DYNAMIQUES TEMPORELLES DES COMMUNAUTÉS VÉGÉTALES FORESTIÈRES EN RÉPONSE AUX CHANGEMENTS GLOBAUX.

APPROCHE COMPARATIVE ENTRE BRYOPHYTES ET TRACHÉOPHYTES VIA L'ÉCOLOGIE HISTORIQUE

par

Antoine Becker-Scarpitta

Thèse présentée au Département de biologie en vue

de l'obtention du grade de docteur ès sciences (Ph.D.)

FACULTÉ DES SCIENCES

UNIVERSITÉ DE SHERBROOKE

Sherbrooke, Québec, Canada, 16 juillet 2018

Le 16 juillet 2018

le jury a accepté la thèse de Monsieur Antoine Becker-Scarpitta
dans sa version finale.

Membres du jury

Professeur Mark Vellend
Directeur de recherche
Département de Biologie, Université de Sherbrooke, QC, Canada

Professeur Guillaume Decocq
Évaluateur externe
Université de Picardie Jules Vernes, France

Professeure Stéphanie Pellerin
Évaluateur interne
Département des sciences Biologiques, Université de Montréal, QC, Canada

Professeur Bill Shipley
Président-rapporteur
Département de Biologie, Université de Sherbrooke, QC, Canada

" Soudain! L'instinct du garde chasse refait surface. Sentant l'appel des bryophytes, sorte de phytoplancton sylvestre, le Becker becquette chaque mouvement de ce discret, mais non moins vital, muscinées. Les sens à vif et le regard exercé des années durant, par le florilège végétal des cimes Normandes ; dans une pose, par l'exercice, presque sclérosée, Scarpitta jette à cet être le tendre désabusement de celui qui sait. Héritage des temps anciens, son large appendice nasal, gavé du suc forestier suivant l'averse, signe la fin de ce subtil moment d'attention dans une brève expiration. Et accompagnant d'un imperceptible frétillement de moustache les logorrhées des ovipares environnants, en héro solitaire du monde chlorophyllien, il retourne à l'insu de tous aux frasques bassement terrestres du quotidien. »

Elmôttacimbillah Belmouhoub

SOMMAIRE

Depuis environ deux siècles les activités humaines modernes ont profondément modifié les conditions environnementales sur la surface de la Terre. De nombreuses études ont mis en évidence une réponse de la végétation face à ces changements. Cependant, il persiste plusieurs incompréhensions. Premièrement, les réponses des communautés varient fortement entre les études, et les mécanismes responsables de cette variation sont encore mal connus. Deuxièmement, malgré leur importance écologique, les bryophytes restent largement sous étudiées dans les études temporelles, limitant notre compréhension de leur dynamique temporelle. Ce doctorat a pour objectif d'apporter des éléments de réponses à ces deux points.

Les trois projets de recherche gravitent autour de la grande question : quels sont les effets des changements environnementaux sur la biodiversité? Les hypothèses que j'ai développées se construisent autour de ces deux grandes questions (i) Quels sont les effets des dépositions et du réchauffement de la température sur la végétation forestière? (ii) Il y a-t-il une différence de sensibilité entre bryophytes et trachéophytes face aux changements environnementaux?

Le chapitre 2 teste l'hypothèse que les bryophytes sont plus sensibles que les plantes vasculaires face aux dépositions atmosphériques et au réchauffement de la température dans une région industrielle du nord-ouest de la France. Le chapitre 3 teste les mécanismes de réponse de la végétation forestière le long d'un gradient de réchauffement climatique dans l'est du Canada. Enfin, le chapitre 4 est une approche mixe entre les deux premiers chapitres, il teste la réponse des plantes vasculaires et des bryophytes face à différentes intensités de réchauffement de la température sur des gradients altitudinaux dans l'est de la province de Québec.

Dans les trois chapitres, j'ai utilisé les méthodes de l'écologie historique. Après un long travail d'archive, j'ai rééchantillonné des relevés botaniques faits dans les années 1970. La sélection des sites à rééchantillonner suit un protocole finement détaillé afin de minimiser tous effets confondants. Les résultats des trois chapitres mettent en évidence le lien direct entre réponse de végétation et changements environnementaux. Premièrement, les bryophytes sont plus sensibles aux dépositions atmosphériques que les plantes vasculaires (chapitre 2). Secondement, les changements temporels de la végétation vasculaire sont plus grands dans les zones ou le réchauffement climatique fut le plus fort (chapitre 3). Dernièrement, face au réchauffement climatique, les réponses des bryophytes et plantes vasculaires diffèrent selon la propriété de la communauté qui est étudiée (chapitre 4). Les trois chapitres, montrent un changement systématique de la composition des communautés, sans pour autant de changement de la richesse spécifique.

Ce doctorat fournit trois exemples de la force des méthodes historiques dans la compréhension des mécanismes de réponse de la végétation face aux changements globaux. Mes travaux supportent l'importance d'analyser la dynamique de la végétation avec une vision holistique. La compréhension des mécanismes liés à la dynamique temporelle de la végétation doit passer par l'étude de plusieurs groupes taxonomiques, avec différentes propriétés des communautés sur plusieurs échelles spatiales.

Mots clés : affinités écologiques, biodiversité, bryophytes, changements globaux, composition des communautés, déposition atmosphérique, diversité, dynamique temporelle des communautés, écologie des communautés, écologie historique, étude à long terme, forêt tempérée, gradient altitudinal, plantes vasculaires, réchauffement climatique, trachéophytes, végétation forestière

ABSTRACT

For at least the past two centuries, human activities have caused strong environmental changes in the biosphere. Many studies have shown responses of vegetation to global changes. However, many unknowns remain. First, most explicitly temporal studies have been conducted at a single site with a common intensity of environmental changes and historical land-use legacies. Results are highly variable among studies, and we have a very limited understanding of mechanisms underlying this variation. Second, despite the major contribution of bryophytes to ecosystem functioning, very few temporal studies have focused on bryophytes. This Ph.D. contributes to filling these two knowledge gaps.

The overarching question for the three research projects presented here is: what is the impact of environmental change on biodiversity? We built a set of hypotheses around two main questions: (i) What is the effect of environmental changes on forest vegetation? (ii) Which taxon, bryophytes or vascular plants, is most sensitive to global changes?

Chapter 2 tests the hypothesis that bryophytes are more sensitive than vascular plants to the combination of atmospheric deposition and warming in an industrial region in north-eastern France. Chapter 3 tests the hypothesis that forest vegetation changes have been greatest in regions with the strongest warming trends along a continental gradient in eastern Canada. The last chapter combines the two first approaches, quantifying temporal changes in bryophyte and vascular plant communities in sites with different warming intensities along elevational gradients in eastern Canada.

To answer to these questions, I used an historical ecological approach by resurveying botanical plots initially surveyed in the 1970s. Plot selection followed a reproducible and detailed procedure to minimize confounding factors. Our results show a direct effect of global changes on forest vegetation. First, bryophytes appear more sensitive to atmospheric deposition than vascular plants (Chapter 2). Second, temporal changes in vascular plant communities were stronger in areas where warming has been greatest (Chapter 3). Third, in response to warming, changes in bryophyte and vascular plant communities show idiosyncratic differences, depending on the community property under study (Chapter 4). Results of the three chapters clearly show systematic changes in community composition, that are not necessarily accompanied by changes in local diversity.

In sum, we provide empirical evidence that historical ecology is a powerful method to disentangling mechanisms of vegetation response to global changes. Only a holistic approach based on different biodiversity components, different spatial scales and wide variety of community properties permit an understanding of the complexity of temporal dynamics of vegetation.

REMERCIEMENTS

Ces quatre années n'ont pas été qu'une formation académique. Le doctorat permet de se perdre, se retrouver, d'explorer différents recoins de la pensée, il permet de prendre le temps de comprendre, d'expérimenter, d'échouer et d'accomplir. Le développement personnel est riche quoi que parfois dur, la détresse et le stress font partie intégrante du paysage émotionnel du doctorant. Cependant, le plus beau souvenir que je garderai de ces quatre années c'est vous. Vous qui avez marché avec moi, qui m'avez porté, soutenu, encouragé, secoué parfois. Je vais essayer ici de remercier l'ensemble des personnes grâce à qui ce projet a été initié, a vu le jour et a pu se réaliser dans les meilleures conditions. Il se peut que ce développement soit long, pour les impatients : un grand merci général à tous.

Pour commencer, je remercie très chaleureusement et en toute sincérité mon directeur de thèse Mark Vellend. Tu as su me donner une entière liberté sur la conduite de mon projet tout en me guidant lorsque j'étais dans le brouillard. Tes conseils ont toujours été bons et judicieux. Les relations entre étudiant et directeur peuvent être compliqué, mais dans notre cas elle fût productive, intelligente et toujours très amicales. Un grand merci de m'avoir offert la possibilité de mener ce projet dans ton laboratoire. Au moment où tu m'as accepté en doctorat, j'étais sur le point de quitter le milieu académique pour découvrir le milieu de la diplomatie. Si j'avais à reprendre ce choix, 100 fois encore je choisirais le doctorat dans ton laboratoire. Un grand merci à toi.

Un grand merci à Bill Shipley, qui a eu un rôle tout particulier dans mon doctorat. Tu as toujours pris le temps de répondre à mes questions, parfois à mon surplus de questions (et de détresse) notamment lorsque Mark était en sabbatique. Un merci également à Stéphanie Pellerin qui m'a accueilli dans son laboratoire de l'Institut de Recherche Biologie Végétale de l'Université de Montréal. Merci d'avoir accepté d'être sur mon comité de conseiller, ton apport a été grandement bénéfique à ce projet. J'espère avoir la chance de continuer à travailler avec toi. Merci à vous deux d'avoir accepté d'évaluer cette thèse. Merci à Guillaume Decocq d'avoir accepté d'être l'examinateur externe.

Merci aux assistants de terrain, Diane, Mélissa et Sarah pour leur aide et leur investissement sur le terrain. Ce fut un plaisir de travailler avec vous trois. Vous avez grandement contribué à ce projet et je vous en suis sincèrement reconnaissant et reconnaissez ici un accomplissement collectif. Merci à Michael Belluau et Audrey Bourret pour la relecture du manuscrit et pour avoir fait le gabarit formaté de ce document.

Merci à Arnault Lalanne, pour le suivi intégral de mon parcours étudiant. Tu as été un inconditionnel soutien depuis presque 10 ans… (j'ai eu un coup de massue en faisant le calcul!). Notre rencontre a débuté lorsque j'étais jeune étudiant en Gestion Forestière au château, je suis heureux d'avoir eu la chance de rester sous ton aile tout ce temps. Nos discussions ont toujours été très fertiles et ont façonné mon développement scientifique. J'espère poursuivre notre collaboration sur de nouveaux projets. Dans l'élan des mentors, un grand merci à Jean-Yves Massenet, Jacques Bardat, Emmanuelle Porcher et Jacques Lefebvre vous avez été des éléments clés dans mon parcours académique et personnel.

Comme je le disais en introduction des remerciements, si mon expérience au doctorat a été si bonne c'est grandement grâce à vous. Premièrement merci à ceux avec j'ai vécu, avec qui j'ai partagé la folie de l'épuisement, les vicissitudes du quotidien, l'ennuie des longs hivers et la joie de manger ensemble, merci à Hipo, Will, Zoli, Arikiki, J., Fannette, et Gab. Au passage, mes excuses répétées pour ces derniers mois d'absence totale.

Merci aux inconditionnels et éternelles : Mich, Raph, La Poupina, Titine, Antoine T., Clarence, Alex, Mélanie, Étienne, Steve, Julie, Amanda, David, Christina, Diane, François, Claire, Cédric, Lou, Rocio, Françoise, Geneviève, Cesc, Benjamin, Sébastien. Un merci au Labo du Prof Dom qui a apporté un vent de fraicheur et de reproductibilité à Sherbrooke, Dominique, Guillaume, Ida, Amaël, Azenor, Claire, la fripouille de Cazelles. À l'esquade Brésilienne : Will, Pedro, Guilherme et Day. Une pensé pour mes collègues de terrain avec ce fût un plaisir de travailler Pascal, Guillaume, Pauline et Romain (on a tellement de choses à vérifier! tellement de questions! prend des notes, tu as du papier?). Merci aux bryophiles chimistes pour leurs invitations sur le terrain dans le Nord! Merci à Anthony, Pedro, Zak et Cam pour le refuge à Montréal, la transition Paris-Sherbrooke fut tellement plus facile grâce à vous. Merci à la Team des physiciens Shaheen, Simon et Pierre.

À ma Team Française, mes acolytes avec qui j'ai fait mes premiers pas dans le monde de la recherche : Théo-groux, Karlos, Moumourad, Shank-Nawak le Meyer des Dallas, Charles dit le Thevenardier, Gauvin, Daphné. À Pauline qui, malgré les 14000 km qui nous séparent, a fait partie intégrante de mon paysage amical durant toute cette thèse. À ma Team Franco-Turco-Tunisienne qui m'a fait renaitre tel un Phoenix avec ce magnifique séjour en Tunisie, merci à Skander & Jamilla, Mourad & Colombine, Karl & Justine, et la toute la Team, aychek louled. Merci à Émilien pour ton accueil en Allemagne, à quand l'EP MC Bryo & Mister Bell?

Merci à Mathilde pour ton aide et ton soutien pendant mon sprint final, ce dernier mois sans toi aurait été vraiment dur. Une pensée pour 'Sigerbert le boiteux' pour ses tentatives de sabotage de ma thèse en s'allongeant systématiquement sur mon clavier. Dans la même lignée, une pensée pour 'Stach double gras' qui a écouté avec attention mes répétitions de conférence, son œil vif, mais incertain ne m'a jamais convaincu de son intérêt pour mes travaux.

À ma famille, mes parents, ma fratrie (ils se reconnaitront tous) pour leur éternel et indéfectible soutien dans mon parcours et plus généralement dans ma vie. Durant ce doctorat j'ai manqué beaucoup d'événements familiaux (dont probablement le plus incongru !!), mais j'ai eu la chance d'être présent pour la naissance de Jules, merci à lui pour ce parfait timing. Chez nous la famille est un concept étendu, alors merci aux Becker, Scarpitta, Anclin, Brument, Picori, Isabel, Paquin et aux Kianička.

Je finirai par te remercier toi, toi que j'ai rencontré au début de ce projet et que j'ai retrouvé à sa fin. Toi qui as partagé et contribué à la joie, la folie et l'insouciance de mes premiers pas dans cette aventure et qui a supporté et enduré ma tourmente, ma détresse et mon instabilité des derniers instants. L'espèce Homo doctorantus n'est pas simple à supporter en fin de parcours, selon les manuels il redevient Homo normalus variété supracoolus une fois le tout déposé. Ta constante bonne humeur m'a été vitale pendant ces longs mois d'écriture. Merci pour ton calme, ta bienveillance, tes blagues et tes encouragements. Maintenant, nous allons pouvoir nous retrouver, voyager au gré de nos envies pour vivre de brocoli et de Bolchoï frais ☺. Merci ma Nikita. J'ai hâte de passer aux prochaines étapes, à deux cette fois.

TABLE DES MATIÈRES

LISTE DES ABRÉVIATIONS

BP	Before Present (avant 1950)	p. 12
CTI	Community Temperature Index	p. 63
CWM	Community Weighted Mean	p. 43
GBIF	Global Biodiversity Information Facility	p. 68
LMM	Linear Mixed-effect Models	p. 69
NMDS	Non-metric Multi-Dimentional Scaling	p. 70
PCA	Principal component Analysis	p. 44
PERMANOVA	PERmutational Multivariate ANalysis Of Variance	p. 44
PERMDISP	PERMutation test for multivariate homogeneity of group DISPersions	p. 44
RA	Relative Abundance	p. 69
R2	Coefficient de détermination	p. 64
R2m	Coefficient de détermination marginal	p. 70
R2c	Coefficient de détermination conditionnelle	p. 70
SE	Standard Error	p. 71
STI	Species Temperature Index	p. 43

LISTE DES TABLEAUX

LISTE DES FIGURES

CHAPITRE 1

INTRODUCTION GENERALE

1.1. Écologie des communautés, revue historique et synthétique des théories

L'écologie des communautés est une discipline qui se focalise sur les processus et les mécanismes de coexistence des espèces dans le temps et dans l'espace. L'objectif de celle-ci est d'expliquer les patrons de composition de la diversité biologique, leurs variations spatio-temporelles, ainsi que les liens qu'ont les espèces entre elles et avec leur environnement (Vellend, 2016; Vellend et Orrock, 2009).

L'objet d'étude, soit l'unité de base de cette discipline, est un concept purement théorique: c'est la communauté. Cette dernière est définie comme un assemblage plurispécifique, vivant sur une échelle spatiale déterminée à un temps donné (Gauch, 1982). Au sein de cette définition, les limites spatiales et temporelles sont floues et varient suivant l'objectif dans lequel est utilisée la communauté (Isselin-Nondedeu, 2014). Il est également possible de définir la communauté comme un assemblage taxonomique, fonctionnel, phénologique (i.e. synusie) voire même sous forme d'un réseau d'interactions. La notion de contour de la communauté peut varier en fonction de la nature même des organismes la composant ; ainsi, une communauté de prairie s'étudiera aisément sur quelques mètres carrés, alors qu'une communauté forestière de fin de succession s'étudiera sur plusieurs centaines de mètres carrés (Van Der Maarel et Franklin, 2013). De même, la dimension temporelle est parfois floue et peut s'échelonner sur différentes échelles selon que l'on étudie la dynamique à très long terme (sur des échelles géologiques), à moyen long terme (du siècle à plusieurs décennies) ou à court terme (variations interannuelles ou saisonnières).

Comparée à l'approche centrée sur l'espèce, l'étude des communautés offre des propriétés émergentes telles que la diversité, la composition en espèce ou en traits fonctionnels, l’équitabilité, l’entropie (i.e. distribution des abondances) ou le lien entre chacune de ces propriétés avec l’environnement (Vellend, 2016).

Dans les sections suivantes, je présenterai les avancées théoriques qui ont été développées pour expliquer les patrons spatiaux et les dynamiques spatio-temporelles des communautés. Ce développement me permettra de poser les bases théoriques de l’étude des communautés en vue de présenter la démarche scientifique. Compte tenu du fait que ma recherche est intégralement centrée sur les communautés végétales forestières, mon discours et mes exemples seront orientés vers celles-ci.

1.1.1. Définition et classification des communautés végétales

Depuis l’émergence de l’écologie des communautés, de nombreux modèles ont été développés dans le but d’expliquer, de comprendre et de classer les observations empiriques de la biodiversité.

Pour commencer, Clements (1916) adopte une vision de la communauté tel un super-organisme, où chaque espèce est interdépendante des autres. Autrement dit, pour Clements, une communauté devient un nouvel objet possédant des propriétés et des fonctions propres et indépendantes des éléments la composant. Il adopte ainsi une vision finie et délimitée de la notion de communauté. Pour lui, les successions végétales sur un gradient environnemental sont des états discrets partants d’un état pionnier jusqu'à un état climacique, qu’il nomme série. Le climax est un état d’équilibre avec son environnement, donc stable dans le temps, et, défini pour chaque région en fonction des caractéristiques pédoclimatiques locales. Clements décrit donc un processus déterministe, la succession des communautés.

Gleason, (1926) s’oppose aux positions de Clements : il décrit une vision plus « individualiste » des communautés, arguant que chaque espèce entretient des contraintes de survie, compétition et reproduction (colonisation, dispersion) dictées par les paramètres abiotiques de l’environnement. Pour lui, les communautés sont des groupements d’espèces, dont les caractéristiques biologiques et écologiques permettent leur établissement et leur croissance dans un milieu particulier. Il observe ainsi une variation progressive dans la composition des communautés le long d'un axe environnemental décrivant un continuum écologique. La principale opposition à la vision de Clements tient dans le caractère stochastique des réponses des espèces à leurs environnements.

De la même manière que Gleason, Tansley, (1935) rejette l'idée de « super-organisme » des communautés. Pour lui, les communautés sont des conceptions intellectuelles de l'homme pour simplifier l'observation de la nature sans limites écologiques fixes. Il définit la notion d'écosystème comme une unité fonctionnelle issue des interactions entre les différents organismes des communautés (biocénose) et des paramètres environnementaux (biotope).

Durant cette même période, certains écologues-botanistes se penchent sur des méthodes plus quantitatives pour étudier les communautés végétales. Braun-Blanquet et al., (1952) définit ainsi une conception floristico-statistique des communautés avec une classification hiérarchique des assemblages d'espèces. Sa méthode quantitative est basée sur des cooccurrences d'espèces caractéristiques d'une association, c'est l'élément fondateur de la phytosociologie SIGMAtiste (Station Internationale de Géobotanique Méditerranéenne et Alpine) également appelé école « Zuricho-Montpelliéraine ». Dans ce cadre de pensée, les communautés sont distinctes et se retrouvent partout où les conditions des milieux sont similaires. Cette école, héritée des travaux de Clements, a motivé une grande partie des recherches en écologie végétale des années 1940 à 1980 en Europe jusqu'à très récemment, ainsi qu'en Amérique du Nord. Jugée par certains comme trop complexe, trop restrictive et trop lourde du fait de sa nomenclature (i.e. la syntaxonomie), elle est progressivement délaissée pour des objectifs différents ou des méthodes plus accessibles. Elle a néanmoins laissé un important héritage éco-botanique tant en Europe qu'en Amérique du Nord. On lui doit par exemple de très nombreuses études phytoécologiques, ainsi qu'une importante partie des protocoles d'étude de la végétation (i.e. les coefficients d'abondance-dominance de Braun-Blanquet ou l'étude stratifiée de la végétation). Plus tard, ces méthodes seront affinées grâce au développement des méthodes numériques d'ordination (Bray et Curtis, 1957).

Afin d'évaluer les effets des changements globaux sur la composition des communautés, nous avons utilisé des relevés faits dans les années 1970 comme « état initial » ou « état original ». Durant cette période, les descriptions de la végétation étaient essentiellement faites avec des protocoles phytosociologiques : des relevés stratifiés de la végétation sur une surface fixe, avec attribution de coefficient d'abondance-dominance de Braun-Blanquet pour chaque espèce renseignant leur recouvrement de la surface délimité. Pour le reste de ce document, une communauté sera donc définie comme l'assemblage d'espèces inventoriées sur la surface définie par les auteurs des études historiques utilisées.

1.1.2. Modèles des interactions entre espèces et concept de niches écologiques

Lotka, (1925) et Volterra, (1926) ont proposé indépendamment et presque simultanément une modélisation simpliste de l'influence de la compétition inter et intraspécifique sur la croissance des populations au sein d'une communauté. Les modèles développés par Lotka et Volterra se basent sur (i) les liens de compétition qui existent entre les espèces et (ii) la capacité de charge biotique de l'écosystème (valeur K). Dans leur formulation, ils n'intègrent ni les structures d'âge de la population, ni les variations géno- et phénotypiques des individus, ni la migration et enfin le modèle n'est pas défini spatialement. Ils postulent que les vitesses de variation de la densité des populations sont déterminées par les densités de ces mêmes populations. Ceci a mené à la formulation du principe d'exclusion compétitive défini par Gause, (1936). Il stipule que si deux espèces ou populations sont écologiquement proches et partagent la même ressource limitante (i.e. plusieurs espèces dans une même niche), celles-ci ne peuvent cohabiter par effet de compétition. Deux issues sont alors possibles : (i) l'une des deux espèces prend le dessus et exclue l'autre ou (ii) on observe un déplacement de niche d'une des deux espèces (changement plastique ou génétique). La coexistence au sein d'une communauté n'est possible que si des espèces ont des niches écologiques différentes. Plus tardivement, Tilman, (1982) formalisera mathématiquement la dynamique de la compétition pour la ressource (R*). Ce développement théorique a permis d'affiner la compréhension des mécanismes de coexistence dans les communautés.

Hutchinson, (1957) a redéfini le concept de niche écologique comme une caractéristique de l'espèce plutôt que de l'habitat. Il délimite la notion de niche à un espace (ou « hypervolume ») à *n*-dimension correspondante à ensemble de *n*-ressource (paramètres abiotiques) ou à une utilisation de l’espace à des fins d’alimentation, de reproduction et de protection. Les différentes dimensions définissent la gamme de tolérance, autrement dit les conditions qui permettent à une espèce de survivre et se reproduire. Une distinction est faite entre la niche fondamentale et la niche réalisée. Premièrement, la valeur théorique de la niche fondamentale, correspondant à l’ensemble des conditions abiotiques sous lesquelles une espèce, en l’absence d’interactions biotiques, peut entretenir un taux de croissance de la population positif. Autrement dit, la niche fondamentale est la répartition d’une espèce basée uniquement sur les conditions environnementales. Deuxièmement, la niche réalisée correspond à l’ensemble des conditions abiotiques en présence d’interactions biotiques sous lesquelles une espèce entretient un taux de croissance de la population positif, c'est-à-dire, l’espace écologique où une espèce a survécu aux interactions avec d’autres espèces (Pulliam, 2000). Selon sa vision, les espèces sont dépendantes de leur environnement et chacune tient une place particulière selon ses exigences et son pouvoir de compétition. Ce revirement dans la vision de niche était assez révolutionnaire à l’époque où Hutchison l’a énoncée (Cherrett et al., 1989). Cette conception théorique a pour objectif d’expliquer les lois d’assemblage et de coexistence des espèces dans une communauté. Plus tard, des précisions sont apportées sur le principe de niche, notamment sur le rôle des espèces dans l’écosystème. En effet, il est important de considérer une espèce comme un élément qui modifie son environnement et donc celui des autres espèces environnantes (Pulliam, 2000). Cette vision a été plus largement décrite par Chase et Leibold, (2003), qui différencient (i) les besoins d’un organisme (i.e. les impacts d’un paramètre écologique sur un organisme) et (ii) les impacts de l’organisme sur ce même paramètre écologique. Une niche se définit alors comme la réunion des besoins et des impacts d’un individu par rapport aux facteurs écologiques. Somme toute, c’est une approche couplée de la vision d’Hutchison, centrée sur les besoins des espèces et d’Elton ou MacArthur, centrée sur les impacts des espèces sur l’environnement.

