + PNP_WI (**) | 0.21 | 0.2651 (*) | |
| M14 | + M1 ( ) + NP_IT (.) | 0.46 | 0.2576 (*) | |
| M12 | + M1 (*) +PO_3 types (**) | 0.51 | 0.2562 (*) | |
| M11 | + M1 (*) +PO_WI (**) | 0.64 | 0.2521 (*) | |
| M10 | + M1 (.) + PO_LF (*) | 1.06 | 0.2396 (*) | |
| M5 | + M1 (*) + PNP_LF (*) | 1.40 | 0.229 (*) | |
| **Dispersal mode – Birds** | | | | Proportion of species with bird-dispersed seeds |
| M16 | - M1 (**) - NP_WI (.) | 0.00 | 0.2537 (*) | |
| M17 | - M1 (**) - NP_3 types ( ) | 1.42 | 0.2033 (*) | |
| **Dispersal mode – Wind** | | | | Proportion of species with wind-dispersed seeds[c] |
| M9 | + M1 (**) + PO_IT (*) | 0.00 | 0.2769 (**) | |
| M16 | + M1 (**) + NP_WI (**) | 0.58 | 0.3665 (**) | |
| M13 | + NP_Dim.1 ( ) + NP_Dim.2 ( ) + NP_Dim.3 (*) | 1.25 | 0.1629 (.) | |

[a] The p-values are shown for models and explanatory variables as follows: (***) $p \le 0.001$; (**) $0.001 < p \le 0.01$; (*) $0.01 < p \le 0.05$; (.) $0.05 < p \le 0.1$; ( ) $p > 0.1$.

[b] Square root transformation.

[c] Power 4 transformation.

# CONCLUSION GÉNÉRALE

## 4.1 Une vue d'ensemble de la thèse

Le territoire forestier du sud du Québec est hautement fragmenté et les usages et activités liés à l'agriculture et l'exploitation forestière ont façonné ses paysages au cours des 200 dernières années (Bouchard & Domon, 1997; Brisson & Bouchard, 2006; Domon & Bouchard, 2007; Simard & Bouchard, 1996). Plusieurs études ont montré que les conditions du paysage pouvaient affecter la structure et la composition des communautés forestières locales (Bellemare et al., 2002; de Blois et al., 2001; Douda, 2010; Jamoneau et al., 2011; Jules & Shahani, 2003; Kimberley et al., 2016; Lloren et al., 2020; Takkis et al., 2018). Il est désormais également reconnu que les conditions passées, locales ou du paysage, pouvaient continuer d'affecter la structure des communautés pendant plusieurs décennies et siècles suite à un événement ou une perturbation (Dambrine et al., 2007; Dupouey et al., 2002). Dans ce contexte, cette thèse avait pour objectif principal de faire l'étude de communautés forestières végétales situées au sein de forêts fragmentées sous l'angle de leur mémoire écologique et, plus précisément, de leur relation avec des legs paysagers et différents filtres écologiques ayant agi au fil du temps et à travers différentes échelles spatiales.

Dans le chapitre 1, nous avons déterminé si les conditions passées à l'échelle du peuplement et du paysage influençaient la structure et la composition des communautés d'arbres et d'arbustes actuelles situées au sein de forêts fragmentées résultant de deux siècles d'activités anthropiques. Nous avons montré que les perturbations et la structure du paysage constituaient des facteurs importants influençant les patrons de diversité et d'abondance des communautés d'arbres et d'arbustes étudiées et que leur influence persistait à travers le temps. Ces communautés sont ainsi caractérisées par une mémoire écologique prenant la forme d'un délai de réponse suite à des changements survenus dans le passé dans la structure du paysage (Kuussaari et al., 2009; Nagelkerke et al., 2002; With, 2007). Nous avons également montré que les conditions d'habitat plus récentes ou actuelles pouvaient aussi être importantes pour expliquer l'abondance de certaines espèces d'arbres et d'arbustes, laissant entrevoir que des filtres écologiques plus récents (ex., perturbations, conditions biotiques et abiotiques) avaient la capacité d'effacer la mémoire lointaine des communautés.