Il faut noter que Hutchinson n’est pas le premier à utiliser ce terme. En effet, Grinnell, (1917) définissait la niche d’habitat comme tout ce qui conditionne l’existence d’une espèce à un endroit donné, déterminée par les facteurs biotiques et abiotiques. Il a établi un système hiérarchique pour classer et organiser la répartition des paramètres biotiques et abiotiques dans un système emboîté (royaume, régions, zones de vies, associations végétales, niches écologiques). Durant la même période, et pas de manière indépendante, Elton, (1927) a repris le concept de niche et la redéfinissait selon une orientation plus fonctionnelle, basé sur les liens trophiques entre les espèces (Cherrett et al., 1989).

Mes recherches utiliseront une approche basée sur ce concept de niche écologique d'Hutchinson. Les patrons de diversité végétale étant très fortement marqués par le climat (Whittaker, 1975), une hypothèse centrale est qu'une modification des conditions climatiques entraînera un changement de distribution des espèces donc un changement de composition et/ou une restructuration des distributions d'abondances d'espèces à échelle locale.

1.1.3. La dispersion et l'écologie des communautés à grande échelle

Les contributions présentées précédemment se fondent sur le principe général que les espèces occupent un espace particulier où elles sont les mieux adaptées et s'illustrent comme les meilleures « compétitrices ». Ces modèles se basent sur deux grandes hypothèses: (i) la spécialisation écologique est déterminée par la sélection naturelle, car chaque espèce (a fortiori chaque individu) est adaptée biologiquement à survivre dans un espace écologique donné ; (ii) l'assemblage des communautés est défini par la sélection des espèces les plus performantes dans un environnement donné (filtrage de l'habitat). Les concepts théoriques, qui suivent, ont été développés à partir d'autres hypothèses.

MacArthur et Wilson, (1963, 1967) ont développé un pan majeur de la théorie en écologie des communautés avec la théorie de la biogéographie insulaire. Dans cette approche, la diversité (i.e. richesse spécifique) d'une île - *sensu stricto* dans son développement initial, mais *sensu lato* dans la théorie finale - est le résultat d'un équilibre entre les processus de colonisation et d'extinction, le processus central étant la dispersion. Ce modèle prédit que le taux de colonisation est directement dépendant (i) du nombre d'espèces déjà installées sur l'île: si les habitats sont tous occupés, la probabilité de colonisation sera faible et (ii) de la distance au continent (réservoir d'espèces) : plus une île sera éloignée moins sa diversité sera grande. En effet, une richesse spécifique locale élevée et une île de petite taille entraîneront de la compétition et augmenteront ainsi les probabilités d'extinction. Enfin, le dernier volet de la théorie prend en compte la distance entre l'île et le continent représentant le réservoir d'espèces. Plus une île sera éloignée de la réserve d'espèces, plus ses taux d'immigration et de colonisation seront faibles. Ainsi, une petite île éloignée sera plus pauvre en espèces qu'une grosse île proche du continent. Cette théorie, initialement formulée pour des îles réelles, a été appliquée à tous les écosystèmes continentaux fragmentés (e.g. mare en paysage agricole, tourbière en contexte forestier…) (Hanski, 2001; Hanski et Ovaskainen, 2003). Ces travaux apportent de très bons éléments de réflexion pour la biogéographie et la biologie de la conservation à une époque où la fragmentation des habitats est une question centrale dans le maintien de la biodiversité. La théorie des îles marque un changement dans notre perception des communautés. Les patrons de diversité ne sont plus mis relation avec les ressources ou les conditions environnementales (i.e. sélection des espèces), mais comme le résultat des processus de colonisation et d'extinction.

À partir de ces travaux, Levins, (1969) proposa une nouvelle notion pour l'étude des communautés, la métapopulation. Ce concept vise à considérer les populations comme connectées entre elles par la dispersion, permettant ainsi un flux d'individus assurant le maintien de cette population dans le paysage. Plus précisément, il décrit les populations comme des éléments discontinus, représentées par des îlots d'habitats isolés spatialement et réparties dans une matrice de « non-habitat », mais connectées entre eux par des processus de dispersion et de colonisation. Ces échanges permettent d'équilibrer la métapopulation soumise à des extinctions locales au niveau des populations par la dispersion. Deux effets sont discernables: (i) l'effet masse, qui est le maintien d'une population non compétitive dans des habitats défavorables, entretenus par un fort taux d'immigration grâce à la dispersion (Shmida et Wilson, 1985), et (ii) l'effet de sauvetage, qui correspond à l'immigration d'individus d'une même espèce dans une population qui permettra de compenser les taux d'extinction locaux grâce à un apport génétique et démographique (Brown et Kodric-Brown, 1977). Leibold et al., (2004), élargiront cette conception aux métacommunautés. Ils définiront le concept suivant 4 paradigmes :

- la dynamique des îlots: compris entre la compétition et la colonisation, extinction et dispersion ;
- le filtrage des espèces : modèle déterministe basé sur les besoins écologiques des espèces;

- l’effet de masse : modèle des communautés puits/sources pilotées par la dispersion ;
- la neutralité : équivalence fonctionnelle des espèces (voir paragraphe suivant).

De nombreux écologistes critiquent l’approche trop simpliste des modèles basés sur la compétition (Chave, 2004). Les avancées statistiques et les méthodes d’écologie expérimentale permettent de mener des études fines sur les interactions entre les espèces. Ainsi certains auteurs ont changé de paradigme en adaptant des hypothèses issues de la génétique des populations à l’écologie des communautés : la théorie neutre. Cette approche conceptuelle fait un pont entre les mécanismes contrôlant les fréquences d’allèles dans un gène à la fréquence des espèces dans une communauté.

C’est dans ce cadre qu’en 2001, Hubbell publia « *The unified neutral theory of biodiversity and biogeography* » où il propose une théorie complémentaire à la théorie des niches et inspiré de la théorie des îles : la théorie neutre. Il suggère que la dérive (*via* la stochasticité démographique) permet d’expliquer les assemblages des communautés. Le modèle neutre considère que les extinctions (perte d’espèces) sont régies par la dérive stochastique alors que les apparitions (gains d’espèces) sont pilotées par la spéciation et la dispersion aléatoire (immigration) (Adler et al., 2007). Autrement dit, les patrons de distribution d’espèce sont fonction de (i) la taille de la métacommunauté, (ii) du taux de dispersion des espèces de la communauté et (iii) du taux de spéciation (Bell, 2001; Chave, 2004; Hubbell, 2001). Ainsi, les espèces d’un même niveau trophique sont égales en termes de valeur sélective, c’est-à-dire qu’aucune espèce n’est favorisée par rapport à une autre. Ici, le concept de niche est négligé, aucune adaptation ne procure un avantage écologique dans un environnement donné. Toutes les espèces d’une communauté sont fonctionnellement équivalentes vis-à-vis de leur valeur sélective et des relations interspécifiques. Le modèle a une forme spatialement explicite puisqu’il tient compte de l’origine de la propagule (i.e. provenance de la communauté locale ou de la métacommunauté) (Gravel et al., 2011). L’écosystème dispose d’un certain équilibre appelé jeu à somme nulle : les abondances totales des espèces sont constantes, les apparitions compensent les extinctions : c’est un modèle saturé. Le terme « théorie neutre » est directement issu de l’analogie avec les travaux de Kimura, (1983) sur les gènes neutres en génétique des populations.

La vision neutraliste des communautés a fortement animé la discipline (McGill et Collins, 2003; Yu et al., 1998). En effet, la théorie d'Hubbell réfute l'existence des patrons d'espèces et donc de la reproductibilité de ces assemblages dans l'espace. Pour lui, il n'y a pas d'adaptations procurant un avantage compétitif dans un environnement donné. De nombreux développements empiriques ont démonté et contredit les prédictions basées sur la composition et l'abondance des espèces (Gilbert et Lechowicz, 2004; Kelly et al., 2008; Leibold, 2008). Néanmoins, la théorie neutre permet d'expliquer certains patrons (Bell, 2001; Hubbell, 2001), la diversité étant pilotée par des processus stochastiques (pas de limite dans la dispersion) et déterministes (dispersion limitée). La théorie des niches et théorie neutraliste considèrent différents mécanismes pour expliquer les patrons observés (Leibold et McPeek, 2006), elles sont complémentaires et definissent deux extrêmes logiques d'un gradient continu (Chave, 2004). En effet, les deux types de processus pourraient intervenir dans différents contextes écologiques et échelles spatiales (Gravel et al., 2006).

Les concepts utilisés pour le cadre théorique de mes recherches ne pourront pas intégrer de prime abord la théorie neutre. En effet, il est impossible de lier des changements de structure ou de composition avec des changements écologiques si la condition de base ne considère pas que chaque espèce possède une enveloppe écologique définie et est en adéquation avec son habitat. Mes hypothèses ne seront donc pas écrites en tenant compte de ces processus. Par ailleurs, nous garderons en tête ces travaux lors de l'interprétation des données. Si les hypothèses développées avec les enveloppes écologiques ne sont pas vérifiées, l'interprétation des mécanismes *via* l'approche neutre sera une option à considérer. Je tiens ici à mentionner l'apport considérable que peut offrir la théorie neutre pour l'étude de l'assemblage des communautés de bryophytes (Fenton et Bergeron, 2013). Ce groupe présente en effet plusieurs caractéristiques s'alignant avec certaines conditions d'application de la théorie neutre (dispersion illimitée et une faible relation aux variables environnementales).

1.1.4. L’intégration des points de vue théoriques dans les études contemporaines

Toutes ces recherches ont permis d’aborder la question de l’assemblage des espèces selon différentes positions conceptuelles. Ainsi, l’écologie des communautés n’a jamais vraiment fait consensus. Néanmoins, les diverses constructions théoriques permettent de concevoir les communautés vivantes selon différents angles d’approche. La nature met à rude épreuve qui veut l’étudier, gardons en mémoire que : « […] *les systèmes ne sont point dans la nature, mais seulement dans l’esprit des hommes* » (C. Bernard). Pour comprendre la complexité et la diversité des interactions entre les organismes et les liens qu’ils ont avec leur environnement, il est nécessaire d’utiliser des modèles stochastiques et déterministes. Pour répondre à des questions complexes et diversifiées, il est nécessaire de disposer d’une multitude de théories et d’approches à complexité variable (Alonso et al., 2006).

Ma recherche porte sur deux grands groupes taxonomiques végétaux: les trachéophytes et les bryophytes. Ces deux groupes sont caractérisés par des processus de dispersion, de colonisation, et de compétition très différente. Ainsi, nous allons devoir utiliser différentes approches théoriques (stochastiques ou déterministes) pour concevoir mes hypothèses.

1.1.5. Conception synthétique de l’assemblage des communautés

Comme nous venons de le voir, les théories cherchant à comprendre la dynamique des communautés ne manquent pas. Dans cette partie, notre objectif est de présenter de manière concise les principaux processus impliqués dans l’assemblage des communautés.

Les théories précédemment décrites sont toutes construites sur quatre principes fondamentaux, hérités et adaptés de la génétique des populations. Les quatre processus à l’origine de la diversité génétique sont transférables aux mécanismes permettant la diversité spécifique au sein des communautés : la dérive écologique, la dispersion, la sélection et la spéciation (Vellend, 2010). Les modèles associés aux théories précédentes se basent sur un ou plusieurs de ces processus. Malgré la proximité dans les mécanismes à l’œuvre dans l’écologie des communautés et la génétique des populations, il existe une grande différence entre les deux disciplines : la génétique des populations aborde ses questions dans le sens « processus centré » tandis que l'écologie des communautés se base sur une approche « patrons centrés » (Vellend et Orrock, 2009). Cette différence dans l'orientation des hypothèses n'altère pas l'utilisation des quatre mécanismes. Ce regard synthétique et conceptuel permet de recadrer et de réorganiser les différentes théories développées jusqu'à maintenant en écologie des communautés.

D'une façon moins théorique, l'assemblage des communautés est régi par de nombreux processus locaux et régionaux. Les interactions biotiques telles que la compétition, la prédation ou le mutualisme peuvent affecter les abondances et les distributions locales des espèces (Hoeinghaus et al., 2007). Les caractéristiques abiotiques (paramètres environnementaux locaux ou régionaux) modulent ces interactions biotiques et influent sur la capacité des espèces à se maintenir dans la communauté (Dunson et Travis, 1991; Hairston et al., 1960). De plus, les facteurs historiques (locaux ou régionaux) conditionnent les assemblages locaux d'espèces (Hermy et Verheyen, 2007; Hoeinghaus et al., 2007; Vanhellemont et al., 2014). Enfin, les pressions anthropiques jouent aujourd'hui un rôle prépondérant dans les patrons de répartition de la biodiversité, les parties suivantes en présenteront les grandes tendances (Vellend et al., 2017).

Mes recherches se basent sur des comparaisons historiques des communautés locales sur une large échelle spatiale. Je dois intégrer les processus locaux, régionaux, historiques, biotiques et anthropiques dans l'interprétation des structures observées. C'est pourquoi la construction des hypothèses intégrera les cadres théoriques précédemment développés, afin d'intégrer l'ensemble des processus locaux et régionaux impliqués dans l'assemblage des communautés.

1.2. Brève histoire paléobotanique Nord-Américaine

Depuis environ une trentaine d'années, l'étude des réponses de la biodiversité aux changements globaux motive une très importante part de la recherche en écologie. Pourtant la biodiversité n'a jamais été stable dans le temps. Sur des échelles temporelles suffisamment longues (e.g. géologique), les espèces évoluent, leurs distributions sont dynamiques et les patrons de diversité se déplacent au rythme des changements bioclimatiques et des interactions biotiques (Harrison et Sanchez Goñi, 2010; Lyons et al., 2016). Comprendre les changements de végétation qui se sont opérés sur de longues périodes de temps permet d'émettre des prédictions sur l'effet du réchauffement actuel et futur sur les patrons de distribution des espèces. Le propos ici n'a pas pour objectif de décrire en détail les successions végétales de l'Holocène (les 12 000 dernières années), mais de donner une perspective paléoécologique des liens climat-végétation.

Le nord-est de l'Amérique a subi de nombreuses vagues de glaciation. Depuis le début de l'époque du Quaternaire (1.8 million d'années) la zone arctique, boréale et le nord de la zone tempérée ont été recouverts environ tous les 100 000 ans d'une épaisse couche de glace (Richard et Grondin, 2009). La glaciation dite Wisconsinien est le dernier épisode glaciaire en Amérique du Nord la glace a atteint son étendue maximum aux alentours de 18 000 ans BP (Dyke, 2005). À cette période, la marge sud du glacier recouvre le nord des États-Unis, à cette époque la toundra et la forêt boréale occupent la majeure partie des États-Unis tandis que les forêts mixtes sont confinées dans le sud des états Américains (~35°N). Le retrait de la glace débute autour de 13 000 ans BP et permet la migration de la végétation vers le nord (Delcourt et Delcourt, 1983; Delcourt et al., 1982). Durant la phase de déglaciation, la vitesse de colonisation des biomes peut atteindre 100 à 200 m/an (Dyke 2005). À partir de 7 000 ans BP les conditions climatiques sont relativement stables et la distribution des forêts mixtes ressemble dans les grandes lignes à ce que nous connaissons aujourd'hui (Delcourt et Delcourt 1983, Dyke 2005). Enfin, à partir de 5 000 ans BP, le patron de distribution des biomes au Canada est similaire à la distribution actuelle.

Les limites de distribution à hautes latitudes et altitudes des grands types de végétations coïncident avec les patrons bioclimatiques. Aujourd'hui à la limite nord de la toundra herbacée, on peut tracer grossièrement une isocline correspondant à une température moyenne en juillet d'environ 3°C ; la toundra arbustive ~7.5°C ; la toundra forestière ~10°C ; pour finir la forêt boréale qui est comprise entre ~13°C et 17°C, correspondant respectivement à la limite sud du front arctique hivernal et estival (Dyke 2005). Dans la partie méridionale du Québec, les forêts feuillues sont vieilles de 8 000 ans, mais ont subi de grandes modifications dans leur composition (Richard, 1995). Une des causes est le réchauffement périodique de la température, qui a fait varier la proportion de *Fagus* et d'*Acer* dans le paysage forestier. Par une dispersion plus efficace, les *Acer* répondent plus rapidement que les *Fagus* aux réchauffements. Ils ont donc rapidement dominé le paysage botanique de la région. La seconde explication est l'intervention de l'homme dans la composition des forêts.

Il est évident que cette délimitation est grossière, mais elle dresse une bonne image du lien entre végétation et climat sur de larges échelles spatio-temporelles. En affinant ce lien, il ne faut pas occulter une forte interaction entre température et précipitation. Par exemple, lorsque la température est suffisamment élevée pour soutenir la croissance, mais les précipitations sont trop faibles, alors les espèces arbustives laissent place aux prairies et steppes. Ce mécanisme explique en partie la distribution est-ouest des biomes en Amérique du Nord (Dyke 2005). La distribution actuelle des biomes est le résultat d'environ 14 000 ans de successions végétales, mais il serait très restrictif de confiner cette dynamique au seul fait des conditions climatiques. La distribution des biomes sur des échelles géologiques est influencée par plusieurs événements stochastiques tels que les feux, les épidémies, les événements climatiques extrêmes et bien sûr plus récemment par les interactions avec l'espèce humaine (Richard et Grondin, 2009; William, 2006).

À chaque période de glaciation ou de réchauffement, les forêts ont migré, évolué et se sont adaptées aux nouvelles conditions environnementales. Aujourd'hui, les changements de biodiversité sont observables à l'échelle humaine. La vitesse d'augmentation de la température engendre des conséquences écologiques assez inquiétantes. D'où l'importance d'étudier les réactions de tous les composants de la biodiversité. Ce doctorat utilise l'approche de l'écologie historique pour tester l'effet du réchauffement de la température observée depuis environ 40 ans sur la structure et la composition des communautés végétales forestières. Les changements climatiques modifient les conditions locales de survie et de reproduction des espèces (théorie des niches). Les réponses des communautés à échelle locales sont (i) un changement des structures d'abondances des espèces et (ii) un changement de composition des communautés. À large échelle spatiale, on prédit un déplacement des distributions des espèces en lien avec les patrons spatiaux de changement climatique.

1.3. Les perturbations sous l’Anthropocène

1.3.1. Les changements globaux

La dynamique des cycles naturels, c’est-à-dire les échanges entre atmosphère, biosphère et hydrosphère est contrôlée par des facteurs naturels tels que la circulation thermohaline, le climat, le volcanisme, la tectonique des plaques, etc. Depuis environ un siècle, l’activité humaine a largement perturbé cet équilibre. Le développement des sociétés occidentales s’est basé sur l’industrialisation, l’agriculture, l’exploitation forestière pour soutenir le niveau de vie acquis, libérer de nouvelles terres pour les villes, les cultures ou les voies de déplacement. Ceci a eu pour effet (i) la libération d’importantes quantités de gaz à effet de serre (e.g. CO_2, SO_x, CH_4, NO_x…) essentiellement due à la combustion des énergies fossiles carbonées et (ii) un changement d’utilisation des sols entraînant des conversions d’habitat ou la fragmentation des écosystèmes. La recherche scientifique s’intéresse aujourd’hui à comprendre, évaluer et prédire l’impact de ces perturbations sur les milieux naturels, semi-naturels et les communautés les composant (McGill et al., 2015; Root et al., 2003; Sala et al., 2000; Vellend et al., 2017). Parmi les grands mécanismes impliqués dans les changements globaux, voici les plus caractéristiques (UICN 2010) :

- changements climatiques : augmentation de la température, perturbation du régime des pluies, fréquence et intensité des événements climatiques extrêmes, etc.;
- pollution chimique: modification de la composition de l’atmosphère, pollution des eaux et des sols, etc.;
- changement de l’utilisation et d’occupations des sols : urbanisation, agriculture, déforestation, conversion des écosystèmes naturels et semi-naturels en agroécosystèmes, etc.;
- crise biologique : surexploitation, invasion biologique, chasse, homogénéisation biotique, etc.

Les changements environnementaux contemporains se caractérisent par leur vitesse et intensité. À titre d'exemple, l'augmentation de la température moyenne annuelle à la surface de la Terre est d'environ 0.85°C entre 1880 et 2012 (IPCC, 2014). Plus spécifiquement, on rapporte qu'à partir de 1979 cette augmentation atteint + 0.17°C (± 0.05) selon (Smith et Reynolds, 2005) par décennie depuis les 50 dernières années. On associe cette hausse aux effets anthropiques (Huber et Knutti, 2012; IPCC, 2014). Voici quelques exemples de conséquences directes des changements climatiques sur les écosystèmes terrestres :

- augmentation des températures;
- augmentation des épisodes climatiques extrêmes et de leur intensité : canicule, inondation, tempêtes… (Coumou et Rahmstorf, 2012);
- perturbation du régime des pluies : augmentation des précipitations dans l'hémisphère nord, et diminution dans une grande partie de l'hémisphère sud et dans les zones déjà arides (Wentz et al., 2007).

Notons que ces modifications ne vont pas avoir les mêmes effets sur l'ensemble de la planète. Par exemple, les augmentations de température et les changements du régime des pluies ne sont pas uniformes (IPCC, 2014). Ainsi, les zones de hautes latitudes et altitudes sont sujettes à de plus forts risques de réchauffement que les zones tempérées (Magurran et al., 2010; Parmesan et al., 2000; Root et al., 2003).

1.3.1.1. Les dépositions atmosphériques

Le développement de l'agriculture intensive en Europe et en Amérique à la fin de la Seconde Guerre mondiale et l'industrialisation de masse des pays développés ont entraîné une importante libération de particules dans l'atmosphère (Bouwman et al., 2002). Les principales particules impliquées sont les composés azotés sous la forme NH_4, NO_x et sulfurés SO_x issu de la combustion d'énergie fossile, de l'agriculture et de l'industrie (Bobbink et al., 2010; Galloway et al., 2008). Les dépôts atmosphériques de ce type ont pour conséquence l'acidification et l'eutrophisation des écosystèmes. Ils conduisent entre autres à une diminution de la diversité des communautés végétales (Field et al., 2014; Soons et al., 2017; Stevens et al., 2010). De ce fait, ils sont considérés comme une des principales menaces pour le fonctionnement et la structure des écosystèmes (Bobbink et al., 2010; Field et al., 2014; Phoenix et al., 2012) ainsi que pour la biodiversité (Dise et Wright, 1995; Sala et al., 2000; Vellend et al., 2017).

Les dépositions atmosphériques sont étudiées dans le chapitre 2 pour comprendre les changements à long terme de la phytocénose d'une forêt située dans un bassin industriel du nord-ouest de la France. Les chapitres 3 et 4 ont été établis dans le but d'éviter les zones industrialisées du Québec méridional.

1.3.1.2. *Le réchauffement de la température*

Le 5^{e} rapport du GIEC (Groupe d'Experts Intergouvernemental sur l'Évolution du Climat – nomé ici IPCC de son acronyme anglais) établit très clairement le lien entre l'intensité des activités humaines et les perturbations du système climatiques (IPCC, 2014). Le relargage de gaz à effet de serre dans l'atmosphère a modifié les flux radiatifs de la Terre entraînant un réchauffement de la température sur la surface du globe. Celui-ci s'est initié dans la seconde moitié du 20^{e} siècle entraînant une diminution des épaisseurs de glace, une augmentation du niveau de la mer et un réchauffement des eaux de surface.

Les principales préoccupations autour de ce débat concernent la rapidité de l'augmentation. Lorsque j'ai proposé ce projet de doctorat en mai 2015, j'expliquais à mon jury que la concentration en dioxyde de carbone à la surface du globe venait tout juste de passer la barre symbolique des 400 ppm. Sur une perspective historique à large échelle, c'est 100 ppm au-dessus de la plus haute concentration atteinte dans les 800 000 années avant 1850. Deux ans plus tard, en mai 2017, la même source d'information (NOAA, https://climate.gov) indique 410 ppm. Entre 2015 et 2016, il y a eu la plus grande augmentation de CO_2 depuis les 60 dernières années de mesures (NOAA, https://climate.gov , 10 décembre 2017).

La Figure 1.2 présente le gradient est-ouest d'augmentation de la température dans la province du Québec. Il correspond à un gradient de continentalité, soit de distance à la mer. Les importantes masses d'eau atlantiques agissent comme un tampon climatique et peuvent expliquer en partie les faibles augmentations de température observées (Yagouti et al., 2008).

Le régime des précipitations est faiblement perturbé pour l'ensemble du Québec avec une augmentation de 18 mm par décennie. Seules les écorégions du nord semblent subir des augmentations significatives des précipitations, et la variation spatiale est très importante (Berteaux, 2014). Si la moyenne totale annuelle montre une tendance à la hausse, la pluviométrie estivale ne montre pas de tendance globale, certaines régions subissent une diminution significative (Yagouti et al., 2008). D'une manière générale, la quantité de neige a diminué pour le sud Québec.

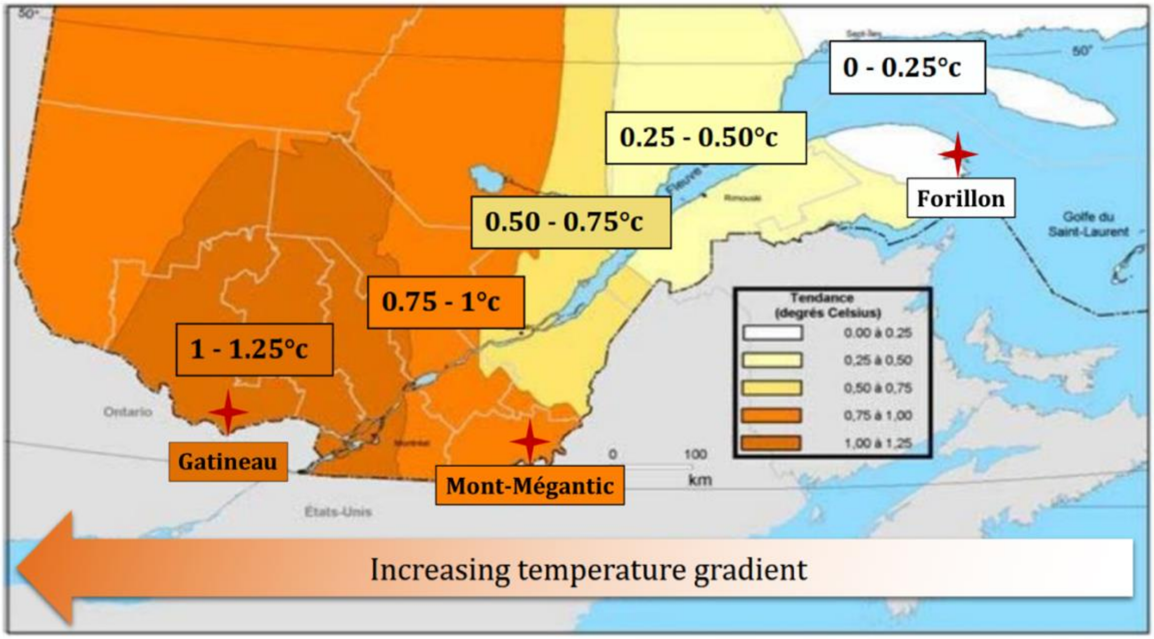


Figure 1.2 – Gradient d'augmentation des températures moyennes annuelles au Québec entre 1960 et 2005 (tirée de Yagouti et al. 2006) et situation géographique des sites d'étude du chapitre 3 et 4.

1.3.1.3. Le changement d'utilisation des sols

Le changement d'utilisation des sols est une des pressions majeures qui pèse sur la biodiversité (McGill, 2015; Newbold et al., 2015; Sala et al., 2000). La conversion des écosystèmes naturels vers des systèmes agricoles intensifs et urbains entraîne généralement une perte de diversité végétale (Vellend et al, 2017). Le changement d'utilisation du sol associe donc deux mécanismes : la fragmentation des habitats et la perte d'habitat. La fragmentation s'intéresse aux résidus d'écosystèmes naturels laissés à la suite d'un changement d'utilisation du sol d'une région. Elle peut également être divisée en deux mécanismes distincts : l'isolation de l'habitat qui renvoie aux prédictions issues de la théorie des îles et l'effet bordure entre les résidus des habitats naturels et les habitats anthropiques créés par la conversion de l'habitat (Fahrig, 2003). Dans une méta-analyse, (Ibáñez et al., 2014) montre que globalement, les effets positifs et négatifs de la fragmentation sur la diversité végétale sont comparables et montrent une grande variabilité. Il est difficile d'établir une tendance précise des effets de la fragmentation, les processus sont complexes et dépendent du contexte écologique, des groupes taxonomiques et des métriques utilisées. Cependant, il est indéniable que la fragmentation a un effet sur la composition taxonomique et fonctionnelle des communautés (Fahrig, 2003; Ibáñez et al., 2014; Laurance et al., 2011; Magnago et al., 2014; Vellend et al., 2017).

Dans chacune de mes études, j'ai sélectionné les sites et les points dans le but d'éviter les effets de changement d'utilisation du sol. Ainsi les sites d'études sont des parcs nationaux (provinciaux ou fédéraux) assurant un bon état de conservation des forêts depuis l'établissement du statut de protection.

1.3.2. Réponses des communautés aux changements globaux

Cette section présente le concept cœur du sujet de recherche : quelles sont les conséquences des changements environnementaux à large échelle sur les patrons d'assemblage et de distribution des espèces? Mes recherches sont axées sur les communautés végétales, ainsi le discours et les exemples seront particulièrement orientés vers les plantes. En parallèle des trois objectifs principaux de cette thèse, j'ai participé à une revue de la littérature visant à synthétiser les changements de biodiversité végétale en réponse aux perturbations environnementales de l'Anthropocène, voir Annexe C.

La capacité des organismes à se maintenir et à prospérer dans un écosystème dépend de l'adéquation entre leur enveloppe écologique avec les conditions abiotiques qu'offre cet habitat le tout modulé par les interactions avec les autres espèces. Une perturbation environnementale même légère peut donc entraîner des modifications de structure, de composition et de répartition des communautés végétales (Fox, 2013; Sala et al., 2000; Smith et al., 2009). De la même manière, les relations biotiques (e.g. facilitation, compétition, coopération, prédation…) jouent un rôle crucial dans le maintien de la diversité (Barabás et al., 2018; Chesson, 2000; Elith et Leathwick, 2009; HilleRisLambers et al., 2012).

Au niveau local, l'assemblage des espèces est fortement influencé par les perturbations environnementales (Grime, 1977; Smith et al., 2009; Vellend et al., 2017). Les changements environnementaux entraînent des modifications de composition et de structure dans les communautés biotiques, mais les différents groupes taxonomiques, ou *a fortiori* les différentes espèces, ne sont pas tous pilotés par les mêmes paramètres environnementaux et n'offrent pas une réponse similaire à une même perturbation (Bagella, 2014; Bertrand et al., 2011; Delgado et Ederra, 2013; Lalanne et al., 2008, 2010; Økland et al., 2004; Vittoz et al., 2010). La littérature en écologie des communautés commence à offrir de nombreux cas d'études évaluant les effets des changements environnementaux sur les systèmes biologiques ou sur les communautés vivantes. Cependant, ces études sont souvent menées sur les trachéophytes, très peu de données sont disponibles pour les bryophytes.

1.3.2.1. *Migration et déplacement des espèces*

Une des prédictions de la théorie des niches écologiques est une adéquation entre les conditions environnementales et les exigences écologiques des espèces d'une communauté. Le climat est un déterminant central de la distribution des plantes, de fait un changement de température à large échelle entraîne un changement local de l'assemblage et des espèces (Bertrand et al., 2011;

Chen et al., 2011; Gornish et Tylianakis, 2013; Lenoir et al., 2008; Parmesan, 2006; Urban, 2015; Walther, 2010). De nombreux travaux ont mis en relation une migration des espèces en réponse à l'augmentation de la température vers les pôles (Colwell et al., 2008; Lesica et McCune, 2004; Parmesan et al., 1999; Walther et al., 2005) ou en altitude (Cannone et Pignatti, 2014; Kelly et Goulden, 2008; Parolo et Rossi, 2008; Pauli et al., 2007; Savage et Vellend, 2015). En effet, le réchauffement climatique mondial pousse les espèces, ou certains écosystèmes à migrer vers leurs *optima* climatiques (Klanderud et Birks, 2003; Pauli et al., 2012; Walther, 2010). Les chapitres 3 et 4 explorent les dynamiques temporelles des communautés sur des gradients altitudinaux. Par souci de cohésion, je centrerai mon discours autour des migrations altitudinales des espèces végétales.

Dans une méta-analyse Chen et al., (2011) rapporte un taux global de migration en altitude d'environ 11 m.décennie $^{-1}$. En Amérique du Nord, il existe une grande variation dans les taux de migration allant de ~22 m.décennie^{-1} en Californie (Kelly et Goulden, 2008) à aucune migration observée dans le Montana (Klasner et Fagre, 2002). Ailleurs dans le monde, on retrouve cette grande variabilité des taux de migration : Alpes de 4 à 24 m.décennie^{-1} (Parolo et Rossi, 2008; Pauli et al., 1996), Andes Péruviennes ~30 m.décennie^{-1} (Feeley et al., 2011), Hawaii ~13 m.décennie^{-1} (Koide et al., 2017), Himalaya Indienne de 14 à 19 m.décennie^{-1} (Dubey et al., 2003), Taiwan ~36 m.décennie^{-1} (Jump et al., 2012). Toutefois, la comparaison directe de ces indices est assez difficile du fait des différences locales de réchauffement, de méthodes (type de données utilisé : herbier ou relevés de communauté) ou bien de succession végétale (i.e. dynamique forestière sur le gradient altitudinal, Bodin et al., 2013).

La grande variabilité des taux de migration laisse apparaître un décalage de réponse « *time-lag* » de la migration des communautés par rapport à la vélocité du réchauffement de la température (Bertrand et al., 2011). Ce retard de réponse se traduit par une inadéquation entre les enveloppes climatiques des communautés locales avec les conditions climatiques de la région. Cela peut traduire plusieurs processus : (i) un manque de réponse due à une trop faible ou trop lente augmentation de la température compensée par la plasticité des espèces de la communauté; (ii) une incapacité à la dispersion dictée par le pouvoir de dispersion des espèces; (iii) l'interaction avec d'autres variables climatiques comme la disponibilité en eau ou (iv) une matrice paysagère fragmentée rendant impossible la colonisation (Corlett et Westcott, 2013). La synergie entre ces qutres processus suggère une multitude de réponses en fonction des espèces et/ou des groupes fonctionnels ou taxonomiques face au réchauffement climatique. L'illustration parait évidente lorsqu'on compare le pouvoir de dispersion, sexué ou non, d'une bryophyte à celui d'un chêne dans un paysage agricole. Les temps de réponse et la capacité de colonisation jouent un rôle prépondérant dans la capacité de mouvement des espèces sessiles tel que les végétaux. Ainsi la capacité de mouvement de certaines espèces dépendra de leur aptitude à l'acclimatation, l'adaptation ou la micro-mobilité vers des refuges favorables.

1.3.2.2. Thermophilisation des communautés

Une des conséquences directes de la migration et du déplacement des espèces est la thermophilisation des communautés. Cela se manifeste par deux mécanismes : (i) une disparition ou diminution en abondance des espèces nordiques caractéristiques des milieux boréalo-alpins voire arctiques au profit de (ii) l'augmentation en nombre et en abondance des espèces méridionales ayant des affinités à des températures plus grandes (Bates et al., 2005; Damschen et al., 2010; De Frenne et al., 2013; Gottfried et al., 2012; Harrison et al., 2010; Stockli et al., 2012).

Il existe de grandes différences dans l'intensité et la magnitude de ce phénomène en fonction des espèces et des situations géographiques (Bertrand et al., 2011). D'autre part, il existe très peu d'études à long terme sur la réponse des bryophytes aux changements climatiques (Bates et al., 2005; Bergamini et al., 2009; Vanneste et al., 2017). Curieusement, les bryophytes ont souvent été présentées comme de bons indicateurs des changements climatiques (Gignac, 2001; He et al., 2016; Molau et Alatalo, 1998; Tuba et al., 2011). Cependant, il y a un manque considérable de preuves publiées qui testent *in natura* la sensibilité des communautés de bryophytes au réchauffement de la température à large échelle. Il est à noter qu'à l'inverse certains auteurs soutiennent que les bryophytes ont une large gamme de tolérance thermique, diminuant leur sensibilité aux changements de température à large échelle (Hudson et Henry, 2010; Vanneste et al., 2017). Dans une section suivante (*1.4.2*), j'établirai le lien entre les caractéristiques bio-écologiques des bryophytes et les arguments qui soutiennent l'une et l'autre de ces suppositions. Les chapitres 2 et 4 seront des contributions au développement de cette question.

1.3.2.3. *Homogénéisation biotique*

L'homogénéisation biotique se defini comme une augmentation de la ressemblance des assemblages d'espèces au sein d'une région. Les mécanismes sous-jacents à l'homogénéisation biotique sont (i) la perte de diversité et (ii) un changement de composition des communmautés. À l'échelle régionale, une prédiction quantitative est la diminution de la diversité-β dans un paysage (Mouquet et Loreau, 2003; Olden et Rooney, 2006). À échelle locale, une prédiction qualitative est le remplacement (en présence ou en abondance) des espèces spécialistes par des espèces généralistes (Clavel et al., 2011; Heinrichs et Schmidt, 2016; Savage et Vellend, 2015; Zwiener et al., 2017). Les espèces spécialistes se définissent par une niche écologique étroite, c'est-à-dire avec une faible valence écologique, elles sont dites *sténoèces*. À l'inverse, les espèces généralistes sont caractérisées par une niche écologique plus large, donc avec une forte valence écologique, on les nomme *euryèces*. Ces dernières sont plus tolérantes aux modifications de leur environnement donc plus résilient dans un contexte de changement global. Cette question pourrait aisément s'aborder sous l'angle de l'écologie fonctionnelle végétale *via* la classification C-S-R de Grime, (1977). D'un point de vue encore plus théorique, on pourrait émettre des hypothèses sur les réponses respectives des stratégies *r* et *K* (MacArthur et Wilson, 1967) face aux changements globaux.

1.3.2.4. *Eutrophisation et acidification*

Entre 1860 et 2005, la production d'azote réactif est passée de 15 à 187 Tg N an^{-1} (Galloway et al., 2008). Depuis 1970, date utilisée comme référence temporelle dans mes travaux, la population mondiale a augmenté de 78% et la création d'azote réactive a augmenté de 120%. Très généralement, les dépositions atmosphériques azotées sont composées de nitrate (NO_{3^-})

engendrant l’eutrophisation ou la nitrification et d’ammonium (NH_{4+}) entraînant l’acidification (Erisman et de Vries, 2000; Pannek et al., 2015). Les retombées atmosphériques, ainsi que les fertilisations directes ou les ruissellements sont responsables d’une perte de diversité et d’un changement de composition des communautés (Diekmann et Dupré, 1997; Field et al., 2014; Sala et al., 2000; Thimonier et al., 1994).

Les mécanismes sous-jacents à la perte de diversité sont (i) l’augmentation de la dominance de quelques espèces à fort pouvoir compétitif (i.e. espèces nitrophiles, ubiquistes) et (ii) l’acidification du sol (Vellend et al., 2017). L’eutrophisation consiste en un remplacement des espèces locales par des espèces nitrophiles à caractère rudéral. L’acidification est le processus inverse, c’est-à-dire un remplacement des communautés locales par des espèces acidiphiles. Ces deux processus apparaissent généralement de pair et ils seront particulièrement étudiés dans le chapitre 2. Le site d’études est une forêt d’étude située dans un important bassin urbano-industriel du nord-ouest de la France. Le choix des sites pour les chapitres 3 et 4 s’est orienté vers des zones les plus éloignées des centres industriels afin de minimiser l’effet des dépositions pour se concentrer sur le réchauffement climatique.

1.3.2.5. Adaptions, microévolutions et évolution

Mentionnons les quelques études traitant des processus adaptatifs ou évolutifs des espèces aux changements environnementaux (Aitken et al., 2008; Parmesan, 2006; Thomas et al., 2001). Celles-ci sont toutefois controversées du fait de la lenteur du processus évolutif et de la vitesse des changements observés (Gienapp et al., 2008). Le taux de spéciation sous l’Anthropocène est relativement comparable au taux d’extinction et semble être, pour l’instant un mécanisme négligeable (Vellend et al., 2017), bien que cela soit encore débattu (McGill et al., 2015). C’est encore un processus méconnu et nous manquons de synthèse à large échelle. La capacité d’adaptation et d’évolution des plantes face aux changements globaux est encore très mal connue et comprise (Corlett et Westcott, 2013).

1.3.2.6. *Barrières à la dispersion*

Une des réponses des espèces aux changements globaux se manifeste par la capacité de migration afin de rejoindre des conditions écologiques plus favorables. Cette mobilité se mesure par la capacité de dispersion divisée en deux éléments très différents (i) les traits d'histoire de vie de l'espèce, par exemple la distance de dispersion des propagules ou le nombre de propagules produit et (ii) la qualité de la matrice environnementale, mesurable, entre autres, par la continuité écologique ou le niveau de fragmentation des écosystèmes. La fragmentation des habitats créer une discontinuité conduisant à un ralentissant ou un blocage des déplacements d'espèces (Higgins et al., 2003; Pearson et Dawson, 2005). De même, l'occupation des fragments par des communautés peut également ralentir voire stopper la dispersion et la colonisation des espèces en mouvement (Corlett et Westcott, 2013). Le cadre théorique des niches rencontre ici celui des îles et des métapopulations/communautés. On peut mettre en liens les interactions entre dispersion, dynamique des fragments et filtrage environnemental des espèces. Si la connectivité diminue, l'isolement de l'habitat augmente, la théorie des îles émet la prédiction que la diversité est une fonction de la taille et de l'isolement du fragment. Si la dispersion augmente dans le paysage, la richesse locale en espèce augmente jusqu'à un maximum avant de diminuer du fait de la dominance des quelques espèces avec une forte dispersion (Mouquet et Loreau, 2003).

Enfin, notons que les interactions biotiques jouent un rôle non négligeable dans les possibilités de déplacement. Ainsi, une récente étude de notre laboratoire a montré que la migration en altitude de l'érable à sucre (*Acer saccharum*) au Québec est en partie limitée par la prédation des graines par des micromammifères (Brown et Vellend, 2014).

Pour terminer, il est bon de noter que les capacités de déplacements des aires de répartition d'espèces sont extrêmement variables entre les espèces (Parmesan et al., 1999; Thomas et al., 2001). Les taxons qui ne parviendront pas à s'adapter ni à migrer sont les cibles de l'extinction (Thomas et al., 2004). Ainsi certaines grandes caractéristiques sont associées aux espèces ou populations « sujettes » à la disparition (d'après Aitken et al., 2008):

- une faible répartition ;
- sédentaires ;
- spécialistes ;
- faible effectif ;
- une variance génétique faible ;
- un temps de génération élevé.

1.4. Cadre méthodologique

1.4.1. L'écologie historique en science de la végétation

Depuis le début du XX^{e} siècle, la recherche en écologie végétale avait pour but de décrire les patrons spatiaux et les assemblages d'espèces (Dengler et al., 2011). Aujourd'hui, ces précieuses données de végétation peuvent être utilisées comme référence temporelle pour évaluer les effets des changements environnementaux sur la végétation (Chytrý et al., 2014; Hédl et al., 2017; Stockli et al., 2012; Tingley et Beissinger, 2009; Vellend et al., 2013). Ces informations peuvent être compilées à partir de plusieurs sources, telles que (i) des suivis de composition de la végétation sur des points de relevé permanents (i.e. *monitoring*) ; (ii) des herbiers ou des bases de données d'occurrences et (iii) des rééchantillonnages d'anciens sites. Mes recherches utiliseront cette dernière méthode, qui est considérée comme la plus fiable des différentes approches existantes dans l'utilisation de données historiques (Chytrý et al., 2014).

Les études phytosociologiques ont servi à décrire, classifier et cartographier la végétation dans de nombreuses régions (Schaminée et al., 2009). Ces relevés botaniques deviennent une ressource de qualité pour tester des hypothèses sur la dynamique temporelle de la végétation (Bertrand et al., 2011; Chytrý et al., 2014; Dengler et al., 2011; Hédl et al., 2017; Lenoir et al., 2008; Vellend et al., 2013). L'avantage des relevés phytosociologiques est l'homogénéité de la méthodologie d'inventaire. Les relevés sont toujours faits suivant le même protocole: un relevé par strate de toutes les espèces présentes sur une surface donnée, avec l'attribution d'un indice d'abondance dominance et dans certains cas un coefficient de sociabilité. Cette constance dans la méthodologie offre une opportunité unique de comparer des relevés réalisés dans différentes régions à différentes époques. Notre recherche se basera essentiellement sur le rééchantillonnage de sites historiques.

Néanmoins, lorsque nous travaillons en forêt avec des données datant de ~40 ans, une attention particulière doit être prise vis-à-vis de la gestion forestière menée depuis le temps des premiers relevés. En effet, la dynamique des peuplements forestiers est fortement soumise à la gestion humaine. Cependant, certains massifs forestiers sont protégés depuis quelques décennies (e.g. parcs nationaux, zones de conservations, réserves faunistiques…). Afin de minimiser les effets confondants tels que l'ouverture de la canopée par exploitation forestière nous avons sélectionné des sites bénéficiant d'un statut de protection limitant les activités humaines.

1.4.2. Les communautés végétales

Les impacts des changements écologiques sur la biodiversité peuvent être étudiés à différents niveaux : à l'échelle individuelle, spécifique, des communautés ou des écosystèmes. À l'échelle individuelle, il est possible d'étudier les variations phénologiques, c'est-à-dire le suivi temporel des événements biologiques (i.e. débourrement, floraison, fructification). Cela renseigne la réaction des espèces vis-à-vis des changements sur le plan biologique. À l'échelle spécifique, les changements de répartition de quelques espèces cibles ayant des écologies très particulières sont utilisés comme « sentinelle » (Gignac, 2001). Une autre approche consiste à étudier les communautés. Plus fiable et plus puissante, elle se base sur la réponse combinée de plusieurs espèces (Gignac, 2001). J'utiliserai cette approche avec une attention particulière envers:

- les modifications structurelles, approche quantitative liée aux indices de biodiversité ;
- les modifications de composition, approche qualitative liée à l'identité des espèces ;
- les modifications autoécologiques : affinités écologiques des espèces.

La littérature contient très peu d'études utilisant des suivis à long terme de bryophytes forestières pour évaluer les impacts des changements climatiques. Elle contient également relativement peu d'études analysant la réponse comparée des deux groupes (bryophytes et trachéophytes). Ceci s'explique par la difficulté des identifications, le manque cruel de bryologues et la rareté des inventaires historiques complets des bryophytes comparativement aux plantes vasculaires. Pourtant, les bryophytes sont souvent considérées très informatives comme indicateurs de certains changements environnementaux (Bates et al., 2005; Frahm et Klaus, 2001; Frego, 2007; Gignac, 2001; Kapfer et al., 2012; Raabe et al., 2010). De plus, les bryophytes constituent une part importante de la diversité végétale et participent au fonctionnement des écosystèmes forestiers.

1.4.3. Les *Embryophyta*, notes botaniques

Les plantes terrestres sont englobées dans le grand groupe des *Embryophyta*. Ils ont pour point commun (i) un développement de l'embryon dans une structure reproductive multicellulaire, les spores ; (ii) une couche de sporopollénine autour des spores et (iii) la présence de composés biochimiques secondaires, tel que des flavonoïdes. Les *Embryophyta* comprennent les *bryophyta* (ou *bryobionta*) et les *polysporangiophyta* (ou *tracheophyta*) (Chase et Reveal, 2009; Shaw et Renzaglia, 2004). Les *bryophyta* sont un groupe composé de 3 lignées :

- *Marchantiophyta* (les hépatiques) ;
- *Bryophyta* ou *Musci* (les mousses à proprement parler) ;
- *Anthocerophyta* (les anthocérotes).

Les *polysporangiophyta* sont composées de plusieurs groupes :

- *Lycophyta*
- *Euphyllophyta (Moniliformopsa* et *Spermatophyta*).

Note : Pour le reste de ce document « bryophytes » avec une minuscule correspond au grand groupe comprenant les trois lignées : Marchantiophytes, Anthocerotes, Bryophytes et « Bryophytes » avec une majuscule se réfère au phylum des mousses sensu stricto (i.e. *Bryophyta*).

Les bryophytes représentent le second plus gros groupe des « plantes », après le groupe des *Magnoliophyta* (i.e. les plantes à fleurs, estimées à 350 000 espèces) avec des estimations comprises entre 15 000 et 25 000 espèces (Frahm, 2008; Vanderpoorten et Goffinet, 2009). Les bryophytes se retrouvent dans tous les écosystèmes terrestres même extrêmes, où elles sont parfois l'espèce dominante (e.g. les forêts boréales, les steppes arides, tourbières, les milieux minéraux : roches, sols maigres, etc..).

1.4.3.1. *Caractéristiques bioécologiques comparées des bryophytes et des trachéophytes*

Cette section a pour objectif de préciser les caractéristiques bioécologiques spécifiques des deux groupes permettant de soutenir les hypothèses développées dans cette thèse. Les chapitres 2 et 4 établissent des comparaisons temporelles de la réponse des communautés de bryophytes et de trachéophytes dans leur réponse aux changements globaux.