Les conditions liées aux années 1930-40 et 1958 qui affectent encore les communautés 57 à 85 ans plus tard impliquent que ces dernières ne sont pas en équilibre avec les conditions d'habitat actuelles. Dans notre aire d'étude, le déclin agricole est survenu autour des années 1950 et les forêts se sont par la suite régénérées en plusieurs endroits sur le territoire (Domon & Bouchard, 2007). Les espèces associées à la période allant de 1930-40 à 1958 pourraient donc être l'objet d'un délai de réponse lié à un crédit de colonisation (*colonization credit*), qui impliquerait une lente augmentation des populations de ces espèces jusqu'à l'atteinte d'un nouvel équilibre avec les conditions de paysage actuelles, où la forêt est plus abondante (Jackson & Sax, 2010; Nagelkerke et al., 2002; With, 2007). Une autre hypothèse veut que les espèces longévives puissent être associées à une période plus lointaine non étudiée dans le cadre de ce projet. Dans ce cas, ces espèces pourraient être des reliques associées à la structure du paysage qui prévalait lors de la période précoloniale (autour de 1785), alors que les forêts étaient plus abondantes et moins fragmentées (Domon & Bouchard, 2007). Selon cette hypothèse, nous observerions plutôt un délai de réponse lié à une dette d'extinction (*extinction debt*) qui ne serait pas encore complètement payée (Hanski & Ovaskainen, 2002; Jackson & Sax, 2010; Kuussaari et al., 2009; Tilman et al., 1994). Dans ce cas, les espèces pourraient continuer à décliner dans le futur jusqu'à ce que les communautés soient en équilibre avec le paysage actuel, plus fragmenté.

Dans le chapitre 2, nous avons d'abord cherché à savoir si la structure fonctionnelle associée aux traits de réponses des communautés forestières d'arbres situées au sein de paysages fragmentés portait une mémoire écologique liée aux conditions d'habitat du passé. Nous avons par la suite investigué comment la valeur et la diversité des traits de réponses de ces communautés d'arbres actuelles variaient au sein des paysages historiquement plus perturbés. Pour ce faire, nous avons créé des trajectoires d'évolution des paysages à travers les 85 dernières années en intégrant les classes d'usages du sol des quatre périodes temporelles. Cette approche originale nous a permis d'avoir une vision d'ensemble et plus en profondeur des grands changements s'étant opérés de façon concurrente sur le territoire au cours de cette période, plutôt que d'avoir une vision morcelée restreinte à l'occupation du sol pour chaque période analysée séparément.

Nos résultats indiquent que la structure fonctionnelle des communautés étudiées porte une mémoire écologique liée aux conditions d'habitat des années 1930-40 et 1958, mais que les conditions plus récentes ou actuelles sont également importantes. L'analyse des trajectoires de paysages indique par la suite que l'altération des legs paysagers, à travers des perturbations continues au fil du temps, peut conduire à une érosion de la diversité de réponses et à un filtrage des traits de réponses favorisant les espèces qui possèdent des graines se dispersant sur de plus longues distances par le vent ou les mammifères. Les trajectoires moins perturbées (davantage forestières au fil du temps) favorisent quant à elles une plus grande diversité de réponses et les espèces dispersant leurs graines par les oiseaux et capables de se reproduire végétativement. Ainsi, les espèces des communautés situées au sein de paysages historiquement plus perturbés possèdent une meilleure capacité de colonisation, mais une persistance locale plus faible à travers le mécanisme de reproduction végétative, ce qui est en accord avec les études montrant l'existence d'un compromis entre la capacité de colonisation des plantes et leur persistance (Cody, 2006; Ehrlén & van Groenendael, 1998; Honnay & Bossuyt, 2005; Ozinga et al., 2007; Stöcklin & Winkler, 2004).