Les bryophytes sont considérées comme le groupe le plus prospère après les angiospermes. Sur plusieurs points, ils se démarquent par leur singularité : nombre d'espèces, la diversité de leur forme de vie, la diversité d'habitat qu'ils colonisent, et leur large distribution spatiale (Tuba et al., 2011). Avec une histoire évolutive longue d'environ 450 millions d'années, les bryophytes représentent également le plus vieux groupe végétal sur Terre marquant un lien évolutif entre les plantes aquatiques et les plantes terrestres (Shaw et Renzaglia, 2004).

1.4.3.2. *Biologie et morpho-anatomie*

La grande majorité des bryophytes n'ont ni de tissus méristématiques, ni de structure secondaire (lignine), ni de système vasculaire. À noter que certaines espèces possèdent des cellules plus ou moins spécialisées assurant la conduction de l'eau et de certains nutriments e.g. *Polytrichum, Politrichastrum, Dawsonia*… (Glime, 2007; Goffinet et Shaw, 2008; Ligrone et al., 2000). Leur taille varie de quelques millimètres pour la mousse *Buxbaumia aphylla* ou l'hépatique *Monocarpus* sp., jusqu'à quelques mètres pour *Frontalis* sp., qui vit dans l'eau (Glime, 2007). Les racines de bryophytes ont une fonction d'encrage et non d'absorption. Leurs feuilles n'ont pas de cuticule ni de stomates ce qui implique une alimentation en eau du type exohydrique, c'est-à-dire que l'absorption se fait directement au niveau des feuilles par capillarité. Autrement dit, il n'y a pas (ou très rarement) de circulation ascendante de l'eau dans la plante. Leur teneur en eau est fonction de la quantité d'eau dans le milieu environnant : elles sont dites poïkilohydriques. Ces caractéristiques impliquent deux conséquences écologiques : (i) elles ont une très large tolérance à la sécheresse, car elles peuvent rester de longues périodes desséchées en gardant la capacité de reprendre leurs activités une fois réhydratée. Cette aptitude à la dessiccation leur permet d'occuper des environnements très limités en eau et leur confère une importante résistante aux variations de température (Glime, 2007; Lee et La Roi, 1979; Proctor, 1990; Vittoz et al., 2010); (ii) L'absence de cuticule et l'alimentation exohydrique les rendent très sensibles aux dépositions atmosphériques (Rydin, 2008; Turetsky, 2003; Vanderpoorten et Goffinet, 2009). La présence de polluants dans les précipitations peut avoir un effet cytotoxique direct conduisant à la mort de la plante. Ces caractéristiques permettent de poser différentes hypothèses selon le type de pression environnementale testée. Il est attendu que les bryophytes soient sensibles aux dépositions, mais résistantes aux réchauffements de la température.

À l'inverse, les trachéophytes possèdent des structures secondaires, parfois très développées, leur conférant des tailles plus importantes et des architectures plus complexes. Leur vascularisation efficace permet le transport ascendant de l'eau et des minéraux et descendant des sucres transformés. L'eau et les minéraux sont absorbés par le système racinaire. Leurs feuilles présentent des stomates et une cuticule, ces deux éléments permettent une régulation de la teneur en eau de la plante (Proctor, 1990). Ces caractéristiques biologiques leur permettent des prouesses d'un point de vue de l'architecture, mais les rendent sensibles aux sécheresses. En effet, leur teneur en eau ne peut descendre sous le « point de flétrissement », niveau auquel les plantes ne sont plus capables de se réhydrater tant les structures cellulaires sont endommagées. Ainsi, la littérature met en avant une plus grande sensibilité des plantes vasculaires aux variations de température, notamment dans l'accomplissement du cycle végétatif.

1.4.3.3. *Reproduction*

Les bryophytes ont une reproduction sexuée particulière : un cycle digénétique, diplo-haplophasique à dominance gamétophytique (i.e. à haplophase dominante). Cela signifie une alternance des générations et une dépendance forte des deux générations. Le gamétophyte correspond à la plante chlorophyllienne, il est haploïde (n chromosomes) et produit des gamètes diploïdes ($2n$ chromosomes). La fécondation de ces gamètes est étroitement liée à la présence de l'eau. Elle donne naissance au sporophyte qui vit aux dépens du gamétophyte. Le sporophyte produira des spores redevenues haploïdes (n) par méiose. La germination de ces spores donnera une nouvelle génération de gamétophytes.

Le cycle de reproduction, la dispersion des gamètes et des spores ainsi que la germination des protonémas (i.e. forme juvénile des gamétophytes) sont très fortement dépendants de l'eau (Glime, 2007; Hedderson et Longton, 1996; Proctor, 1990). Ce cycle de reproduction sexuée rapide, associé à leur forte capacité de dispersion permet aux bryophytes de répondre rapidement aux variations environnementales (Raabe et al., 2010; Tuba et al., 2011). Cependant, il semblerait que la reproduction végétative par fragmentation du gamétophyte domine hors des écosystèmes arctiques/alpins (Longton, 1988). Une hypothèse intuitive, quoique non validée, est qu'il existe un lien entre la diversité des différences non plastiques des bryophytes (i.e. génotypes) dans leur capacité à occuper une large gamme d'habitats (Hedderson et Longton, 1996) ou bien à supporter d'importantes variations environnementales (Cronberg, 2004).

Les trachéophytes angiospermes ont une reproduction axée sur la production de graines. Dans ce groupe, les sporophytes sont réduits aux ovaires et grains de pollen. La pollinisation est complexe et peut faire intervenir de nombreux acteurs extérieurs (e.g. pollinisateurs), mais contrairement aux bryophytes la présence de l'eau n'est pas une condition *sine qua non*. La fécondation des gamètes produit des graines, qui protègent l'embryon et assurent une persistance dans les écosystèmes. L'immense variabilité morphologique des graines implique des stratégies de dispersion très différentes. D'une manière assez générale, les plantes herbacées forestières possèdent une faible capacité de dispersion comparée aux bryophytes (Eriksson, 2000).

En résumé, les bryophytes se caractérisent par : l'ectohydrisme et le poïkilohydrisme, l'absence de structure secondaire et d'un système racinaire fonctionnel pour l'absorption de l'eau, une reproduction très fortement dépendante de l'eau et de grandes capacités de dispersion. Elles ont de très bons mécanismes de tolérance à la sécheresse et aux variations de température, mais une grande sensibilité aux dépositions atmosphériques. *A contrario*, les trachéophytes possèdent une cuticule fonctionnelle et des stomates, des racines absorbantes, un système vasculaire efficace dans la circulation interne de l'eau, une architecture complexe, une reproduction non dépendante de l'eau, avec une grande variété de stratégies de dispersion des diaspores. Elles ont une défense externe contre les dépositions, mais une grande sensibilité aux sécheresses prolongées. Ces grandes caractéristiques biologiques vont conditionner l'écologie spécifique des deux groupes.

1.4.3.4. Écologie

La première différence écologique entre trachéophytes et bryophytes tient dans le cycle de végétation. Dans les forêts tempérées, la grande majorité des bryophytes sont sempervirentes, c'est-à-dire que leurs formes chlorophylliennes persistent et croissent durant l'hiver, tandis que les plantes vasculaires sont pour la plupart saisonnières et croissent durant la saison de végétation (Raunkiaer, 1904).

Les bryophytes, par l'absence de racines d'absorption, ont la capacité d'occuper des substrats très divers et souvent inutilisables pour les autres plantes (exception faite de quelques épihytes tropicales type *Bromeliaceae)*, tels que des débris ligneux, des substrats minéraux bruts, des troncs… Il y a donc une forte relation entre la diversité des bryophytes et la quantité de microhabitats disponibles (Bruun et al., 2006; Grytnes et al., 2006; Zechmeister et al., 2003). De fait, la diversité de la bryoflore est plus fortement affectée par des facteurs microécologiques que macro-écologiques (Bergamini et al., 2009; Raabe et al., 2010; Sporn et al., 2009).

Le mode de dispersion très efficace et leur large tolérance écologique confèrent aux bryophytes des aires de répartition très vastes (Frahm, 2008; Shaw, 2001). Ce pouvoir de dispersion, associé à une forte production de spores, leur offre une forte possibilité de mouvement en cas de modification des conditions écologiques (Bergamini et al., 2009; Zechmeister et al., 2003). Enfin, elles possèdent une plus large gamme de tolérance altitudinale (Lee et La Roi, 1979; Vittoz et al., 2010), participant ainsi grandement à la biodiversité et au fonctionnement de certains écosystèmes alpins ou de hautes latitudes (Alatalo et al., 2014; Lindo et Gonzalez, 2010; Rydin, 2008; Seppelt et al., 1992; Turetsky, 2003).

À l'échelle globale, la diversité des plantes vasculaires est très inéquitablement répartie (Kreft et Jetz, 2007). Les tropiques accueillent une plus grande diversité d'espèces que les écosystèmes tempérés ou boréaux (Barthlott et al., 2005, 2007; Kier et al., 2005). En revanche, il est plus difficile d'établir de telles délimitations pour les bryophytes (Geffert et al., 2013). Premièrement, la diversité bryologique des forêts tropicales est très mal connue. Deuxièmement, il y a une grande méconnaissance des distributions des bryophytes connues. Cependant, selon les données disponibles, la diversité des bryophytes ne suit pas le patron communément décrit pour les plantes vasculaires (Geffert et al., 2013; von Konrat et al., 2008). La diversité des mousses (Bryophytes *sensu stricto*) dans les forêts tempérées, boréales et dans la toundra est comparable à la diversité présente dans les régions tropicales (Geffert et al., 2013). Pour les hépatiques (Marchantiophytes) les *hot-spot* de diversité ne correspondent pas à ceux décrits pour les autres groupes taxonomiques (von Konrat et al., 2008).

Les bryophytes et les plantes vasculaires ont différentes caractéristiques bioécologiques. Les modes de persistance dans l'écosystème, les cycles de végétation, les modes d'alimentation en eau et éléments nutritifs et les stratégies de dispersion offrent aux deux groupes des caractéristiques écologiques différentes (Bagella, 2014). Basés sur ce constat, nous émettons l'hypothèse que la nature et l'intensité des réponses aux changements environnementaux seront différentes entre les deux groupes. Comme nous l'avons précédemment noté, il est commun de lire que les bryophytes devraient être utilisées comme « sentinelles » du réchauffement climatique (Gignac, 2001; He et al., 2016; Tuba et al., 2011). Cependant, le manque de preuves scientifiques publiées sur la sensibilité comparée des deux groupes m'a largement motivé à tester ces hypothèses. Mes travaux sont une contribution dans la compréhension des mécanismes de réponse de la bryoflore face aux changements environnementaux (Alatalo et al., 2014; Vanneste et al., 2017).

1.5. Objectif de la recherche

Ce travail de doctorat s'inscrit dans le courant de l'écologie scientifique du 21^{e} siècle: évaluer l'impact des activités humaines sur les systèmes biotiques et identifier les trajectoires à long terme de la biodiversité. La question cœur de ce doctorat est : quels sont les effets des changements globaux sur la biodiversité? Les trois chapitres suivants développent un ensemble cohérent d'hypothèses gravitant autour de deux axes majeurs :

- Évaluer l'effet des changements environnementaux sur la végétation forestière (déposition et réchauffement de la température);
- Comparer la sensibilité de deux grands groupes taxonomiques face aux changements environnementaux (bryophytes et trachéophytes);

Afin de répondre à mes hypothèses, j'utiliserai dans les trois chapitres les méthodes de l'écologie historique, soit le rééchantillonnage d'anciens relevés de la végétation. J'ai développé une méthodologie claire et précise visant à contrôler l'histoire des sites, les biais taxonomiques et reproduire à la lettre les protocoles d'inventaires.

Plusieurs études attestent une réponse des plantes vasculaires face aux changements globaux. Cependant, ces études sont pour la plupart à échelle très locale et incluent très rarement les communautés de bryophytes. Notre compréhension des mécanismes de réponse de la végétation face aux changements globaux est largement biaisée. De plus, malgré un manque notable de preuves scientifiques robustes, les bryophytes sont souvent présentées comme un bon bio-indicateur des changements climatiques. Pourtant, les bryophytes participent à la diversité et jouent un rôle important dans le fonctionnement des écosystèmes.

Dans le second chapitre, j'ai testé l'effet des dépositions atmosphérique et du réchauffement de la température sur la végétation forestière. Plus particulièrement, l'hypothèse testée était : les bryophytes sont plus sensibles que les plantes vasculaires face à ces deux pressions environnementales. Le site d'étude se trouve dans une région industrielle du nord-ouest de la France. Entre 2009 et 2012, nous avons rééchantillonné des relevés botaniques réalisés initialement en 1976. Les analyses portaient sur les changements de diversité-γ, -α, -β, de composition et des affinités des communautés (CWM) à la température, l'humidité, l'azote, le pH et a lumière.

Le troisième chapitre analyse la réponse de la végétation vasculaire sur un gradient à large échelle de réchauffement de la température au Québec. L'hypothèse de travail est : il y a une relation entre le degré d'augmentation de la température et la magnitude des changements de communauté. Les trois sites d'études se situent dans le Québec méridional, et couvrent un gradient d'augmentation de la température d'est en ouest. Tout d'abord le Parc National de la Gatineau qui se situe à l'extrême ouest de la province, là où le réchauffement fût le plus important, puis le Parc National du Mont-Mégantic qui se situe au milieu de la province, caractérisé par un réchauffement intermédiaire, enfin le Parc National de Forillon qui se situe à l'extrême est de la province, sur la façade atlantique, là où le réchauffement fût le plus faible. Nous avons revisité des inventaires botaniques réalisés entre 1970 et 1976. Les analyses se sont axées sur les changements de diversité-γ, -α, -β, de composition et d'affinité des communautés à la température (CTI).

Le quatrième et dernier chapitre compare les dynamiques temporelles des communautés de bryophytes et de plantes vasculaires sur un gradient altitudinal dans deux sites contrastés d'un point de vue de l'augmentation de la température. Nous avons testé l'hypothèse que les bryophytes étaient moins sensibles que les plantes vasculaires face au réchauffement de la température. Les sites d'études sont le Parc National de Forillon et du Mont-Mégantic. Les analyses de ce chapitre seront similaires au chapitre 3.

2- CHAPITRE 2

LONG-TERM COMMUNITY CHANGE: BRYOPHYTES ARE MORE RESPONSIVE THAN VASCULAR PLANTS TO NITROGEN DEPOSITION AND WARMING

2.1. Description de l'article et contribution

Dans le contexte actuel des changements globaux, les communautés et les écosystèmes sont fortement affectés dans leurs compositions et leurs fonctionnements. Les études sur les changements temporels de la végétation sont nombreuses dans la littérature. Cependant, la quasi-majorité de ces études sont orientées vers les plantes vasculaires, et très peu d'entre elles traitent des bryophytes. Pourtant les bryophytes ont un rôle central dans le fonctionnement des écosystèmes et contribuent la diversité locale.

Ce premier chapitre pose la question : quels sont les effets des changements globaux sur la diversité végétale forestière dans le nord-ouest de la France, région fortement touchée par les dépositions atmosphériques et le réchauffement climatique? Nous avons testé les hypothèses suivantes : (i) les dépositions atmosphériques et le réchauffement de la température sont des moteurs de changement de la végétation et (ii) les bryophytes sont plus sensibles que les plantes vasculaires. Pour répondre tester ces hypothèses, nous avons rééchantillonné les plantes vasculaires et les bryophytes sur des sites inventoriés 35 ans auparavant. Nous avons testé les changements temporels de diversité, composition et affinités écologiques des communautés des deux groupes.

Les résultats soutiennent les hypothèses, les communautés de bryophytes montrent plus grande intensité de changement de richesse, de composition et d'affinités écologiques que les plantes vasculaires. Globalement, les plus grands changements observés dans les communautés de bryophytes, suggèrent que les nombreuses études traitant des réponses temporelles des plantes vasculaires pourraient sous-estimer la sensibilité élargie de la végétation, notamment pour les cryptogames.

J'ai construit ce projet conjointement avec Arnault Lalanne et Mark Vellend. Les données historiques ont été recueillies par Jacques Bardat et les données récentes par mes soins. C'est grâce à ce projet que j'ai été initié à la bryologie par Jacques Bardat et Arnault Lalanne. Les analyses ont été conduites avec l'aide de Mark Vellend et Pierre Legendre. J'ai rédigé le manuscrit conjointement avec Mark Vellend et commenté par Arnault Lalanne. Cet article a été soumis le 15 novembre 2016, accepté le 2 août 2017 et mis en ligne le 28 novembre 2017.

Citation:

Becker-Scarpitta, A., J. Bardat, A. Lalanne, and M. Vellend. 2017. Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming. *Journal of Vegetation Science* 28:1220–1229.

2.1.1.1. Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming

Antoine Becker Scarpitta[1], Jacques Bardat[2], Arnault Lalanne[3], Mark Vellend[1]

1 : Département de Biologie, Faculté des sciences, Université de Sherbrooke, 2500, Boulevard de l'Université, Sherbrooke J1K 2R1, Québec, Canada.

2 : Muséum National d'Histoire Naturelle, Paris, France.

3 : Université de Bretagne Occidentale, EA 2219 Géo-architecture, UFR Sciences et Techniques, CS 93867, 29238 Brest, Cedex 3,

Contact: Becker Scarpitta, A.: corresponding author, Bardat, J., Lalanne, A., Vellend, M.

Contributions: AL and ABS deigned the study, JB and ABS collected data. ABS and MV led data analyses and writing of the manuscript, with input from all authors.

Keywords: temporal changes, legacy data, long-term study, community ecology, temperate forest, bryophytes, vascular plants, multivariate analysis, global changes, warming, nitrogen deposition, plant ecology

Nomenclature: TNRS. iPlant Collaborative. v4.0. [Accessed: Feb 2017] for vascular plants; TAXREF: Gargominy et al. 2016 for bryophytes.

2.1.2. Abstract

Aims: Many studies of vegetation change over multiple decades have focused on vascular plants, but very few on bryophytes, despite the importance of bryophytes for overall plant biodiversity and ecosystem functioning. Using a repeated survey of vascular plants and bryophytes in a forest ecosystem, we tested predictions of the hypotheses that (i) vegetation change has been driven by nitrogen deposition and climate warming, and (ii) bryophytes are more responsive to environmental change than vascular plants.

Location: A lowland temperate forest of northwestern France.

Methods: In forest plots initially surveyed in 1976, we re-surveyed both vascular plants and bryophytes in 2009 and 2012 respectively. We analysed changes in alpha diversity, beta diversity, and species composition, and we used community-weighted mean (CWM) values of species affinities for temperature, light, pH, soil moisture and nitrogen to assess the temporal responses potentially caused by warming, nitrogen deposition, or possibly a changing light regime.

Results: We observed significantly increased species richness of bryophytes and decreased richness of vascular plants. Community affinities to nitrogen, pH and temperature increased significantly for bryophytes, but not for vascular plants, although the change over time in nitrogen affinities for vascular plants was qualitatively in the predicted direction. Bryophytes showed a greater magnitude of temporal community change than vascular plants both in terms of overall species composition and environmental affinities indicating a higher responsiveness of bryophytes to environmental change.

Conclusion: Overall, the result of more marked temporal community change for bryophytes suggests that the many studies of changes in vascular plant communities over time might underestimate the sensitivity of the broader plant community (including cryptogams) to environmental change.

2.1.3. Introduction

Spatial variation in plant community composition is strongly influenced by abiotic factors (e.g., soil chemistry and climatic conditions), site history, and biotic interactions. Changes in such factors are therefore expected to cause temporal changes in the structure and composition of plant communities (Smith et al. 2009; De Keersmaeker et al. 2014; McGill et al. 2015; Kempel et al. 2015; Vellend et al. 2017). However, for long-lived perennial plants, which dominate most of the world's vegetation, temporal responses may take many decades to manifest, thus requiring long-term monitoring or the use of historical data to document (Vellend, et al. 2013; Chytrý et al. 2014)

In recent decades, anthropogenic global changes have caused major modifications of the physical and chemical characteristics of the Earth's surface, with important consequences for the structure of ecological communities (Poiani et al. 2000; Rooney et al. 2004; Wiegmann & Waller 2006; Bernhardt-Römermann et al. 2015). In communities that have not undergone major land-use transitions, dominant global change factors include climate change (especially warming) and atmospheric nitrogen deposition (Field et al. 1992). As predicted by climate warming, several studies have documented "thermophilization" – decreased abundance of cold-adapted species and/or increases in warm-adapted species (Bertrand et al. 2011; De Frenne et al. 2013) – or shifts in species distributions toward higher altitudes (Le Roux & McGeoch 2008; Savage & Vellend 2015) and latitudes (Chen et al. 2011). In the context of nitrogen deposition, other studies have documented "eutrophication" of vegetation, involving a shift in composition toward more N-demanding species (Thimonier et al. 1994; Gilliam 2007; Delgado & Ederra 2013) and a decrease of species richness and evenness (Bobbink et al. 2010; Armitage et al. 2014; Field et al. 2014).

A powerful and increasingly prevalent method for assessing the pattern and causes of long-term vegetation change involves "legacy data", such as phytosociological plots that were initially surveyed decades ago (Vellend et al. 2013; Chytrý et al. 2014). Using data on species' ecological affinities (Diekmann 2003) such as Ellenberg indices (Ellenberg 1988), we can formulate *a priori* predictions about how communities should have changed over time under different hypotheses (e.g., a strong influence of warming or nutrient deposition) (Diekmann 2003; Delgado & Ederra 2013), and then test these predictions (Hédl et al. 2017).

Many legacy studies have been conducted to date, but almost all of them have focused only on vascular plants, despite the fact that bryophytes are major contributors to both plant diversity and ecosystem functioning (Turetsky 2003; Lindo & Gonzalez 2010). Bryophyte communities fix both carbon and nitrogen, often enhance soil organic matter content and water retention, capture nutrients from the air, and provide habitat for a diverse community of microorganisms and invertebrates (During & Tooren 1990; Turetsky 2003; Vanderpoorten & Goffinet 2009; Lindo & Gonzalez 2010).

Different taxa do not necessarily respond in a similar fashion or with the same intensity to environmental change (Grytnes et al. 2006; Bagella 2014), and it has been hypothesized that bryophytes and vascular plants might respond differently (Möls et al. 2013). However, these taxa have very rarely been studied jointly in long-term temporal analyses (Økland et al. 2004; Lalanne et al. 2008; Lalanne et al. 2010), likely due to the paucity of historical data available for bryophytes (Gignac 2001, Molau & Altalo 1998, but see Delgado & Ederra 2013). We thus have extremely limited knowledge of how these different components of the plant community compare in terms of the nature and magnitude of long-term responses to environmental change. Nevertheless, our knowledge of the basic biology of vascular plants and bryophytes provides a basis for hypotheses related to their relative sensitivity to environmental change. For instance, widespread dispersal of bryophyte spores (Vanderpoorten & Goffinet 2009) can permit more rapid colonization of suitable habitats, thus accelerating community responses to environmental change (Cottenie & DeMeester 2004). In addition, because bryophytes absorb water through above-ground tissues, they should be more responsive than vascular plants to the chemical composition of rainfall (Turetsky 2003; Bobbink et al. 2010).

Here we report an analysis of community changes over ~35 years for both understorey vascular plants (i.e., herbaceous plants, ferns & shrubs) and bryophytes (i.e., mosses & liverworts) in a lowland forested region of north-west France, initially surveyed in 1976 (Bardat 1978), and then re-surveyed in 2009 and 2012 using the same protocols and location. Here we used community-weighted mean (CWM) values of species affinities for temperature, light, pH, soil moisture and nitrogen to assess the temporal responses potentially caused by warming, nitrogen deposition, or possibly a changing light regime.

We first conducted exploratory analyses of temporal changes in multivariate species composition and diversity, and then tested the following specific hypotheses and predictions: (i) Nitrogen deposition and climate warming have had a major influence on changes in plant community composition. *Predictions*: For both vascular plants and bryophytes, community-weighted means for ecological affinities to nitrogen, pH and temperature should have increased over the ~35-year period. (ii) Bryophyte communities are more responsive to environmental change than understorey vascular plant communities. *Prediction*: The magnitude of community responses has been greater for bryophytes than for vascular plants. Specifically, we expect larger increases for bryophytes than for vascular plants in the analyses described under hypothesis (i).

2.1.4. Materials and Methods

2.1.4.1. Study area

Field work was conducted in a 7450 ha site located in the Brotonne forest (Normandy, France; 49.4–49.52°; 0.65–0.80°), an Atlantic *Fagus-Quercus* even-aged forest dominated by *Fagus sylvatica* L., *Quercus robur* L. and *Quercus petraea* L. Elevation ranges from 0 to 200 m, with distinct geological and soil types: plateaus are characterized by quaternary loess (silt) with variable amounts of clay; slopes are calcareous; and valleys are covered mostly by old alluvial soils. The climate is oceanic, with an average annual rainfall of 800-900 mm evenly distributed throughout the year, and a mean annual temperature of 10 °C. Our study region, Upper

Normandy, was a major industrial region in France, with a high level of atmospheric nutrient deposition, especially NO_x (NO, NO_2), and SO_x (SO_2, SO_3), which reached their peaks in the 1970s and 1980s in France, with subsequent declines (PRQA 2009; CITEPA 2003). Thus, while soils continue to accumulate nitrogen from the atmosphere, soil acidity may have declined in recent decades. The region has also experienced considerable climate warming over the past half century (Fig. 2.1). Beech forests in this region are managed for harvesting as even-age stands, with a cutting cycle of ~140 years. Although we selected plots without any recent anthropogenic or natural disturbances (e.g., clearing, planting, or windstorms), successional shifts in the light regime might contribute to temporal community change.