Dans le chapitre 3, nous avons posé la question à savoir si les arbres résiduels dans le paysage étaient associés à la composition et la structure des communautés d'arbres et d'arbustes des forêts environnantes et si, par le fait même, ils pouvaient contribuer à la mémoire écologique externe de ces communautés. Nos résultats ont d'abord montré que les arbres résiduels dans le paysage avaient un effet positif sur la connectivité et que leur contribution relevait surtout de leur rôle en tant que pas japonais. Par la suite, nous avons montré que les arbres résiduels contribuaient à augmenter l'évidence (*strength of evidence*) des modèles expliquant la diversité spécifique ainsi que la diversité de réponses des traits liés à la dispersion des graines et à la reproduction des arbustes dans les communautés forestières. Les arbres résiduels dans le paysage ont également contribué à augmenter l'évidence de quatre modèles expliquant la composition des communautés d'arbres, notamment en ce qui a trait à la proportion des espèces se reproduisant de manière sexuée et dispersant leurs graines par le vent. Finalement, les arbres résiduels persistants (présents en 2015 et en 1983) ne se sont pas révélés plus importants que les arbres résiduels non-persistants (présents seulement en 2015) pour expliquer la composition et la structure des communautés d'arbres et d'arbustes.

L'association entre les patrons des communautés forestières et les variables de connectivité calculées à partir des arbres résiduels suggère que ces derniers peuvent agir comme sources de propagules se dispersant dans les forêts avoisinantes, tel que proposé par Levin (1995) et démontré par Aldrich & Hamrick (1998). Cette association suggère également que les arbres résiduels peuvent favoriser le déplacement des animaux dispersant les propagules en milieu ouvert (Fischer & Lindenmayer, 2002; Harvey, 2000; Lindenmayer & Laurance, 2017; Manning et al., 2006), tel qu'anticipé avec nos analyses de réseaux où les arbres résiduels ont agi à titre de pas japonais pour les trois distances de dispersion testées. Les arbres résiduels peuvent en effet attirer de nombreuses espèces capables de disperser des propagules et ainsi représenter des points chauds (*hotspots*) pour la dispersion (Harvey, 2000; Herrera & García, 2009; Lindenmayer & Laurance, 2017). Cependant, l'association entre les communautés forestières et les arbres résiduels pourrait aussi indiquer que ces derniers sont plutôt le résultat d'une dispersion efficace des propagules en provenance des forêts avoisinantes plutôt que d'être eux-mêmes des points chauds favorisant la dispersion, bien que ces deux options puissent être vraies et avoir cours simultanément. Les arbres résiduels sont donc des éléments interconnectés avec les communautés forestières adjacentes à travers des processus comme la dispersion des propagules et du pollen (Levin, 1995) et pourraient contribuer à leur mémoire écologique externe (Johnstone et al., 2016).

## 4.2 Importance de l'étude et perspectives

Cette étude prend toute son importance dans un contexte d'aménagement du territoire et forestier. En effet, elle soulève des réflexions quant à l'incertitude associée aux délais de réponses des communautés forestières aménagées, aux interactions possibles entre ces communautés transitoires et des stresseurs liés aux changements globaux ainsi qu'aux meilleurs moyens à mettre en place pour assurer une transition en douceur. Nos résultats ont en effet montré que l'usage et les perturbations du territoire pouvaient avoir un impact négatif durable sur les communautés forestières, notamment en ce qui a trait à la diversité des traits fonctionnels de réponses. Il est généralement admis qu'une diminution de la diversité de réponses peut entraîner une diminution de la résilience des écosystèmes et réduire leur capacité à faire face aux perturbations futures (Elmqvist et al., 2003; Hooper et al., 2005; Mori et al., 2013; Naeem & Wright, 2003; Walker, 1995). Selon cette hypothèse, notre étude suggère que les communautés situées dans des paysages historiquement plus perturbés pourraient éprouver des difficultés à s'adapter à de nouvelles perturbations dû à leur plus faible diversité de réponses. Il est également possible que certaines espèces possédant une meilleure capacité de colonisation dans les paysages historiquement plus perturbés ne soient pas bien adaptées à faire face à de nouvelles perturbations. Par exemple, les espèces qui dispersent leurs graines par le vent sur de très longues distances pourraient avoir des difficultés à tolérer des sécheresses plus sévères et fréquentes, surtout durant la phase de régénération, puisque les graines plus petites sont généralement moins tolérantes à divers facteurs de stress (Muller-Landau, 2010).