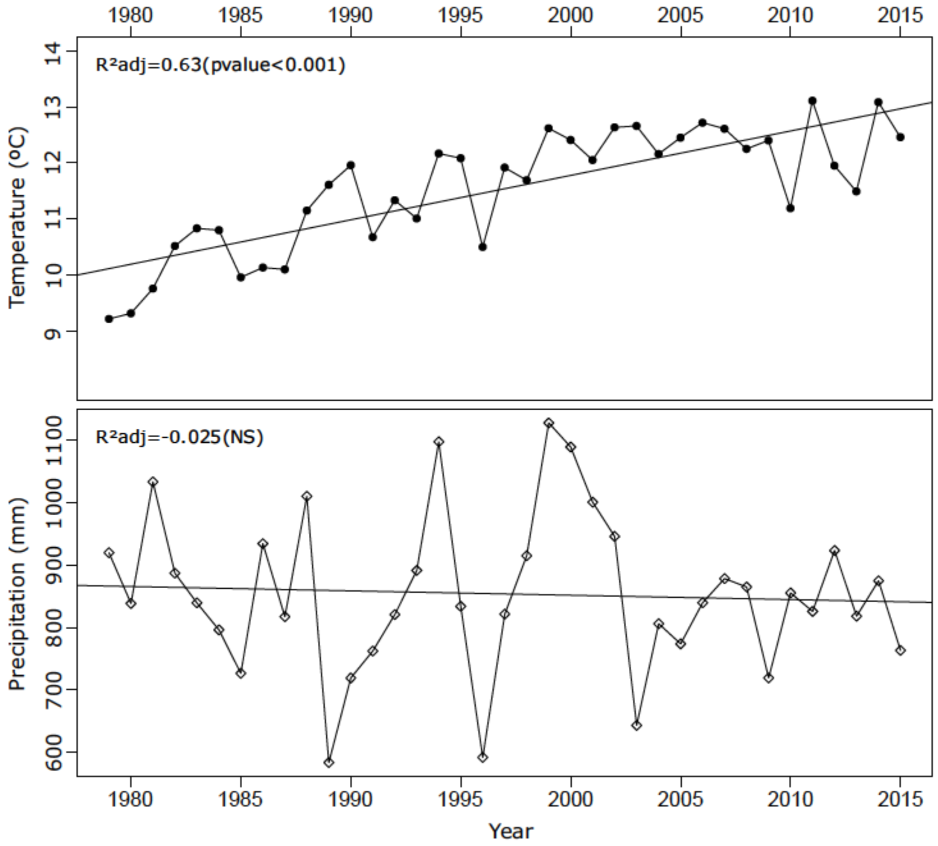


Figure 2.1 - Temporal trends in mean annual temperature and total annual precipitation, calculated from monthly mean values between January 1979 and December 2015.

Data are from the Météo-France meteorological station in Jumièges (n. 76378001), [49.434, 0.821], located 7 km from the study site.

2.1.4.2. Plot selection and field data collection

Between 1975 and 1977, 500 plots within the study area were surveyed during spring and summer (Bardat 1978). Plots in the original survey were mapped at a fine scale (1/5000), and we were able to relocate the old plots with high precision using QGIS 2.8.2. For the recent surveys, we selected plots according to three criteria: (i) plots must occur in one of two oak and beech forest Natura 2000 habitats: *Endymio non scriptae-Fagetum sylvaticae* (Durin et al.,

1967) and *Ilici aquifolii-Fagetum sylvaticae* (Durin et al., 1967, Royer et al. 2006); (ii) plots must not have experienced major disturbances (e.g., clear-cutting) in recent decades; (iii) plots have maintained forest cover since the 1970s. Applying these criteria resulted in 74 plots for vascular plant sampling, 46 of which were also used for bryophyte sampling (bryophyte plots require a comparatively greater investment of resources given time-consuming identifications).

Using identical methods for the two-time periods, the abundance of all species of vascular plants (herbaceous species, ferns, shrubs, & trees) and bryophytes (*Bryophyta* & *Marchantiophyta*) were recorded following a phytosociological approach (Bardat 1978). In each plot (400m^2) or subplot (see below), the abundance of all vascular plant and bryophyte species present in the plot was recorded using Braun-Blanquet's phytosociological coefficients (abundance-dominance index) (Braun-Blanquet, 1952) (see Appendix A-S1 & A-S2 for frequency of occurrence of all species). For vascular plants, the recent surveys were conducted in 2009 during two-time windows – in April for spring flowering species and in June/July for summer flowering species – and abundances were recorded for two vegetation layers, shrubs and ground-layer plants. Our analysis thus focused only on understorey plants (i.e., not canopy trees). For bryophytes, recent surveys were conducted in April 2012, and in each plot we sampled up to four microhabitats ("subplots"), corresponding to different substrates: soil, rock, tree stumps, and fallen branches. Not all substrates were present in a given plot, so the total number of subplots (93: 44 soil + 2 rock + 32 stump + 15 branch) is less than 46 * 4, but identical for the two-time periods (balanced design). Because there are only two subplots on rock per year, we removed these from analyses, leaving 91 subplots per year. Because Braun-Blanquet coefficients do not scale linearly with abundance, we first converted each coefficient to the midpoint of the range of proportional cover values for a given coefficient. We merged "+" (some individuals) and "1" (<5% cover) into the same category. We then calculated relative abundances by dividing each species' raw abundance by the sum of abundances across species within a plot.

2.1.4.3. Species ecological affinities

The affinity of each species for different environmental conditions was characterized using Ellenberg and related indicator values for vascular plants from *Plantatt* (Hill et al. 2004 based on Ellenberg et al. 1991) and equivalent indices for bryophytes from *Bryoatt* (Hill et al. 2007, based on Ellenberg et al. 1991). Ellenberg's indices were used for light (L), moisture (F), pH (R), and nitrogen (N) (Appendix A-S3). We did not have directional hypotheses concerning light and moisture affinities, although light was used to test the possibility that increasing canopy cover over time (i.e., decreased light due to forest succession) drove some community changes. For temperature affinities, we calculated a proxy of average annual temperature as the average of July mean temperature (i.e. the warmest month) and January mean temperature (i.e. the coolest month) throughout the range of each species in the United Kingdom (see "Geographic attributes: climatic means" in Hill et al. 2004 for vascular plants and Hill et al. 2007 for bryophytes). For each species, we can consider this "species temperature index" (STI) to represent species' associations with temperature (Thuiller et al. 2005; Devictor et al. 2008).

In each time period, for each plot *k*, we calculated the average for each indicator value *j*, weighted by the relative abundance of each species *i* as follows (Garnier et al. 2004; Shipley et al. 2011):

$$\mathrm{CWM}_{jk} = \sum_i \mathrm{p}_{ik}\,\mathrm{t}_{ij}$$

Where p_{ik} is the relative abundance of species *i* in plot *k*, and t_{ij} the affinity index *j* of species *i*.

2.1.4.4. Statistical analysis

All statistical analysis was done using R v. 3.2.3 (R Foundation for Statistical Computing, Vienna, Austria).

To test for temporal change in species richness (the number of species per plot or subplot) for vascular plants and bryophytes separately, we used linear mixed effect models. Given the difference in data structure between vascular plants (no subplots) and bryophytes (subplots), the models were different for the two taxa. In univariate response models, for bryophytes, we used subplot nested within plot as a random effect (1|plot/subplot), whereas for vascular plants, we used only plot as a random effect (1|plot). In all models, year was a fixed effect factor with two levels. Using plot as a random factor accounts for the fact that the same plot was measured at the two-time points. These analyses were conducted with the *lmer* function in the lme4 package (v. 1.1-10) (Bates et al. 2015).

The calculation of p-values for these kinds of models is not straightforward. Here we report the 95% credible intervals (CrI) for the fixed effect of time using the *sim* function with 2000 simulations by the package arm (v. 1.9-3). The effect of a variable is considered "significant" if the 95% credible interval excludes zero and "highly significant" with 99.9%.

For beta diversity, we tested differences across time with PERMutational analysis of multivariate DISPersion (PERMDISP) using the Bray-Curtis index of compositional dissimilarity in the *betadisper* function in the vegan package (v.2.3-1) (Oksanen et al. 2016). To test for significant temporal shifts in species composition, we used PERmutational Multivariate ANalysis Of VAriance (PERMANOVA), (Anderson 2001) with 999 permutations across all plots in the *adonis* function in vegan, also using the Bray-Curtis dissimilarity index. Permutations involved swapping the data for a given plot (vascular plants) or subplot (bryophytes) across years.

As described above, each plot or subplot was characterized by community-weighted mean values for each of five indicators of environmental affinity. These data were analysed using both multivariate and univariate analyses, separately for vascular plants and bryophytes in all cases. First, in order to visualize relationships between ecological affinities across plots and across time, we performed a principal component analysis (PCA) using normalized (scaled and centered) community-weighted means per plot and year. Secondly, linear mixed effects models were used to test for a difference of community-weighted means (CWM) between years; these univariate models were implemented in the exact same way as the models for species richness described above. See Supplementary materials for more information on CWM models (Appendix A-S4).

2.1.5. Results

2.1.5.1. Diversity and composition

For bryophytes, the total number of species across all sample plots increased from 18 in 1976 to 52 in 2012 (Table 2.1). Of the 37 new species, 30 were present in fewer than 10% of plots in 2012. Three species found in the initial survey in 1976 were not found in the resurvey (*Pleurozium schreberi, Brachythecium velutinum and Hylocomium splendens*). Bryophyte species richness per plot increased over time significantly, by more than two-fold, with the same qualitative trend for Shannon diversity (Table 2.1). Richness increased in all four subplot types (Appendix A-S5). The PERMANOVA analysis showed a significant temporal shift in bryophyte community composition, but there was no significant temporal change in β diversity (PERMDISP, see Table 2.1).

For vascular plants, the total number of species declined from 87 in 1976 to 62 in 2009, while mean plot-scale species richness also showed a significant decrease over time (Table 2.1). As was the case for bryophytes, there was no significant temporal change in β diversity (PERMDISP, Table 2.1), but there was a significant shift in community composition over time (PERMANOVA, Table 2.1).

Table 2.1 - Biodiversity indices for bryophyte and vascular plant communities in 1976 and 2012 or 2009.

	Number of (sub)plots	Total species number	Species richness			PERMDISP			PERMANOVA		
			2.5%	(50%)	97.5%	Dist. to median	F	*P*	F	R^2	*P*
Bryophytes	subplots			per subplot							
1976	(46) 91	18	2.8	**3.3**	3.8	0.56	0.02	0.89	**12.84**	**0.07**	**0.001**
2012	(46) 91	53	6.3	**6.8*****	7.3	0.56					
Vascular plants	plots			per plot							
1976	74	87	14.2	**15.8**	17.4	0.55	0.98	0.33	**6.8**	**0.04**	**0.001**
2009	74	62	8.3	**9.8*****	11.5	0.54					

Species richness differences were tested with linear mixed effect models; 95% credible intervals were calculated using posterior distributions. PERMDISP and PERMANOVA analyses were performed on Bray-Curtis compositional dissimilarities among pairs of plots. Distance to median is the average distance of a plot to the centroid of the plots in that year in multivariate space. Significance levels were calculated based on the position of zero relative to the posterior distributions: * $p<0.05$; ** $p<0.01$; *** $p<0.001$. Bold values indicate significant differences ($p<0.05$).

2.1.5.2. Ecological affinities

For bryophytes, there was a clear multivariate temporal shift in environmental affinities associated with a shift toward higher nitrogen, pH and temperature affinities (Fig. 2.2a). Univariate analyses for bryophytes showed significant temporal increases for average annual temperature, nitrogen and pH affinities (consistent with Fig. 2.2a) and a decrease for light affinity (Table 2.2). There was no significant temporal change of moisture affinity.

In contrast, vascular plants did not show any clear directional multivariate changes, but a small decrease of the CWM multivariate dispersion between 1976 and 2009 (Fig. 2.2b). None of the temporal changes were significant in univariate analyses, although the mean change for nitrogen was qualitatively in the predicted positive direction (95% CrI over time = [-0.1, 0.3], mean = 0.1; see Table 2.2 and Appendix A-S4).

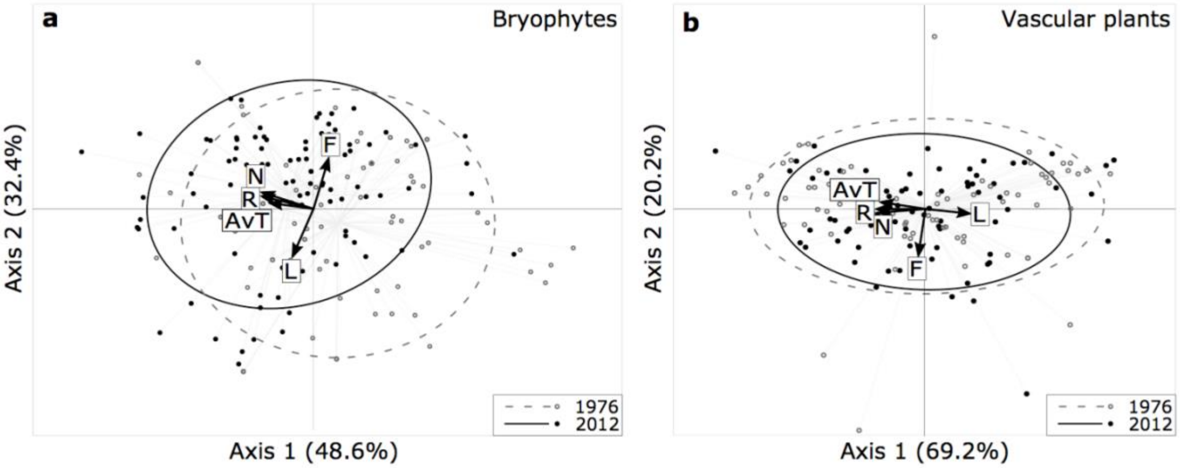


Figure 2.2 - Principal components analysis ordination of community-weighted means (CWM) for affinities with average annual temperature (AvT), light (L), moisture (F), soil pH (R), and nitrogen (N) for (a) bryophytes and (b) vascular plants; 80% confidence ellipses are shown for each time period.

Table 2.2 - Temporal changes of community-weighted means (CWM) of ecological affinities for bryophytes and vascular plants.

		Bryophytes CWM			Vascular plants CWM		
		2.5 %	Estimate (50%)	97.5 %	2.5%	Estimate (50%)	97.5%
AvT - Affinity to average annual temperature	Initial	8.9	8.9	9	9	9	9.1
	Temporal change	0.04	0.1***	0.1	-0.03	-0.001	0.03
R - affinity to pH	Initial	3.7	3.8	4	4.2	4.5	4.7
	Temporal change	0.1	0.3***	0.4	-0.2	0.03	0.3
N - affinity to nitrogen	Initial	3.4	3.5	3.6	4.1	4.3	4.4
	Temporal change	0.3	0.5***	0.6	-0.1	0.1	0.3
L - affinity to light	Initial	4.8	4.9	5.1	5.3	5.4	5.5
	Temporal change	-0.3	-0.2***	-0.04	-0.1	0.04	0.2
F - affinity to moisture	Initial	5.2	5.3	5.4	5.4	5.5	5.6
	Temporal change	-0.1	0.1	0.2	-0.1	0.04	0.1

Coefficient estimates (50%) are the modeled means from linear mixed effect models; also shown are the 95% credible intervals around the means. Initial values are estimates for the 1976 surveys, and temporal changes are the differences between the initial and contemporary (2009 or 2012) surveys. Significance levels were calculated based on the position of zero relative to the posterior distributions: * $p<0.05$; ** $p<0.01$; *** $p<0.001$. Background shading indicates significant differences ($p<0.05$).

2.1.6. Discussion

Support for our first hypothesis – that temperature and nitrogen indices would increase over time – was mixed. Community affinities to nitrogen, pH and temperature increased significantly for bryophytes, but not for vascular plants, although the change over time in nitrogen affinities for vascular plants was suggestive of a weak effect in the predicted direction (Table 2.2). Our second hypothesis – that bryophytes are more responsive to environmental change – was clearly supported by the data. CWM changes for vascular plants were non-significant while those for bryophytes were significant and of substantially greater raw magnitude (Table 2.2).

Bryophytes showed a greater magnitude of temporal community change than vascular plants both in terms of overall species composition (Table 2.1) and environmental affinities (Table 2.2 & Fig. 2.2a). The greater sensitivity of bryophytes than vascular plants to environmental change likely results from aspects of their basic morphology and life history. Bryophytes possessing no vascular system or true roots, and have limited abilities to resist desiccation, with water and nutrients absorbed largely by leaves, thus making them highly sensitive to atmospheric nitrogen inputs and the acidity of rain (Turetsky 2003, Tuba et al. 2011). Compared to vascular plants, bryophytes also have relatively strong dispersal and high spore (or propagule) production, thus increasing the local availability of species from the regional pool (Gignac 2001. Raabe et al. 2010), which can potentially enhance community-level responses to environmental change (Cottenie & De Meester 2004). Few studies have made similar comparisons between bryophytes and vascular plants. In one study, Carleton (1990) found results consistent with ours: higher responsiveness of bryophyte species composition than vascular-plant composition to a lowland-to-upland environmental gradient in the Canadian boreal forest.

Our first hypothesis predicted important roles for climate warming and nitrogen deposition in causing temporal community change. Our results for nitrogen affinities were at least roughly consistent for both bryophytes and vascular plants, but the results were mixed for warming, as discussed in the following paragraphs.

We found a clear and significant shift toward higher nitrogen and pH affinities for bryophytes, which we interpret as indicative of community responses to increased substrate nitrogen and pH. These results are consistent with other studies finding signatures of eutrophication in European forests due to atmospheric nutrient deposition (Bobbink et al. 1998, 2010, Thimonier et al. 1994, Erisman & Vries 2000, Lameire et al. 2000, Baeten et al. 2010, McClean et al. 2011, Verstraeten et al. 2013, Bernhardt-Römermann et al. 2015). Our results for vascular plants were less clear, but not inconsistent with the hypothesis of nitrogen deposition as a driver of vegetation change. Regional studies have shown high levels of NOx, SOx emissions in the study area, with a peak of acidification ~30 years ago (PRQA 2009; CITEPA 2003), likely representing an ultimate source of our observed plant community shifts via ongoing nitrogen accumulation and declining acidification.

Compared to vascular plants, little is known about how bryophytes will respond to nitrogen deposition, although responses might depend on the form of added nitrogen (Verhoeven et al. 2011) or the ecosystem (see Bobbink et al. 2010). We found a shift over time toward more nitrogen demanding and high pH-associated bryophyte species. Interestingly, some species that declined in abundance tend to be associated with acidic and late successional forests (e.g. *Leucobryum glaucum, Eurynchyum striatum, Pleurozium schreberi, Brachythecium velutinum* and *Hylocomium splendens*) while new species or those that increased in abundance were more often associated with rich soils and early or intermediate succession (e.g., *Brachythecium rutabulum, Kindbergia praelonga, Plagiothecium succulentum*) (see Appendix A-S1). Another study in a similar ecological context with corticolous bryophytes found that more mature stands were associated with acidophilous species while early successional stands were characterised by more broadly tolerant species such as *B. rutabulum* or *K. praelonga* (Bardat & Aubert 2007), consistent with increasing acidity of the organic layer during this kind of forest succession (Aubert et al. 2004). However, if anything, the forests in our study have matured during the period of study, so disturbance is not likely to be responsible for the changes we observed. Although we can only speculate as to the precise mechanisms underlying these changes, recovery from the peak of acid deposition might prompt an apparent "successional regression" of bryophyte communities with respect to the natural successional sequence.

We also found a small but significant increase of temperature affinities for bryophyte communities, consistent with the hypothesis of climate warming, but no trend was observed for vascular plants (Table 2.2). Temperature in this region has been steadily rising over the past 40 years (Fig. 2.1). Other legacy studies have shown responses of vascular plant communities to climate warming (Le Roux & McGeoch 2008, Bertrand et al. 2011, Savage & Vellend 2015), and at present we cannot say whether vascular plant communities are simply not responding to warming in our region, or whether the responses are too slow or subtle to have been detected given our time frame, sample size, and measure of temperature affinity. In either case, bryophyte communities do appear more responsive to warming than vascular plant communities, although we consider this conclusion tentative given the small effect size. Our results showed that neither bryophyte nor vascular plant communities showed temporal shifts in moisture affinities (Table 2.2), which is consistent with the lack of temporal trend in precipitation in this region during the period of study (Fig. 2.1).

Changes over time in local-scale plant diversity over the past century have been highly variable (Vellend, et al. 2013; Vellend et al. 2017). Here we found opposite temporal changes of species richness of bryophytes and vascular plants. While bryophytes experienced a near doubling of local species richness, vascular plant richness declined by almost 40% (Table 2.1). One implication of this result is that vascular-plant diversity (more often studied) cannot be used as a proxy for bryophyte diversity (Möls et al. 2013, Bagella 2014). While the change in vascular plant diversity is consistent with expectations based on nitrogen deposition, the increase in bryophyte richness is more difficult to explain. Changes in local richness of the magnitude observed here raise the question of the comparability of the two surveys. However, in this study (unlike many legacy studies) the original surveyor, Jacques Bardat, also took part in the recent survey, which was conducted at the same time of year to control for phenological variation. Observer bias thus cannot account for these large differences. Another potential source of variance is "pseudo-turnover", due to imprecise plot re-location (Fischer & Stöcklin 1997). However, the forest structures and composition in our study site are relatively homogeneous at local scales, and moreover, in 2009 and 2012 plots were likely within 20-30 m of original plots, which might introduce some random variance, but not systematic bias in local richness. There are no plausible reasons to suspect that these results stem from methodological artefacts. Thus, we are confident in the robustness of results.

2.1.7. Conclusion

Our study is one of only a few to compare the relative magnitude of temporal community change for bryophytes and vascular plants (Alatalo et al. 2014). We found that bryophyte and vascular plant communities both showed compositional shifts over time, but bryophyte communities showed responses of a markedly greater magnitude, with directional responses likely related to nutrient deposition, and to a lesser degree warming. These results point to the possibility that the large number of studies of temporal change in vascular plant communities collectively underestimate the magnitude of change in the broader plant community, which includes bryophytes. Our knowledge of long-term changes in communities of bryophytes and other cryptogams (e.g., lichens) is minimal compared to our knowledge of vascular plants (but see Vanneste et al, 2017), despite the major ecosystem-level consequences of cryptogam diversity and composition (Cornelissen et al. 2007). Additional studies in a variety of ecological settings are needed to increase our understanding of these important components of plant communities.

2.1.8. Acknowledgements

We thank the Office National des Forêts for permission to conduct research in the Forêt Domaniale de Brotonne, and Jean-Yves Massenet, Emmanuelle Porcher, and the Muséum National d'Histoire Naturelle de Paris for assistance during the early phases of this project. Three reviewers and the handling editor provided insightful comments and suggestions that greatly improved the paper. MV was supported by the Natural Sciences and Engineering Research Council of Canada.

2.1.9. References

Alatalo, J., Jägerbrand, A., & Molau, U. 2014. Seven years of experimental warming and nutrient addition causes decline of bryophytes and lichens in alpine meadow and heath communities. PeerJ. doi: 10.7287/peerj.preprints.98v1

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32–46.

Armitage, H.F., Britton, A.J., van der Wal, R., & Woodin, S.J. 2014. The relative importance of nitrogen deposition as a driver of Racomitrium heath species composition and richness across Europe. Biological Conservation 171: 224–231.

Aubert, M., Bureau, F., Alard, D., & Bardat, J. 2004. Effect of tree mixture on the humic epipedon and vegetation diversity in managed beech forests (Normandy, France). Canadian Journal of Forest Research 34: 233–248.

Baeten, L., Hermy, M., Van Daele, S., & Verheyen, K. 2010. Unexpected understorey community development after 30 years in ancient and post-agricultural forests. Journal of Ecology 98: 1447–1453.

Bagella, S. 2014. Does cross-taxon analysis show similarity in diversity patterns between vascular plants and bryophytes? Some answers from a literature review. Comptes Rendus Biologies. doi: 10.1016/j.crvi.2014.01.003

Bardat J., 1978. La forêt de Brotonne (Seine-Maritime), étude phyto-écologique. Remarques floristiques, pédologiques et climatiques. Ph.D thesis, Université de Rouen, France.

Bates, D., Mächler, M., Bolker, B., & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67: 1-48.

Bernhardt-Römermann, M., Baeten, L., Craven, D., De Frenne, P., Hédl, R., Lenoir, J., Bert, D., Brunet, J., Chudomelová, (…) & Verheyen, K. 2015. Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. Global Change Biology 21: 3726–3737.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C., & Gégout, J.-C. 2011. Changes in plant community composition lag behind climate warming in lowland forests. Nature 479: 517–520.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, (…) & De Vries, W. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications 20: 30–59.