Conséquemment, notre étude souligne l'importance d'adopter une approche préventive visant à restaurer la diversité des espèces et de leurs traits de réponses et ce, particulièrement dans les forêts situées au sein de paysages ayant été hautement perturbés au fil du temps. Pour y parvenir, il serait opportun de planifier des efforts de reboisement en milieu agricole de manière à favoriser l'augmentation de la résilience du couvert forestier dans son ensemble. En ce sens, les espèces pouvant compléter la diversité fonctionnelle des arbres déjà présents sur le territoire pourraient être favorisées afin d'assurer la capacité d'adaptation des forêts face aux perturbations futures (Messier et al., 2019). Il serait également opportun d'augmenter le degré de connectivité de la matrice agricole, et donc son hétérogénéité, au sein des paysages hautement perturbés (Manning et al., 2009), cette approche se voulant complémentaire à la conservation du couvert forestier actuel. La colonisation des parcelles d'habitats en milieu fragmenté est en effet fortement tributaire de la nature de la matrice qui les entourent, sa composition et la configuration de ses attributs pouvant notamment favoriser ou défavoriser la dispersion des espèces d'une parcelle d'habitat à l'autre (With, 2019). Notre étude appuie l'importance de la matrice dans les paysages agroforestiers fragmentés. En effet, plusieurs éléments de cette dernière (ex., les terres en friche, les pâturages et les zones en régénération), à différentes époques, sont parmi les facteurs les plus influant sur l'abondance des espèces, leur diversité ainsi que la valeur et la diversité de leur traits de réponses au sein des communautés forestières actuelles. L'importance du paysage pour les communautés locales ne relève donc pas strictement des forêts qui y sont présentes, mais également du contexte dans lequel elles sont imbriquées (Franklin & Lindenmayer, 2009).

L'augmentation de la connectivité au sein de la matrice agricole et l'implantation d'espèces possédant des traits de réponses adaptés aux conditions environnementales anticipées dans le futur nécessiteraient cependant l'augmentation de la présence d'arbres en milieu agricole, ce qui peut s'avérer un défi de taille et être en conflit avec les usages actuels du territoire (Benayas et al., 2008; Lust & Muys, 1991). Les travaux réalisés dans le cadre de ce projet nous apportent toutefois une piste de solution potentielle pour parvenir à réintroduire davantage d'arbres en milieu agricole hautement perturbé, tout en limitant les conflits. Cette solution pourrait passer par l'implantation d'un réseau d'arbres résiduels pouvant prendre diverses formes (arbres isolés ou agglomérés en bandes linéaires ou en petits îlots). Concrètement, il pourrait s'agir de restaurer les bandes riveraines, d'implanter différentes solutions agroforestières comme des haies brise-vent et des cultures intercalaires, de conserver les arbres résiduels existants et de restaurer des îlots boisés de petite superficie (Benayas et al., 2008; Manning et al., 2009; Schroth et al., 2004). Ce type de projets devrait être planifié et implanté stratégiquement dans les zones qui ont le potentiel d’augmenter le plus la connectivité une fois restaurées afin d’assurer un impact maximum à l’échelle du paysage. L’importance des arbustes résiduels ainsi que des systèmes agroforestiers pour favoriser la dispersion des arbres et arbustes en milieu agricole devrait d’ailleurs faire l’objet de recherches approfondies dans le futur. Finalement, à la lueur des résultats présentés dans cette thèse, les travaux visant à augmenter la diversité des espèces et de leurs traits de réponses aujourd’hui auront vraisemblablement des impacts positifs durables sur les communautés forestières du futur, surtout dans un contexte de changements globaux.