Bobbink, R., Hornung, M., & Roelofs, J.G.M. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. Journal of Ecology 86: 717–738.

Braun-Blanquet, J., Roussine, N., Negre, R., 1952. Les groupements végétaux de la France méditerranéenne. CNRS, Paris, France.

Carleton, T. 1990. Variation in terricolous bryophyte and macrolichen vegetation along primary gradients in Canadian boreal forests. Journal of vegetation Science 1: 585–594.

Chen, I., Hill, J.K., Ohlemuller, R., Roy, D.B., & Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333: 1024–1026.

Chytrý, M., Tichý, L., Hennekens, S.M., & Schaminée, J.H.J. 2014. Assessing vegetation change using vegetation-plot databases: a risky business. Applied Vegetation Science 17: 32–41.

CITEPA. 2003. Émissions dans l'air en France métropole. Substances impliquées dans les phénomènes d'eutrophisation et de photochimie. Centre interprofessionnel technique d'études de la pollution atmosphérique, Paris, France.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A., & During, H.J. 2007. Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. Annals of Botany 99: 987–1001.

Cottenie, K., & De Meester, L. 2004. Metacommunity structure, synergy of biotic interactions as selective agents and dispersal as fuel. Ecology 85: 114–119.

Delgado, V., & Ederra, A. 2013. Long-term changes (1982–2010) in the bryodiversity of Spanish beech forests assessed by means of Ellenberg indicator values of temperature, nitrogen, light and pH. Biological Conservation 157: 99–107.

Devictor, V., Julliard, R., Couvet, D., & Jiguet, F. 2008. Birds are tracking climate warming, but not fast enough. Proceedings of the Royal Society B: Biological Sciences 275: 2743–2748.

Diekmann, M. 2003. Species indicator values as an important tool in applied plant ecology – a review. Basic and Applied Ecology 4: 493–506.

Durin L., Gehu J.-M., Noirfalise A., Sougnez N., 1967. Les hêtraies atlantiques et leur essaim climatique dans le. Nord-Ouest de la France. Bulletin Société Botanique du Nord-Ouest de la France, Tome 20.

During, H.J., & Tooren, B.F. Van. 1990. Bryophyte interactions with other plants. Botanical Journal of the Linnean Society 104: 79–98.

During, H.J. 1979. Life Strategies of Bryophytes: A Preliminary Review. Lindbergia 5: 2–18.

Ellenberg, H. 1988. Vegetation Ecology of Central Europe Fourth Edition. Cambridge University Press, Camdbrige, UK.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., & Paulißen, D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica IX

Erisman, J.W., & de Vries, W. 2000. Nitrogen deposition and effects on European forests. Environmental Reviews 8: 65–93.

Field, C.B., Chapin, F.S., Matson, P.A., & Mooney, H.A. 1992. Responses of terrestrial Ecosystems to the changing atmosphere: a resource-based approach. Annual Review of Ecology Evolution and Systematics 23: 201–235.

Field, C.D., Dise, N.B., Payne, R.J., Britton, A.J., Emmett, B. a., Helliwell, R.C., Hughes, S., Jones, L., Lees, (…) & Caporn, S.J.M. 2014. The role of nitrogen deposition in widespread plant community change across semi-natural habitats. Ecosystems 17: 864–877.

Fischer, M., & Stöcklin, J. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-1985. Conservation Biology 11: 727–737.

De Frenne, P., Rodriguez-Sanchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Romermann, M., Brown, C.D., Brunet, (…) & Verheyen, K. 2013. Microclimate moderates plant responses to macroclimate warming. Proceedings of the National Academy of Sciences 110: 18561–18565.

Gargominy, O., Tercerie, S., Régnier, C., Ramage, T., Schoelinck, C., Dupont, P., Vandel, E., Daszkiewicz, P., & Poncet, L. 2016. TAXREF v10.0, référentiel taxonomique pour la France, méthodologie, mise en œuvre et diffusion.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.-P. 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85: 2630–2637.

Gignac, L.D. 2001. Bryophytes as Indicators of Climate Change. The Bryologist 104: 410–420.

Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57: 845-858.

Grytnes, J.A., Heegaard, E., & Ihlen, P.G. 2006. Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. Acta Oecologica 29: 241–246.

Hédl, R., Bernhardt-Römermann, M., Grytnes, J.-A., Jurasinski, G., & Ewald, J. 2017. Resurvey of historical vegetation plots: a tool for understanding long-term dynamics of plant communities. Applied Vegetation Science 20: 161–163.

Hill, M.O., Preston, C.D., Bosanquet, S.D.S., & Roy, D.B. 2007. Bryoatt - attributes of British and Irish mosses, liverworts and hornworts. NERC, Centre for Ecology & Hydrology

Hill, M.O., Preston, C.D., & Roy, D.B. 2004. Plantatt atributes of British and Irish plants: status, size, life history, geography and habitats. NERC, Centre for Ecology & Hydrology

De Keersmaeker, L., Onkelinx, T., De Vos, B., Rogiers, N., Vandekerkhove, K., Thomaes, A., De Schrijver, A., Hermy, M., & Verheyen, K. 2014. The analysis of spatio-temporal forest changes (1775–2000) in Flanders (northern Belgium) indicates habitat-specific levels of fragmentation and area loss. Landscape Ecology 30: 247–259.

Kempel, A., Razanajatovo, M., Stein, C., Unsicker, S.B., Auge, H., Weisser, W.W., Fischer, M., & Prati, D. 2015. Herbivore preference drives plant community composition. Ecology 96: 2923–2934.

Lalanne, A., Bardat, J., Lalanne-Amara, F., Gautrot, T., & Ponge, J.-F. 2008. Opposite responses of vascular plant and moss communities to changes in humus form, as expressed by the Humus Index. Journal of Vegetation Science 19: 645–652.

Lalanne, A., Bardat, J., Lalanne-Amara, F., & Ponge, J.F. 2010. Local and regional trends in the ground vegetation of beech forests. Flora: Morphology, Distribution, Functional Ecology of Plants 205: 484–498.

Lameire, S., Hermy, M., & Honnay, O. 2000. Two decades of change in the ground vegetation of a mixed deciduous forest in an agricultural landscape. Journal of Vegetation Science 11: 695–704.

Lindo, Z., & Gonzalez, A. 2010. The bryosphere: An integral and influential component of the Earth's biosphere. Ecosystems 13: 612–627.

McClean, C.J., Berg, L.J.L., Ashmore, M.R., & Preston, C.D. 2011. Atmospheric nitrogen deposition explains patterns of plant species loss. Global Change Biology 17: 2882–2892.

McGill, B.J., Dornelas, M., Gotelli, N.J., & Magurran, A.E. 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology and Evolution 30: 104-113.

Molau, U., & Alatalo, J.M. 1998. Responses of subarctic-alpine plants communities to simulated environmental change, biodiversity of bryophytes, lichens and vascular plants. Ambio 27: 322–329.

Möls, T., Vellak, K., Vellak, A., & Ingerpuu, N. 2013. Global gradients in moss and vascular plant diversity. Biodiversity and Conservation 22: 1537–1551.

Økland, T., Bakkestuen, V., Økland, R.H., & Eilertsen, O. 2004. Changes in forest understorey vegetation in Norway related to long-term soil acidification and climatic change. Journal of Vegetation Science 15: 437–448.

Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Szoecs, E. 2016. Package "vegan" CRAN R-project

Poiani, K.A., Richter, B.D., Anderson, M.G., & Richter, H.E. 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. BioScience 50: 133.

PRQA. 2009. Plan Régional de la Qualité de l'Air en Normandie 2010-2015, Haute-Normandie, France.

Raabe, S., Müller, J., Manthey, M., Dürhammer, O., Teuber, U., Göttlein, A., Förster, B., Brandl, R., & Bässler, C. 2010. Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. Forest Ecology and Management 260: 1956–1964.

Rooney, T.P., Wiegmann, S.M., Rogers, D. a., & Waller, D.M. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conservation Biology 18: 787–798.

Royer, J.M., Felzines, J.C., Misset, C., Thévenin, S., 2006. Synopsis commenté des groupements végétaux de la Bourgogne et de la Champagne-Ardenne. Bulletin de la Société Botanique du Centre-Ouest, n° spécial 25, France.

Le Roux, P.C., & McGeoch, M.A. 2008. Rapid range expansion and community reorganization in response to warming. Global Change Biology 14: 2950–2962.

Savage, J., & Vellend, M. 2015. Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. Ecography 38: 546–555.

Shipley, B., Laughlin, D.C., Sonnier, G., & Ottinowski, R. 2011. A strong test of a maximum entropy model of trait-based community assembly. Ecology 92: 507–517.

Smith, M.D., Knaap, A.K., & Collins, S.L. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. Ecology 90: 3279–3289.

Thimonier, A., Dupouey, J.L., Bost, F., & Becker, M. 1994. Simultaneous eutrophication and acidification of a forest ecosystem in North-East France. New Phytologist 126: 533–539.

Thuiller, W., Lavorel, S., & Araujo, M.B. 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecology and Biogeography 14: 347–357.

Tuba Z., Slack N., Stark L., 2011. Bryophytes ecology and climate change. Cambridge University Press, Cambridge, UK.

Turetsky, M.R. 2003. The role of Bryophytes in carbon and nitrogen cycling. The Bryologist 106: 395–409.

Vanderpoorten, A., & Goffinet, B. 2009. Introduction to Bryophytes. Cambridge University Press, Cambridge, UK.

Vanneste, T., Michelsen, O., Graae, B.J., Kyrkjeeide, M.O., Hassel, K., Lindmo, S., & Frenne, P. De. 2017. Impact of climate change on alpine vegetation of mountain summits in Norway. Ecological Research 32: 579–593.

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J.L., Messier, J., Myers-Smith, I.H., & Sax, D.F. 2017. Plant biodiversity change across scales during the Anthropocene. Annual Review of Plant Biology 68: 563–586.

Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., De Frenne, P., Verheyen, K., & Wipf, S. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proceedings of the National Academy of Sciences of the United States of America 110: 19456–19459.

Vellend, M., Brown, C.D., Kharouba, H.M., McCune, J.L., & Myers-Smith, I.H. 2013. Historical ecology: Using unconventional data sources to test for effects of global environmental change. American Journal of Botany 100: 1294–1305.

Verhoeven, J.T.A., Beltman, B., Dorland, E., Robat, S.A., & Bobbink, R. 2011. Differential effects of ammonium and nitrate deposition on fen phanerogams and bryophytes. Applied Vegetation Science 14: 149–157.

Verstraeten, G., Baeten, L., Van den Broeck, T., De Frenne, P., Demey, A., Tack, W., Muys, B., & Verheyen, K. 2013. Temporal changes in forest plant communities at different site types. Applied Vegetation Science 16: 237–247.

Wiegmann, S.M., & Waller, D.M. 2006. Fifty years of change in northern upland forest understories: Identity and traits of "winner" and "loser" plant species. Biological Conservation 129: 109–123.

2.1.10. Supplementary Materials

- Appendix A-S1: List of bryophyte species and number of occurrences per survey
- Appendix A-S2: List of vascular plant species and number of occurrences per survey
- Appendix A-S3: Simplified explanations of Ellenberg values
- Appendix A-S4: Complete model results of linear mixed-effect models
- Appendix A-S5: Temporal change of bryophyte richness per subplot (microhabitat)

NOTE : Toutes les annexes des chapitres sont regroupées à la fin du document.

3- CHAPITRE 3

FOUR DECADES OF PLANT COMMUNITY CHANGE ALONG A CONTINENTAL GRADIENT OF WARMING

3.1. Description de l'article et contribution

Le réchauffement climatique est un moteur de changement de composition des communautés à échelle locale et de distribution des espèces à échelle globale. Bien que de nombreuses études établissent ce lien, la magnitude du lien est très variable entre les études. La synthèse de ces résultats pose souvent la question de la comparabilité des études tant les effets confondants sont nombreux (e.g. historique du site, perturbations locales…). Ainsi les mécanismes responsables de cette variabilité dans la magnitude de réponse face au réchauffement de la température restent incompris. Ce chapitre pose la question : quel est l'effet d'une différence d'intensité de réchauffement sur la végétation forestière? Nous émettons les prédictions suivantes : les changements temporels de distribution des espèces sur un gradient altitudinal, la diversité, la composition et les affinités à la température des communautés sont toujours plus importants dans les zones où l'intensité du réchauffement est la plus forte.

Pour tester cette hypothèse, j'ai utilisé l'approche historique sur trois sites couvrant un large gradient d'augmentation de la température dans l'est du Canada. J'ai compilé des bases de données historiques de relevé de végétation fait dans trois parcs nationaux au Québec : le parc national de Forillon à l'est de la province où le réchauffement est minime depuis 1960, le parc national du Mont-Mégantic au centre de la province où le réchauffement est intermédiaire et le parc national de la Gatineau à l'extrême ouest où le réchauffement est le plus fort.

Les résultats concernant les changements de distribution des espèces sur le gradient altitudinal, de diversité et de composition soutiennent les hypothèses. Les magnitudes des changements observées sont cohérents avec l'intensité de l'augmentation de la température, ils suivent le gradient : Forillon < Mont-Mégantic < Gatineau. Cependant, contrairement aux prédictions, il n'y a pas eu de changement des affinités des communautés à la température. Ce chapitre met en avant la complexité des tendances temporelles des communautés face à un changement macro-climatique. Il invite à explorer les propriétés fonctionnelles des communautés.

L'idée originale de cet article a été développée conjointement avec Mark Vellend. La prise de données sur le terrain s'est faite avec le concours de Diane Auberson-Lavoie. Le calcul des affinités à la température s'est fait conjointement avec Steve Vissault. J'ai mené les analyses avec l'aide de Mark Vellend, et les commentaires de Guillaume Blanchet et Rapahel Aussenac. J'ai rédigé le manuscrit avec l'appui de Mark Vellend.

Citation :

Ce chapitre est déposé sur bioR*x*iv (doi : http://sci-hub.hk/10.1101/313379 et sera soumis à la revue *Global Change Biology.*

Becker-Scarpitta, A., Vissault, S., and Vellend, M. (2018). Four decades of plant community change along a continental gradient of warming. *bioRxiv*. Doi: http://sci-hub.hk/10.1101/313379

3.2. Four decades of plant community change along a continental gradient of warming

Antoine Becker-Scarpitta*[1], Steve Vissault[1], Mark Vellend[1]

1: Université de Sherbrooke, Département de biologie, 2500 boulevard de l'Université, Sherbrooke, J1K 2R1, Québec, Canada.

ORCID: Becker-Scarpitta A., 0000-0001-9241-091X

Contact: *corresponding author: Becker-Scarpitta A.,

Vissault S.,

Vellend M.,

Contribution: ABS and MV designed the study and wrote the manuscript collaboratively (with ABS as leader); ABS collected and analyzed the data; SV extracted climatic and species distribution data and provided input on the manuscript.

Keywords: climate change, community ecology, forest, historical ecology, legacy data, long-term monitoring, plant community, resurvey, understorey vegetation.

3.2.1. Abstract

Many studies of individual sites have revealed biotic changes consistent with climate warming (e.g., upward elevational distribution shifts), but our understanding of the tremendous variation among studies in the magnitude of such biotic changes is minimal. In this study we re-surveyed forest vegetation plots 40 years after the initial surveys in three protected areas along a west-to-east gradient of increasingly steep recent warming trends in eastern Canada (Québec). Consistent with the hypothesis that climate warming has been an important driver of vegetation change, we found an increasing magnitude of changes in species richness and composition from west to east among the three parks. For the two mountainous parks (Forillon and Mont-Mégantic Parks), we found no changes in elevational species' distributions in the eastern most park where warming has been minimal (Forillon Park), and significant upward distribution shifts in the centrally located park where the recent warming trend has been marked (Mont-Mégantic Park). Community temperature indices (CTI), reflecting the average affinities of locally co-occurring to temperature conditions across their geographic ranges ("species temperature indices"), did not change over time as predicted. However, close examination of the underpinnings of CTI values suggested a high sensitivity to uncertainty in individual species' temperature indices, and so a potentially limited responsiveness to warming. Overall, by testing a priori predictions concerning variation among parks in the direction and magnitude of vegetation changes, we have provided stronger evidence for a link between climate warming and biotic responses than otherwise possible and provided a potential explanation for large variation among studies in warming-related biotic changes.

3.2.2. Introduction

Climate is a dominant driver of large-scale plant distributions (Pearson & Dawson, 2003). On smaller spatial and temporal scales, changes in local climatic conditions can lead to modifications of species' abundances (Vellend et al., 2017), risks of extinction (Parmesan & Yohe, 2003; Rooney et al., 2004; Urban, 2015), phenology (Menzel et al., 2006; Cleland et al., 2007), distributions (Kelly & Goulden, 2008; Lenoir et al., 2008; Bertrand et al., 2011) and local adaptation (Aitken et al., 2008). Although many such changes have been observed in previous studies, the magnitude of response varies tremendously from study to study, and we have only a limited understanding of the processes underlying this variation.

Most of the world's natural vegetation is dominated by long-lived perennials plants (Grime, 1977), and so we expect vegetation responses to environmental change to occur slowly relative to the time span of a few years (or less) typical of ecological studies (Tilman, 1989). A key strategy used to assess longer-term temporal changes in plant communities is the resurvey of plots initially surveyed decades ago, often referred to as "legacy" studies (Vellend et al., 2013a; Chytrý et al., 2014; Hédl et al., 2017; Perring et al., 2017). An important limitation of such studies is their constrained ability to test the ecological mechanisms underlying temporal community change. Indeed, most legacy studies pertain to a single site, meaning a set of plots within an area sharing a similar climate and history, in which case community change might be caused by many local changes, such as ongoing land use (Hermy & Verheyen, 2007; Kampichler et al., 2012; Newbold et al., 2015), historical management legacies (Vanhellemont et al., 2014; Becker et al., 2016; Perring et al., 2017), nitrogen deposition (Becker-Scarpitta et al., 2017) or grazing (Frerker et al., 2014; Vild et al., 2016).

Causes of community change at a single site are often assessed by comparing observed changes in community composition across space or time with predictions based on drivers of interest, such as climate warming. For instance, as predicted by the climate warming hypotheses, many species have experienced a shift in distribution towards higher elevations (Gottfried et al., 2012; Pauli et al., 2012; Stockli et al., 2012; Sproull et al., 2015) or latitudes (Parmesan et al., 1999; Hickling et al., 2006; Boisvert-Marsh et al., 2014; but see VanDerWal et al., 2012). Given that plant species richness tends to be greater in warmer areas, a local-scale increase in richness is also predicted due to warming, at least in the absence of severe moisture stress (Vellend et al., 2017). Finally, if each species is first characterized by its geographic affinity with different temperature conditions (using a "Species Temperature Index"), then the average affinity across species in a local community (the "Community Temperature Index") is predicted to increase in response to warming (Devictor et al. 2008, 2012). Although there have been considerable advances in testing these predictions in single-site studies (local scale), explicit tests of predictions comparing multiple sites (regional scale) are needed to improve our knowledge and ability to predict biodiversity responses to climate changes (Verheyen et al., 2017).

Here we report analyses of changes in forest plant communities over four decades at three sites strategically chosen to be in areas covering a range of recent climate warming trends in eastern North-America (Québec, Canada). To assess temporal changes, we have revisited sites where botanical legacy data were collected in the 1970s, during the time that many provincial parks were being planned and established in Québec. Plots were widely distributed throughout each park and were typically placed in mature forest stands. Since the time of the original surveys, these forests have not experienced any major anthropogenic disturbances, thus minimizing possible confounding causes of vegetation change.

The province of Québec (Canada) spans >1000 km east-west, over which there is a marked gradient of warming over the past ~60 years (see Appendix B-S1 and Yagouti et al., 2008). At the tip of the Gaspé Peninsula, the location of our most easterly site, Forillon National Park (Fig. 3.1), warming has been least pronounced, likely due to the climatic buffering effect of the Atlantic Ocean (see Appendix B-S1). In contrast, Gatineau Park in continental western Québec has experienced marked warming, with Mont-Mégantic Provincial Park in between both geographically and in terms of the magnitude of warming (Fig. 3.1 and B-S1, Yagouti et al., 2008). To the best of our knowledge, no study has used legacy data to specifically test for contrasting vegetation responses in sites with variable warming trends (but see Menzel et al., 2006 for phenological responses to different warming trends).

Our core hypothesis is that areas with greater warming will have experienced stronger vegetation changes than areas with less warming (Chen et al., 2011; Wang et al., 2017). We take advantage of this unique combination of original studies along a warming gradient to perform a regional-scale analysis of temporal change of forest plant communities. Results for Mont-Mégantic, including significant upward elevational distribution shifts and increased local species richness, were reported in a previous paper (Savage & Vellend, 2015), to which we here add data for Gatineau Park (stronger warming trend) and Forillon Park (weaker warming trend). We tested the following specific predictions: (1) Significant upward elevational distribution shifts have occurred at Mont-Mégantic (already observed) but not at Forillon Park (tested in this paper). (Elevational variation in Gatineau Park is minimal – insufficient to test for temporal shifts in species distributions.) The magnitude of (2) the temporal change in species richness, (3) the temporal change in community composition (R^2 from the "time" effect in a multivariate analysis), and (4) the temporal change in Community Temperature Index (CTI) vary in magnitude among parks as follows: Forillon < Mont-Mégantic < Gatineau.

3.2.3. Materials and methods

3.2.3.1. Study region and sites

We studied vegetation change in three north-temperate forest sites in eastern Canada (Québec), spanning ~1000 km from Forillon National Park in eastern Québec, to Mont-Mégantic Provincial Park in central Québec and Gatineau National park in the western part of the province (Fig. 3.1). For all three parks, there has been no logging or forest management during the period of study.

Forillon National Park, located at the eastern extremity of the Gaspé peninsula (48°54′N, 64°21′W), was created in 1970 and covers 245 km^2, with our study plots ranging in elevation from ~50 to 500 m a.s.l.. The vegetation at Forillon is characterized in large part by boreal species, such as *Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss and *Betula papyrifera* Marshall. At low elevation, temperate deciduous or mixed forests are dominated by *Acer saccharum* Marsh. and *Betula alleghaniensis* Britt. (Majcen, 1981).

Mont-Mégantic Provincial Park is located in the Eastern Townships region of Québec (45°27′N, 71°9′W), about 650 southwest of Forillon Park and 15 km north of the U.S. borders with New Hampshire and Maine. The park was created in 1994 (logging ceased in the 1960s prior to park planning) and covers ~55 km^2. Our study plots range in elevation between ~460 and 1100 m a.s.l.. Vegetation patterns are very similar to Forillon, with a somewhat more visually evident elevational gradient: at low elevations, temperate deciduous forests are dominated by *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh. and *Betula alleghaniensis* Britt., while at high elevation boreal forests are composed largely of *Abies balsamea* (L.) Mill. and *Picea rubens* Sar. (Marcotte & Grandtner, 1974).

Gatineau Park is located in southwestern Québec (45°35′N 76°00′W), in the Outaouais region, 360 km west of Mont-Mégantic. The park was established in 1938, covers 361 km^2, with relatively little elevational variation compared to the other parks (250 m elevational range). Contrary to Forillon and Mont-Mégantic, our vegetation sampling was not spread throughout the entire park (access to certain sectors of the part is restricted). Our study area (~30 km^2) is largely dominated by *Acer saccharum* Marsh and *Fagus grandifolia* Ehrh., with a few more southerly tree species such as *Tilia americana* L., *Quercus rubra* L., *Quercus alba* L. or *Fraxinus americana* L. as well.

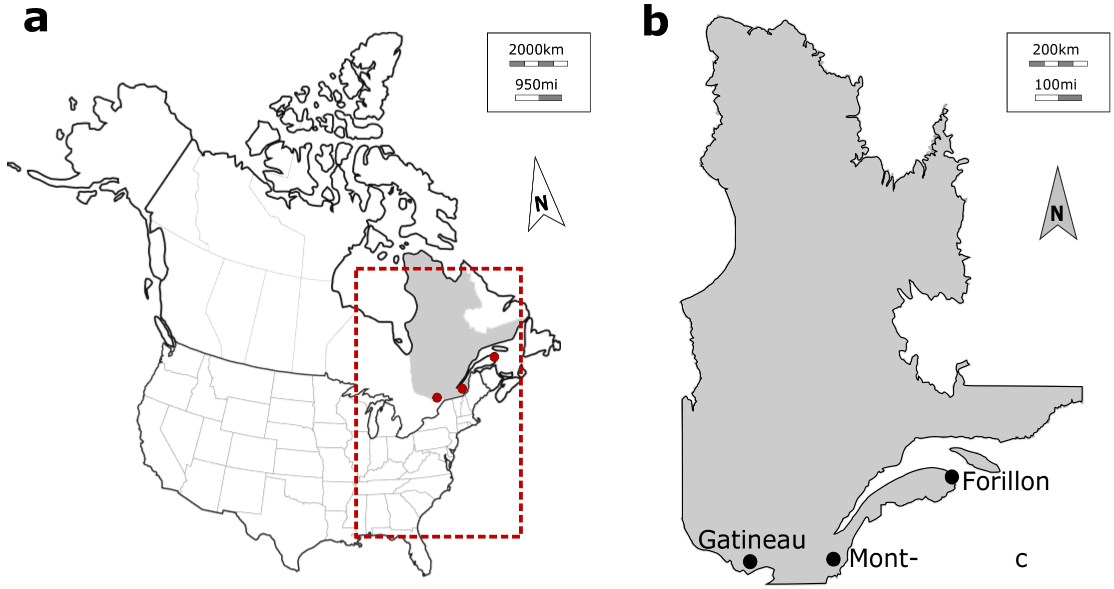


Figure 3.1 - Location of study sites in (a) Canada and (b) the Province of Québec. The red box in (a) shows the area used for extraction of species occurrences in the calculation of Species Temperature Indices (STI): 60°-90°W; 30°- 60°N.