## 4.3 Limites de l’étude

Dans le cadre de ce projet, nous avons mis en lumière des relations entre les patrons observés dans les communautés forestières d’arbres et d’arbustes et des conditions d’habitat à l’échelle locale, du peuplement et du paysage. Bien que de nombreux facteurs explicatifs aient été considérés dans les analyses, il n’a cependant pas été possible de prendre en compte certains d’entre eux qui auraient pu s’avérer importants. C’est le cas notamment de la pression de broutage par le cerf de Virginie (*Odocoileus virginianus*). Une surabondance de cette espèce peut en effet modifier de manière importante la composition forestière, surtout au niveau de la régénération, et ainsi affecter le développement des forêts (Beguin et al., 2016). Dans la même veine, le travail de photo-interprétation n’a pas permis de détecter les perturbations historiques des forêts qui auraient pu avoir lieu en sous-couvert (ex., pâturages en forêt pour les animaux de ferme).

Parmi les facteurs explicatifs retenus figuraient différents indices de connectivité fonctionnelle ayant été calculés par l’entremise d’analyses de réseaux. Pour ce faire, la distance Euclidienne a été utilisée pour caractériser la distance de dispersion possible entre les parcelles d’habitat. Ce faisant, cette approche n’intègre pas la notion d’hétérogénéité de la matrice et considère que les espèces se dispersent en ligne droite selon le chemin le plus court, peu importe les différents types d’habitat rencontrés (Galpern et al., 2011). Cette approche, bien que standard, représente toutefois une simplification de la réalité qui doit être gardée à l’esprit lors de l’interprétation des résultats.

Pour le chapitre 3 spécifiquement, nous avons cartographié les arbres résiduels en territoire agricole. Les arbres résiduels de 2015 ont été identifiés à l’aide d’images satellites à haute résolution, mais sans toutefois faire de photo-interprétation en trois dimensions, ce qui a réduit le niveau de détails pouvant être détectés. Cette approche a été retenue dans un souci d'utiliser une technique uniforme pour identifier les arbres résiduels qui étaient également présents en 1983 et pour lesquels la seule source d'information disponible était les photos aériennes numérisées datant de cette année. De futures études visant à approfondir les connaissances quant à l'effet des arbres résiduels en territoire agricole sur les communautés forestières bénéficieraient de la technologie LiDAR (détection et télémétrie par ondes lumineuses), qui permettrait d'identifier ces arbres avec un niveau de détails beaucoup plus fin (ex. hauteur des arbres, meilleure distinction entre arbres et arbustes, etc.). Les données LiDAR, qui sont disponibles depuis quelques années pour une bonne partie du territoire, vont permettre, à terme, de conduire des analyses spatiotemporelles similaires à celles de la présente étude, mais avec une résolution améliorée.

Enfin, dans le cadre de cette thèse, la végétation forestière a été échantillonnée au sein de 64 sites. L'ensemble de ces sites a été utilisé pour les analyses du chapitre 1, alors que des sous-échantillons ont été utilisés dans le cadre des chapitres 2 et 3. Dans ce contexte, l'emphase a été mise sur l'analyse des espèces les plus abondantes, puisqu'il n'était pas possible d'analyser les données individuelles (abondance relative) de plusieurs espèces, qui étaient présentes dans seulement quelques sites.  Pour les futurs projets visant à étudier les communautés d'arbres et d'arbustes, il serait donc avantageux d'échantillonner un nombre de sites plus élevé afin d'avoir une meilleure représentativité des espèces plus rares et ainsi éviter ce problème. Des analyses d'occurrence (présence/absence) pourraient également être envisagées dans certains cas.

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