3.2.3.2. *Data set*

All original vegetation surveys were conducted using phytosociological methods (Marcotte & Grandtner, 1974; Chartrand, 1976; Majcen, 1981). In fixed-area plots (see below), authors made a full list of vascular plant species in different strata (i.e. canopy trees, shrubs, herbs) with abundance coefficients per species assigned following the scale of Braun-Blanquet et al. (1952). In our analyses, we pooled shrubs and herbs into a single "understorey" stratum and given the limited representation of the tree community in smaller plots (90 m^2, see below), we focused all analyses on the understorey data. For analyses, Braun-Blanquet classes were converted to a percentage value representing the mid-point of a given abundance class.

None of the original survey plots were permanently marked, but for all three parks plot coordinates were reported in maps and/or tables. As such, plots are considered "semi-permanent", which introduces the possibility of pseudo-turnover due to relocation uncertainty (Stockli et al., 2012; Vellend et al., 2013a; Hédl et al., 2017; Kapfer et al., 2017). However, previous studies have shown that conclusions are robust to uncertainty in plot relocation, which adds statistical noise but not systematic bias (Kopecký & Macek, 2015). In our study, original surveyors tended to sample mature forest stands where spatial heterogeneity was relatively low, thus reducing any effects of plot relocation uncertainty. We used original plot maps and environmental descriptions (elevation, slope, aspect) to select potential locations for resurvey plots in a GIS (QGIS Development Team 2016, Open Source Geospatial Foundation Project). Potential locations were visited in the field, with the final location of a given plot determined by the best match to the original location and description. Logistical limitations prevented us from resurveying all original plots in Forillon and Gatineau. At Mont-Mégantic, all plots within the current park boundary were surveyed in 2012 (see Savage & Vellend, 2015). Plot selection for our recent surveys followed several criteria: (i) plots occurred in forest, excluding swamps or bogs; (ii) plots were accessible via <3-4 hours hiking off of trails (abandonment of old forest roads and trails since the 1970s has reduced accessibility); (iii) plots had not obviously experienced recent major natural disturbances (e.g., storms, fire, or insect outbreaks); (iv) in the original survey the plots were sampled in mature stands that have since maintained forest cover (i.e., no early successional dynamics in the intervening period).

At Forillon, the original survey was conducted in June-September 1972 in 256 vegetation plots of 500 m^2 distributed throughout the park (Majcen, 1981). We resurveyed 49 plots during July and August of 2015. At Mont-Mégantic, the vegetation was originally surveyed in 1970 in 94 plots, almost half of which were outside of the current park boundaries. The plot size was 400 m^2 in coniferous forest and 800 m^2 in broadleaved forests (Marcotte & Grandtner, 1974). Among the 94 original plots, 48 were revisited within the current park limits at Mont-Mégantic in 2012, with results reported in Savage & Vellend (2015). In Gatineau Park, surveys were conducted in 1973 in 33 plots of 90 m^2 during the summer in 1973 (Chartrand, 1976) and 28 plots were resurveyed in summer 2016. We harmonized taxonomy across all three parks and two-time periods (see below), so the Mont-Mégantic data are not precisely the same as reported in Savage & Vellend (2015). The study design was perfectly balanced within parks for statistical analysis (i.e., the same number of plots in the original and recent surveys).

3.2.3.3. *Taxonomy*

Our taxonomical reference for vascular plants was the Taxonomic Name Resolution Service v4.0 (assessed in Feb 2017: http://tnrs.iplantcollaborative.org).

Our data set was collected by five different survey teams, one for each of the three original surveys: Forillon: Majcen (1981); Mont-Mégantic: Marcotte & Grandtner (1974); Gatineau: Chartrand (1976), one for the recent Mont-Mégantic survey: Savage & Vellend (2015), and one for the recent Forillon and Gatineau surveys (A. Becker-Scarpitta and assistants). Most plants were identified to the species level in the same way across surveys, such that the only harmonization step for these taxa was to standardize names, which may have changed over time. In many cases, however, coarser levels of taxonomic resolution (e.g., a pair of similar species not identified to the species level) were used in some but not all surveys, or the timing of different surveys created doubt about the likelihood of comparable detection abilities (e.g., for spring ephemeral plants) (see Appendix B-S2 for details on taxonomic standardization). In these cases, the coarser level of resolution was applied to all data sets, or species were removed to maximize comparability. We deposited all specimens identified at the species level to the Marie-Victorin herbarium (Institut de Recherche en Biologie Végétale, Université de Montréal, Canada) and all locations were entered into the GBIF database (GBIF - https://www.gbif.org).

3.2.3.4. *Community Temperature Index (CTI)*

A predicted response of communities to warming is a temporal increase in the Community Temperature Index (CTI), which we calculated for all plots in each survey. CTI was calculated as the abundance-weighted average of the Species Temperature Index (STI) across all species in a given plot. The STI for a given species is the median of the long-term (1960-2010) mean annual temperatures calculated across all known occurrences of the species (Devictor et al., 2008). To calculate STIs, we compiled an independent dataset by extracting all recorded occurrences for each species in the Botanical Information and Ecology Network (BIEN - http://bien.nceas.ucsb.edu/bien/; Enquist et al., 2016) in eastern North America: 60˚ to 90˚W; 30˚ to 60˚N (red box of Fig. 3.1a). We excluded occurrences further west, in order to control the range of variation in precipitation (precipitation decreases markedly to the west of the deciduous forest biome). Our STIs thus reflect temperature affinities under precipitation conditions most comparable to those found in our study region. For each occurrence point, we extracted the annual mean temperature from ANUSPLIN, a model developed by Natural Resources Canada (http://cfs.nrcan.gc.ca/projects/3; McKenney et al. 2006). The abundance-weighted version of CTIw was calculated for each plot *j* as:

$$\mathrm{CTIw}_j = \sum_{i=1}^{S} (\mathrm{STI}_i \, * \, \mathrm{RA}_{ij})$$

The STI of species *i* is weighted by the relative abundance (RA) of species *i* in plot *j* (RA = the species local abundance divided by the sum of all *S* species' abundances in that plot). Given some surprising results concerning CTIw, we also explored analyses of the unweighted version, CTIuw (median STI across species with no weighting for abundance), thus focusing on which species were present in a given plot rather than their relative abundances.

STI values were calculated only for species identified at the species level and with more than 50 occurrences in the BIEN database (see Appendix B-S3 – Species Temperature Index database). Note that compared to Savage & Vellend (2015) we used improved climate data (ANUSPLIN instead of WORLDCLIM) and updated distribution data (BIEN instead of GBIF), thus leading to the potential for different results.

3.2.3.5. *Statistical analysis*

All statistical analyses were performed in R v.3.4.2 (R Foundation for Statistical Computing 2017). To test for upward elevational shifts in species distributions at Forillon and Mont-Mégantic, we selected species occurring in at least four plots per survey in a given park. For each species in each park we calculated the average abundance-weighted elevation across occurrences. We then conducted linear mixed effect models (LMM, function *lmer*, package 'lme4' v.1.1-14, Bates et al., 2015) testing for a fixed effect of time period on abundance-weighted mean elevation, with species as a random effect to account for the paired sampling structure of the data (each species observed in each time period).

We first studied the relationship between α-diversity (species richness) and time using LMMs including time, elevation and the time*elevation interaction (if significant) as fixed effects, and plot ID as a random effect. Because Gatineau has a negligible elevation gradient, we used a model for this park with only time and plot ID as a random effect. Coefficients of determination were expressed as marginal R^2 (R^2m) and conditional R^2 (R^2c) using the function *r.squaredGLMM*, package 'MuMIn' v.1.40.0 (Nakagawa & Schielzeth, 2013).

We then explored temporal change in β-diversity (i.e. the variability in species composition among communities) using permutational analysis of multivariate dispersion (PERMDISP). This analysis assessed the multivariate homogeneity of group dispersions based on Bray-Curtis distances (also called percentage-difference distance), with significance testing via permutation (function *betadisper*, package 'vegan' v.2.4-4, Anderson et al., 2006). A decrease in the multivariate distance between plots and the time-specific centroid is interpreted as biotic homogenization, while an increase indicates biotic differentiation.

To examine changes in community composition over time, we used permutational analysis of variance (PERMANOVA, with Bray-Curtis distances) using 999 permutations (function *adonis*, package 'vegan', Anderson, 2001). We used the R^2 values from the PERMANOVA models as quantification of the magnitude of temporal change in order to compare among parks. We used non-metric multidimensional scaling (NMDS) with Bray-Curtis distances for visualization (function *metaMDS*, package ‘vegan’).

Temporal changes in the Community Temperature Index (CTI) were tested using LMMs for both weighted and unweighted versions of CTI (CTIw and CTIuw, respectively). Model structure was identical to the model for species richness. We included the interaction between time and elevation only if significant.

3.2.4. Results

3.2.4.1. Species elevational distributions

In Forillon, where there has been the least warming in recent decades, there was no significant temporal change, on average, in understorey species’ elevational distributions (original survey mean = 195.4 m ± 12.3 (SE) m; recent = 206.8 m ± 12.3 m, t = 0.85, p = 0.41, Fig. 3.2a, see Appendix B-S4 for species-by-species data). In contrast, a significant upward elevational shift was observed at Mont-Mégantic, which has experience marked warming (original mean = 622.1 ± 10 m, recent mean = 660.94 m ± 10 m, t = 4.67, p < 0.001, Fig. 3.2b). At Mont-Mégantic, on average species’ distributions have shifted 39 m towards higher elevations (~10 m.decade^{-1}), and this was consistent along the spatial gradient (Fig. 3.2b; see also Savage & Vellend 2015).

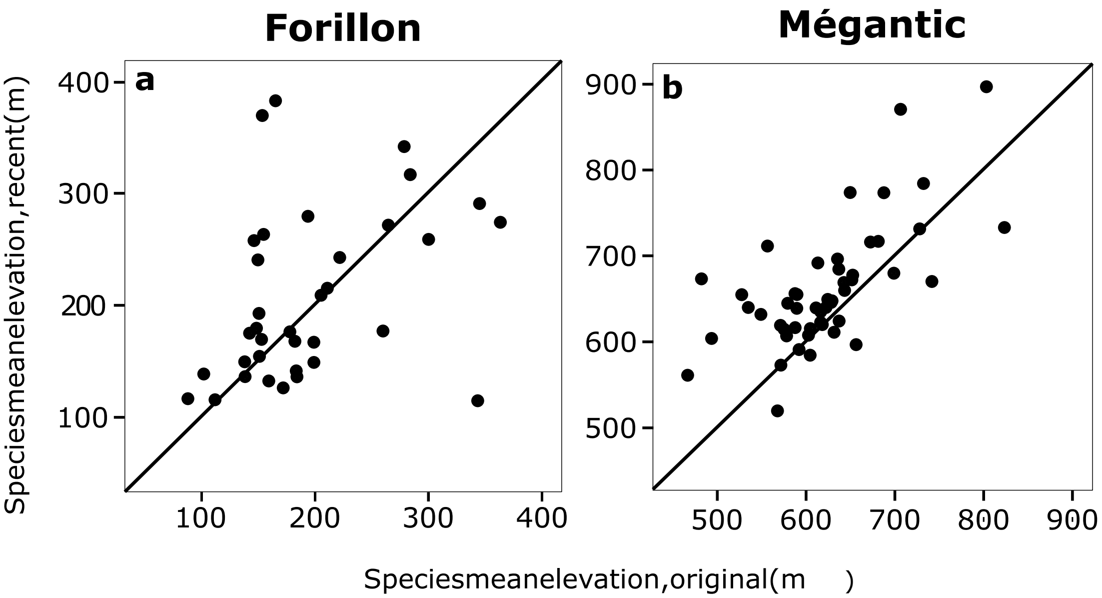


Figure 3.2 – Changes over time in species' elevational distributions at (a) Forillon, n=35 species, F=0.70, p=0.41 – no significant shift in elevation, and (b) Mont-Mégantic, n=50 species, F=22.72, p<0.001 – significant upward shift in elevation.

The diagonal line (1:1) represents no elevational change over time. Each point represents one species (occurring in minimum four plots per survey); see Appendix B-S4 for data.

3.2.4.2. Species richness

At Forillon, for plot-level species richness (α-diversity) we found no significant temporal change (Table 3.1 and 3.2), and the weak negative trend of richness with elevation was not significant (Fig 3d, Table 3.1). Across all plots we observed 18 fewer understorey species in the recent survey (65 species) than in the original survey (83 species); 27 species present in original survey were not found in the recent one, while we found 9 new species (Table 3.2). It is important to note that these are not likely to be gains and losses to and from the entire park, but only to and from this set of semi-permanent plots.

At Mont-Mégantic richness declined significantly with elevation in both time periods (original: $t = -6.97$, $p < 0.001$; recent: $t = -6.91$, $p < 0.001$, Fig. 3.3e and Table 3.1). Similar numbers of understorey plant species overall were found in the recent and original surveys (92 and 87 species, respectively); 8 species from the original survey were not found, while we recorded 13 new species in recent survey (Table 3.2). Mont-Mégantic showed a significant increase over time in the plot-level richness of understorey species (27% increase on average, see Fig. 3.3b and Tables 3.1 and 3.2), and this increase was consistent across the elevational gradient (Fig. 3.3e).

Finally, in Gatineau Park, plot-level species richness increased significantly by an average of 38% ($t = 4.14$, $p < 0.001$, Fig. 3.3c, Table 3.1 and 3.2). Overall, we found 20 more species in the recent survey than in the original survey. Gatineau showed the largest study-wide gain in species, with 32 new species observed in the recent survey and 12 species from the original survey not observed in recent one (Table 3.2).

Table 3.1 – Results of linear mixed models (LMMs) predicting species richness and community temperature indices (CTIw).

	Effect	F value	df	Pr(>|t|)	R^{2}m	R^{2}c
a) Plot richness (α diversity)						
Forillon	Time	3.67	48	0.06	0.04	0.41
	Elevation	1.25	47	0.27		
Mégantic	Time	26.77	47	**<0.001**	0.54	0.74
	Elevation	68.14	46	**<0.001**		
Gatineau	Time	17.15	27	**<0.001**	0.16	0.50
b) Community Temperature Index (CTIw)						
Forillon	Time	0.01	47	0.74	0.01	0.16
	Elevation	0.57	48	0.46		
Mégantic	Time	7.02	46	**0.01**	0.13	0.36
	Elevation	4.57	46	**0.04**		
	Time * Elevation	9.57	46	**0.003**		
Gatineau	Time	1.49	27	0.23	0.01	0.56

R2m is the marginal R2, measuring the proportion of variance explained by fixed effects; R2c is the conditional R2, giving the proportion of variance explained by both fixed and random effects. Bold values indicate significant differences ($p<0.05$).

Table 3.2 – Temporal changes in total species numbers and plot-level species richness (α-diversity).

	Total species number					α-diversity	
	Original	Recent	Shared	Losted	Gained	Original	Recent
Forillon	83	65	56	27	9	18.2 ± 1	16.4 ± 0.8
Mégantic	87	92	79	8	13	**21.2 ± 1.5**	**27.0 ± 1.5**
Gatineau	70	90	58	12	32	**11.6 ± 0.8**	**15.9 ± 0.8**

The total number of species observed across all plots is broken down into those shared, lost, or gained between the original and recent surveys. For plot-level richness, means ± SE are reported. Bold values indicate significant differences ($p<0.05$, see Table 3.1 for statistical tests).

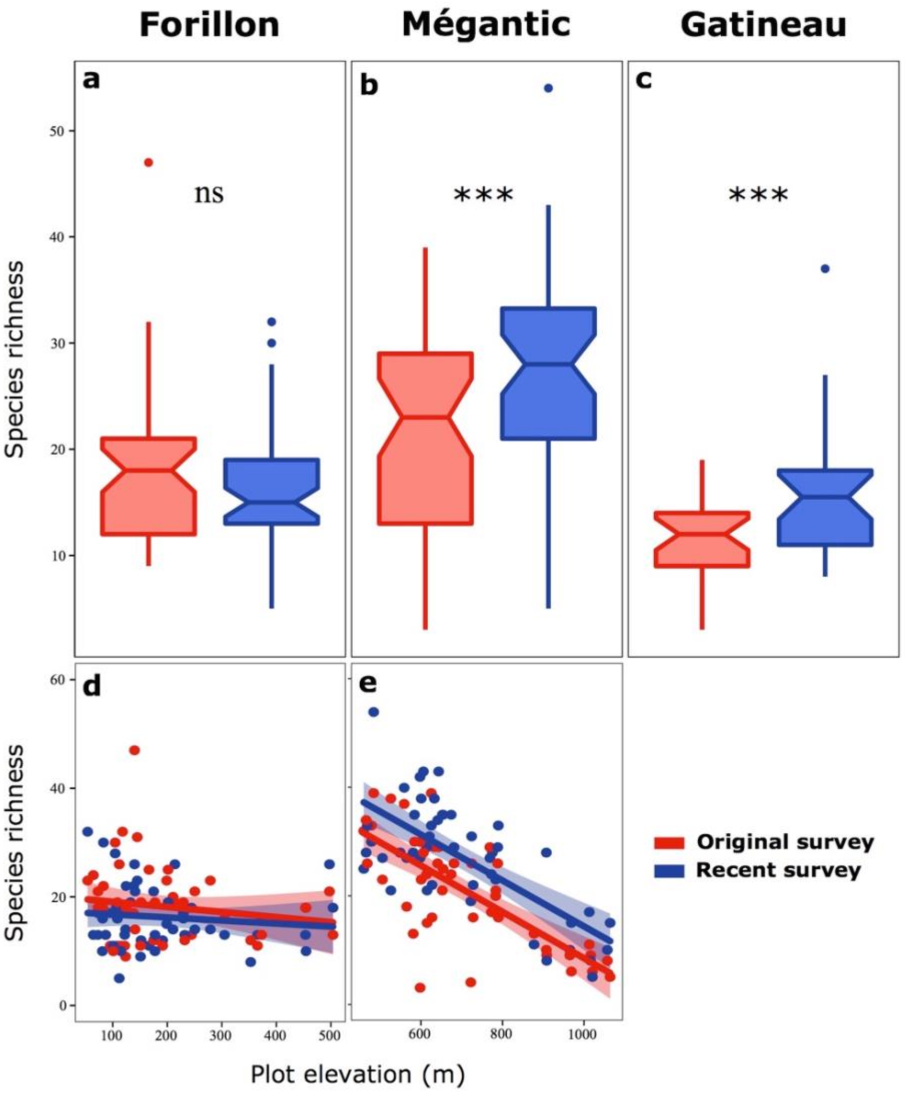


Figure 3.3 – Temporal changes in understorey species richness.

(a-c) Box plots of original and recent species richness per plot in the three parks. (d-e) Linear relationships between species richness and elevation in the original and recent surveys at Forillon (n=49*2 plots, no significant relationship for either original or recent surveys, see Table 3.1), and Mont-Mégantic (n=48*2 plots, significant relationship for both original and recent surveys, see Table 3.1). The colored polygons around each regression line represent 95% confidence intervals. *** $p<0.001$.

3.2.4.3. *Community composition and heterogeneity*

At none of the three sites was there significant temporal change in β-diversity (Table 3.3). However, we observed highly significant shifts in understorey community composition for all study sites (Table 3.3). Although shifts appear fairly subtle in the two-dimensional NMDS ordinations run independently for each park (Fig. 3.4), for Gatineau and Mont-Mégantic the differences are clearly visible in the NMDS run on all plots from all parks together (Fig. 3.5). The magnitude of the understorey compositional shifts (R^2) increased from Forillon (5%) to Mont-Mégantic (8%) to Gatineau (10%) (Table 3.3, Fig 3.5). Appendix B-S5 reports the list of species frequencies.

Table 3.3 – Tests for temporal shifts in β-diversity (PERMDISP) and community composition (PERMANOVA) of understorey communities between original and recent surveys.

	β-diversity				Community composition		
	Original	Recent	F	Pr(<F)	R^2	F	Pr(<F)
Forillon	0.50	0.54	3.53	0.06	0.052	5.26	**<0.001**
Mégantic	0.53	0.50	2.56	0.11	0.076	7.78	**<0.001**
Gatineau	0.56	0.60	3.52	0.70	0.096	5.71	**<0.001**

β-diversity is the mean distance between each plot and the time-specific centroid in multivariate space (Bray-Curtis distances). R^2 is the proportion of variation in community composition explained by time. Statistical significance levels were calculated with 999 permutations. Bold values indicate significant differences ($p<0.05$).

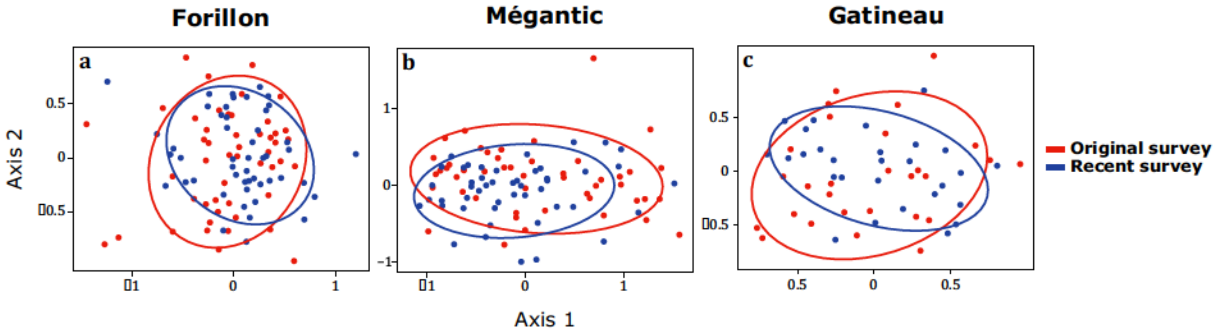


Figure 3.4 – Non-metric multidimensional scaling (NMDS) ordinations of understorey communities across time for (a) Forillon, stress = 0.94; (b) Mont-Mégantic, stress=0.97 and (c) Gatineau, stress=0.97.

Each point represents a survey plot, and colors refer to the time-period of surveys (red: original survey; blue: recent survey). Ellipses show 75% confidence limits for each time-period. We used two dimensions and Bray-Curtis distances. For a single ordination with species names see Appendix B-S6.

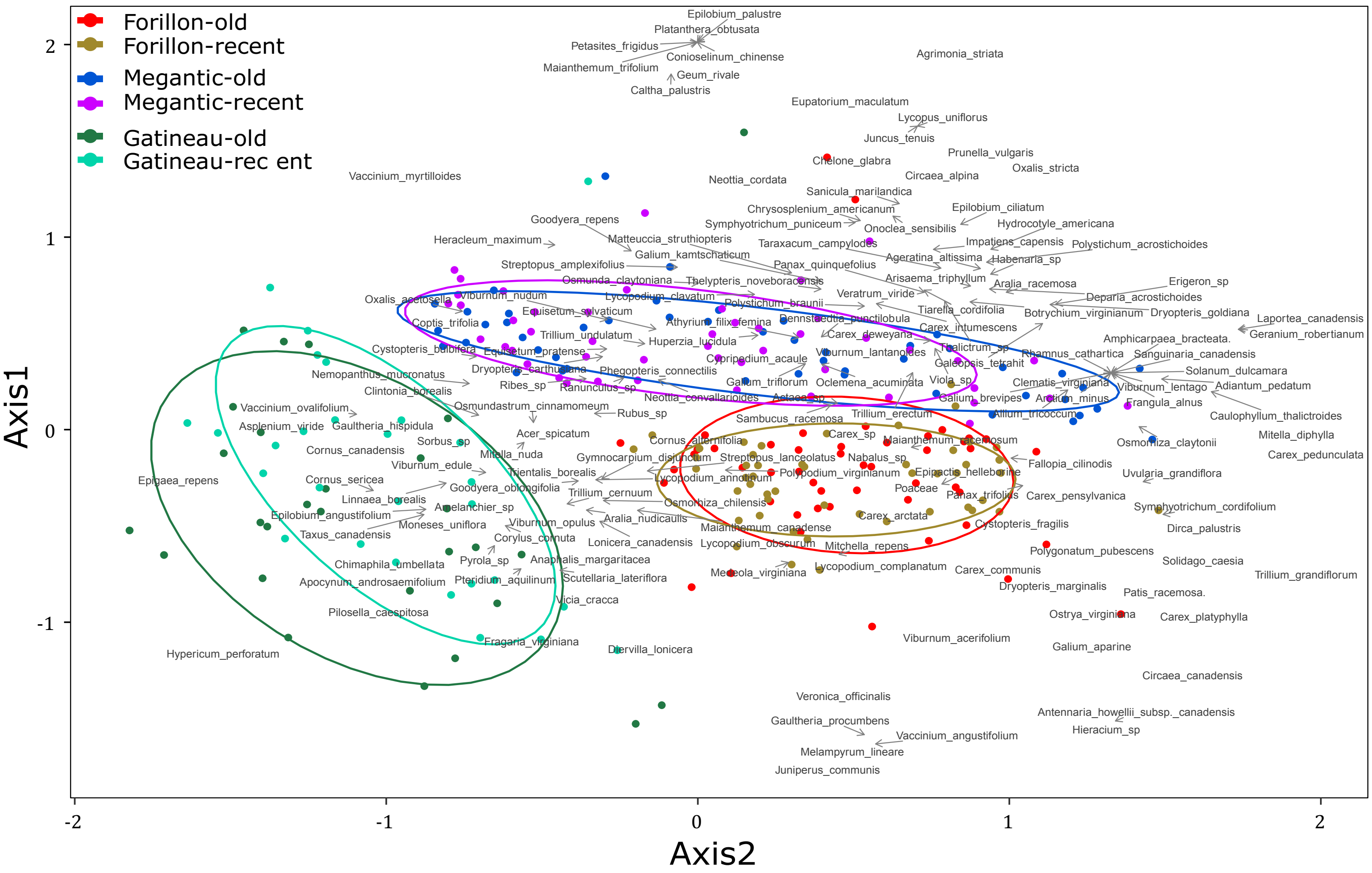


Figure 3.5 – Non-metric multidimensional scaling (NMDS) ordination of understorey community composition of all plots from all parks together for both original and recent surveys; stress=0.96.

Ellipses show 75% confidence limits for each time survey within each park. We used two dimensions and Bray-Curtis distances.

3.2.4.4. *Community temperature indices (CTI)*

The only significant temporal change in Community Temperature Indices (CTIw) was found at Mont-Mégantic, and the change was negative, the opposite of the predicted direction. We detected no significant changes in CTI in Forillon or Gatineau (Fig. 3.6, and Table 3.1). At Forillon, there was no significant relationship between CTI and elevation for either the original or recent survey (Fig. 3.6d and Table 3.1), nor was there any relationship for the original survey at Mont-Mégantic (Fig. 3.6e and Table 3.1). For the recent survey at Mont-Mégantic, there was a significant negative relationship between CTIw and elevation ($t = -3.1$, $p = 0.003$, Fig. 3.6e and Table 3.1), suggesting a decrease over time in the CTIw at high elevations but not low elevations (Fig. 3.6e). When using the unweighted CTI (CTIuw), results were qualitatively the same for Forillon and Gatineau. At Mont-Mégantic, however, we found no effect of time and a clear and significant decrease in CTIuw with elevation for both the original and recent surveys (see Appendix B-S6).

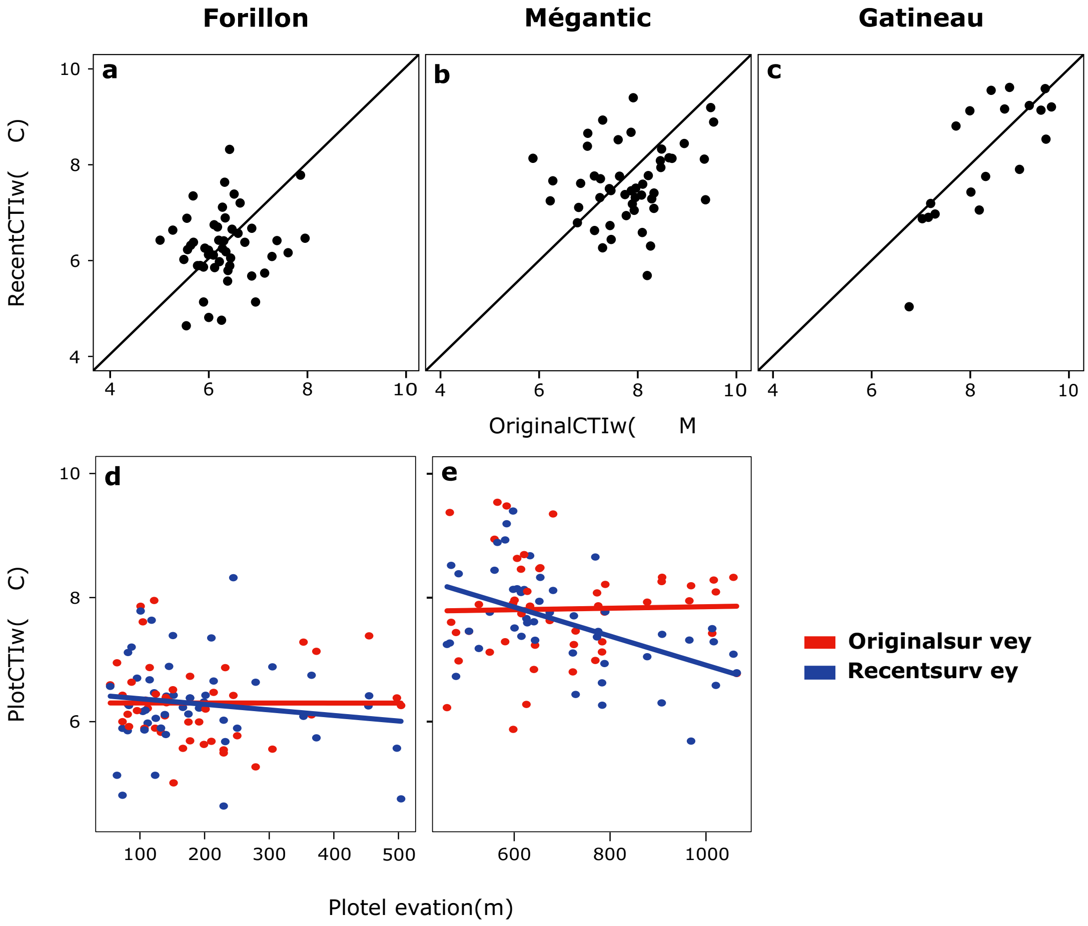


Figure 3.6 – Community Temperature Indices (CTIw) during the two-time periods and across the elevational gradient.

(a-c) Abundance-weighted indices (CTIw) at Forillon, Mont-Mégantic, and Gatineau, with the 1:1 line indicating no temporal change between two times. (d-e) Relationships between CTIw and elevation for each time period at Forillon and Mont-Mégantic. Red and blue illustrate original and recent surveys, respectively. Each point is a plot in all panels.

3.2.5. Discussion

Many studies at single sites have revealed temporal changes in species distributions, community composition, or phenology that are consistent with predictions based on climate warming (Lenoir et al., 2009; Bertrand et al., 2011; Bernhardt-Römermann et al., 2015; Sproull et al., 2015; Ash et al., 2017; Rogora et al., 2018). However, with observational data (i.e., most long-term studies) it is always difficult to rule out alternative causes of temporal community change, such that comparative multi-site studies are needed to strengthen tests of the general hypothesis that biotic change over time has been influenced by climate warming (Verheyen et al., 2017). In this study, we have taken advantage of a natural gradient in the degree of climate warming and of a protected area network in eastern Canada, combining three re-survey efforts totalling 130 plots to test whether greater warming has led to more marked changes in species distributions and community properties. Results were mostly consistent with our predictions, with the magnitude of biotic changes (i.e. elevational distributions, species richness, composition) most often increasing from Forillon Park in eastern Québec, where the warming trend has been relatively weak, to Mont-Mégantic where warming has been moderate, to Gatineau Park in western Québec where the warming trend has been the strongest. Results for community temperature indices were difficult to interpret, as discussed further below.

3.2.5.1. Species' elevational distributions

As predicted, species' mean elevations shifted upward at Mont-Mégantic but not Forillon. There is no elevational gradient in Gatineau Park. On average, species at Mont-Mégantic moved toward higher elevations, as predicted if species are at least partially spatially tracking their temperature optima in response to warming (Kelly & Goulden, 2008; Savage & Vellend, 2015; Sproull et al., 2015).

The rate of elevational shift for the understorey plants at Mont-Mégantic (~10 m.decade^{-1}) is close to the global average of 11 m.decade^{-1} reported in the meta-analysis of Chen et al. (2011), although individual studies have reported higher values (e.g., ~22 m.decade^{-1} in southern

California; Kelly & Goulden, 2008) and lower values (e.g., no shift in elevation in Montana; Klasner & Fagre, 2002). However, direct comparison among studies in different regions is complicated by different degrees of warming over the relevant time frames in different places. Moreover, there has been relatively few studies in North-America, making our study not only a novel general contribution to global change biology, but also a valuable regional-scale contribution to our knowledge of changes in species distributions along elevation gradients in eastern North-America.

Although the gradients in Forillon and Mont-Mégantic cover similar elevational ranges (~500-600 m), the vegetation gradient is less pronounced in Forillon Park than at Mont-Mégantic. For instance, Forillon's high elevation summits are not as predictably dominated by boreal forest as they are at Mont-Mégantic. This can be seen in the weaker relationships between plot richness and CTI with elevation at Forillon contrary to Mont-Mégantic (Figs. 3.3d-e, 3.5d-e, Appendix B-S6). Despite these differences, the clear absence of any shift in elevational distributions in Forillon Park is consistent with the hypothesis that climate warming is the probable cause of elevational distribution shifts at Mont-Megantic (and elsewhere).

3.2.5.2. *Species richness, composition, and heterogeneity*

Since warm areas tend to have higher local plant diversity than cold areas, climate warming is predicted to increase local plant diversity in many regions (Vellend et al., 2017). Consistent with our prediction, there was no significant temporal change in species richness over ~40 years at Forillon but significant increases were found at Mont-Mégantic and Gatineau. Some other studies in regions that have experienced warming have also found increases of local vascular plant diversity (Klanderud & Birks, 2003; Walther et al., 2005; Stockli et al., 2012, Steinbauer et al., 2018), although temporal changes in species richness are highly variable (Verheyen et al., 2012; Vellend et al., 2013b).

We found significant temporal shifts in understorey community composition in all three parks, consistent with many studies in the literature showing species turnover through time (Magurran et al., 2010; Dornelas et al., 2014; Shi et al., 2015). Comparisons among parks were consistent with our predictions, with the magnitude of community shifts (R^2) following the gradient of warming: Forillon < Mont-Mégantic < Gatineau. However, we found no evidence of biotic homogenization, in contrast to many studies in literature (Jurasinski & Kreyling, 2007; Keith et al., 2009; Zwiener et al., 2017). In fact, our earlier study of Mont-Mégantic reported significant biotic homogenization (Savage & Vellend 2015), and the difference with the present study appears to be largely due to differences in data processing and analysis. The raw community data were slightly different given our taxonomic standardization across surveys in different parks and a few differences in which woody plants were considered part of the understorey vs. canopy (e.g., *Acer spicatum* was included in the understorey in the current study but not the earlier one). More importantly, Savage & Vellend (2015) first used a fourth-root transformation of abundance data prior to calculating Bray-Curtis differences (a recommendation in the PRIMER software; Anderson et al., 2008), whereas we saw no clear justification for this in the present study. Applying the same transformation to our data revealed significant biotic homogenization for Mont-Mégantic, but not for the other two parks (results not shown). This is of negligible consequence for the present study, given that we did not have strong *a priori* predictions concerning beta diversity, although it is clear that the earlier result of biotic homogenization was not robust to alternative methods of analysis.

All observational studies involve uncertainty in making inferences about the cause of changes over space or time. Among potentially confounding factors that can underlie temporal community changes, succession is of potentially high importance. However, our study was designed specifically to minimize strong successional dynamics. We resurveyed plots originally surveyed in mature stands that have maintained closed canopies throughout the period of study. Importantly, we have no reason to suspect that forest dynamics (driven by factors other than climate) varies among our three parks in a way that aligns with the gradient of climate warming. As such, the best supported hypothesis for explaining the temporal changes we observed along the east-west gradient is that climate warming is a key driver.

Resurvey studies also raise questions about the comparability of surveys in different years and in different parks (Vellend et al. 2013a). In this study, in order to minimize differences between the six surveys, we paid close attention to taxonomic homogenization, and we consulted with botanists active in the 1970s (e.g., Colette Ansseau, a collaborator of M. Grandtner's, and Z. Majcen) in order to reproduce the exact same field survey methods used in the original studies. One difference among parks we could not avoid was plot size, with smaller plots in Gatineau than in Forillon and Mont-Mégantic. It is predicted that in small communities, the importance of drift (stochastic changes in abundance) in driving community dynamics should be relatively high (Ricklefs & Lovette, 1999; Vellend, 2016). As such, all else being equal, one might have expected reduced detectability of deterministic community change over time in Gatineau, yet we found the opposite: a stronger temporal increase of α-diversity and a stronger directional shift in composition. Thus, if anything, we may have underestimated the difference between Gatineau and the other parks.

3.2.5.3. *Community temperature affinity (CTI)*

The results for Community Temperature Indices (CTI) diverged most strongly from our predictions. Specifically, we failed to detect any temporal increase of CTI in Gatineau, and contrary to our prediction, we found a significant decrease of CTIw for high elevation plots at Mont-Mégantic (see Fig. 3.6e and Table 3.1). This result suggests a "cooling" in terms of community affinities to temperature at high elevation, which has actually been previously observed in the European Alps (Roth et al., 2014). The fact that there was no such trend when using unweighted community temperature indices (CTIuw) indicates that changes in particular species' abundances drove the result for CTIw.

In particular, two of the most abundant species experienced major temporal changes: (i) *Oxalis acetosella* L. (known also as *Oxalis montana* Raf.) decreased in average abundance and (ii) *Dryopteris carthusiana* (Vill.) H.P. Fuchs increased in abundance (see Appendix B-S7). *Oxalis acetosella* had a Species Temperature Index (STI) of 8.6 °C. This species was often found at unusually high abundance in the original surveys at Mont-Mégantic, especially at high elevation (>800 m). On average, *O. acetosella* contributed ~74% to CTIw values for high elevation plots in the original survey, while contributing only ~8% in the recent survey (see Appendix B-S7). Given abundance reductions at high elevation, the abundance-weighted elevation of this species declined more than any other, which represents an exception among the full set of species (*O. acetosella* is the right-most point in Fig. 3.2b), but which has a major effect on CTIw values. In contrast, *Dryopteris carthusiana* (STI = 7.6 °C) was not particularly abundant at high elevation in the original surveys but became very abundant in the recent surveys. The contribution of *D. carthusiana* to CTIw for plots at high elevation (>800 m) increased from ~9.5% to ~47%. At Mont-Mégantic, *O. acetosella* is more strongly associated with high elevation forests (i.e., colder sites) than is *D. carthusiana*, and so their changes in abundance are in one sense consistent with the hypothesis that warming is a major driver of vegetation change. But since the estimated STI (using independent data) was actually higher for *O. acetosella* than *D. carthusiana*, the changes in abundance caused a decline in high-elevation CTIw. In sum, the high sensitivity of CTI to the dynamics of individual species, combined with uncertainty in STI values (see also below), may reduce the degree to which CTI acts as an indicator of climate warming.

The calculation and interpretation of CTI has several limitations. First, Species Temperature Indices (STI) are calculated based on recorded species occurrences, but for many species we have limited knowledge of geographic distributions, especially in northern regions or at high elevation. Second, the assumption that median temperature represents a species' optimum is unverified (Rodriguez-Sanchez et al., 2012). As mentioned above, STI is greater (warmer) for *Oxalis* than for *Dryopteris* due to the more northern distribution of *Dryopteris*. However, in eastern North America *Oxalis* is known to be more abundant in coniferous forests at high elevation while *Dryopteris* is more widely distributed along elevation gradient. Thus, if we used data from occurrences along elevational gradients (i.e., at Mont-Mégantic), *Oxalis* would have a lower STI than *Dryopteris*. In other studies, CTI has been shown to increase as predicted by warming (Devictor et al., 2008; Lindström et al., 2012; Bowler et al., 2015). In our study system, STIs and therefore CTIs come with considerable uncertainty.

In sum, we have provided empirical evidence of vegetation changes in eastern Canada that are largely consistent with the east-west gradient in warming. Explicit comparisons of community change among regions with variable climatic histories appears to be a powerful method for increasing the confidence with which biotic trends can be attributed to climate warming. Many unknowns remain, such as the functional attributes of “loser” and “winner” species, and the extent to which adaptive changes within species might also contribute to warming responses. Continuing to exploit historical data sources of all kinds can help advance global change science.

3.2.6. Acknowledgements

We thank the field and lab assistants who contributed to this project: Diane Auberson-Lavoie, Melissa Paquette, and Sara Gaignard. This work was made possible thanks to the support of park managers, especially Camille-Antoine Ouimet (Mont-Mégantic) and Daniel Sigouin (Forillon). We also thank Guillaume Blanchet, Raphael Aussenac and Joanie Van De Walle for valuable input on various aspects of this project, in particular statistical analysis. Finally, thanks to Pauline Palmas and Arnault Lalanne for providing comments on an earlier version of the manuscript. Funding was provided by the Natural Sciences and Engineering Research Council, Canada.

3.2.7. References

Aitken SN, Yeaman S, Holliday J a., Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications, 1, 95–111.

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26, 32–46.

Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9, 683–693.

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. Plymouth, UK, 214 pp.

Ash JD, Givnish TJ, Waller DM (2017) Tracking lags in historical plant species’ shifts in relation to regional climate change. Global Change Biology, 23, 1305–1315.

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67, 1–48.

Becker T, Spanka J, Schröder L, Leuschner C (2016) Forty years of vegetation change in former coppice-with-standards woodlands as a result of management change and N deposition. Applied Vegetation Science, 20, 304–313.

Becker-Scarpitta A, Bardat J, Lalanne A, Vellend M (2017) Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming. Journal of Vegetation Science, 28, 1220–1229.

Bernhardt-Römermann M, Baeten L, Craven D et al. (2015) Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. Global Change Biology, 21, 3726–3737.

Bertrand R, Lenoir J, Piedallu C et al. (2011) Changes in plant community composition lag behind climate warming in lowland forests. Nature, 479, 517–520.

Boisvert-Marsh L, Périé C, de Blois S (2014) Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere, 5, art83.

Bowler DE, Haase P, Kröncke I et al. (2015) A cross-taxon analysis of the impact of climate change on abundance trends in central Europe. Biological Conservation, 187, 41–50.

Braun-Blanquet J, Roussine N, Nègre R (1952) Les Groupements Végétaux de la France Méditerranéenne, CNRS edn (ed CNRS). Toulouse, 1-297 pp.

Chartrand N (1976) Étude phytosociologique du stade climacique des séries de végétation dans un secteur du parc de la Gatineau. McGill University, Macdonal College, 109 pp.

Chen I, Hill JK, Ohlemuller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science, 333, 1024–1026.

Chytrý M, Tichý L, Hennekens SM, Schaminée JHJ (2014) Assessing vegetation change using vegetation-plot databases: a risky business. Applied Vegetation Science, 17, 32–41.

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends in Ecology and Evolution, 22, 357–365.

Devictor V, Julliard R, Couvet D, Jiguet F (2008) Birds are tracking climate warming, but not fast enough. Proceedings of the Royal Society B: Biological Sciences, 275, 2743–2748.

Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE (2014) Assemblage time series reveal biodiversity change but not systematic loss. Science, 344, 296–299.

Enquist BJ, Condit RR, Peet RK, Schildhauer M, Thiers BM (2016) The Botanical Information and Ecology Network (BIEN): Cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. PeerJ.

Frerker K, Sabo A, Waller D (2014) Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. PLoS ONE, 9, e115843.

Gottfried M, Pauli H, Futschik A et al. (2012) Continent-wide response of mountain vegetation to climate change. Nature Climate Change, 2, 111–115.

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist, 111, 1169–1194.

Hédl R, Bernhardt-Römermann M, Grytnes J-A, Jurasinski G, Ewald J (2017) Resurvey of historical vegetation plots: a tool for understanding long-term dynamics of plant communities. Applied Vegetation Science, 20, 161–163.

Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecological Research, 22, 361–371.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology, 12, 450–455.

Jurasinski G, Kreyling J (2007) Upward shift of alpine plants increases floristic similarity of mountain summits. Journal of Vegetation Science, 18, 711–718.

Kampichler C, van Turnhout C a M, Devictor V, van der Jeugd HP (2012) Large-scale changes in community composition: determining land use and climate change signals. PloS one, 7, e35272.

Kapfer J, Hédl R, Jurasinski G, Kopecký M, Schei FH, Grytnes J-A (2017) Resurveying historical vegetation data - opportunities and challenges. Applied Vegetation Science, 20, 164–171.

Keith S a, Newton AC, Morecroft MD, Bealey CE, Bullock JM (2009) Taxonomic homogenization of woodland plant communities over 70 years. Proceedings of the Royal Society B: Biological Sciences, 276, 3539–3544.

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences, 105, 11823–11826.

Klanderud K, Birks HJB (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. The Holocene, 13, 1–6.

Klasner FL, Fagre DB (2002) A half century of change in Alpine treeline patterns at Glacier National Park, Montana, U.S.A. Arctic, Antarctic, and Alpine Research, 34, 49–56.

Kopecký M, Macek M (2015) Vegetation resurvey is robust to plot location uncertainty. Diversity and Distributions, 21, 322–330.

Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science, 320, 1768–1771.

Lenoir J, Gégout JC, Pierrat JC, Bontemps JD, Dhôte JF (2009) Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006). Ecography, 32, 765–777.

Lindström Å, Green M, Paulson G, Smith HG, Devictor V (2012) Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. Ecography, 36, 313–322.

Magurran AE, Baillie SR, Buckland ST et al. (2010) Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends in Ecology & Évolution, 25, 574–582.

Majcen Z (1981) Les forets du parc national Forillon, Gaspésie, Québec, étude phytosociologique. Université de Laval, 158 pp.

Marcotte G, Grandtner M (1974) Étude écologique de la végétsation forestière du Mont Mégantic. Université de Laval, 156 pp.

McKenney DW, Pedlar JH, Papadopol P, Hutchinson MF (2006) The development of 1901–2000 historical monthly climate models for Canada and the United States. Agricultural and Forest Meteorology, 138, 69–81.

Menzel A, Sparks TH, Estrella N et al. (2006) European phenological response to climate change matches the warming pattern. Global Change Biology, 12, 1969–1976.

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R 2 from generalized linear mixed-effects models. Methods in Ecology and Evolution, 4, 133–142.

Newbold T, Hudson LN, Hill SLL et al. (2015) Global effects of land use on local terrestrial biodiversity. Nature, 520, 45–50.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421, 37–42.

Parmesan C, Ryrholm N, Stefanescu C et al. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature, 399, 579–583.

Pauli H, Gottfried M, Dullinger S et al. (2012) Recent plant diversity changes on Europe's mountain summits. Science, 336, 353–355.

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography, 12, 361–371.

Perring MP, Bernhardt-Römermann M, Baeten L et al. (2017) Global environmental change effects on plant community composition trajectories depend upon management legacies. Global Change Biology.

Ricklefs RE, Lovette IJ (1999) The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. Journal of Animal Ecology, 68, 1142–1160.

Rodriguez-Sanchez F, De Frenne P, Hampe A (2012) Uncertainty in thermal tolerances and climatic debt. Nature Climate Change, 2, 638–639.

Rogora M, Frate L, Carranza ML et al. (2018) Assessment of climate change effects on mountain ecosystems through a cross-site analysis in the Alps and Apennines. Science of The Total Environment, 624, 1429–1442.

Rooney TP, Waller DM (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management*, **181**, 165–176.

Rooney TP, Wiegmann SM, Rogers D a., Waller DM (2004) Biotic impoverishment and homogenization in unfragmented forest understory communities. Conservation Biology, 18, 787–798.

Roth T, Plattner M, Amrhein V (2014) Plants, birds and butterflies: short-Term responses of species communities to climate warming vary by taxon and with altitude. PLoS ONE, 9, e82490.

Savage J, Vellend M (2015) Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. Ecography, 38, 546–555.

Shi Z, Sherry R, Xu X et al. (2015) Evidence for long-term shift in plant community composition under decadal experimental warming. Journal of Ecology, 103, 1131–1140.

Sproull GJ, Quigley MF, Sher A, González E (2015) Long-term changes in composition, diversity and distribution patterns in four herbaceous plant communities along an elevational gradient (ed Collins B). Journal of Vegetation Science, 26, 552–563.

Steinbauer MJ, Grytnes J-A, Jurasinski G et al. (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, **556**, 231–234.

Stockli V, Wipf S, Nilsson C, Rixen C (2012) Using historical plant surveys to track biodiversity on mountain summits. Plant Ecology and Diversity, 4, 415–425.

Tilman D (1989) Ecological Experimentation: Strengths and Conceptual Problems. In: Likens G.E. (eds) Long-Term Studies in Ecology, pp. 136–157. Springer, New York.

Urban MC (2015) Accelerating extinction risk from climate change. Science, 348, 571–573.

VanDerWal J, Murphy HT, Kutt AS, Perkins GC, Bateman BL, Perry JJ, Reside AE (2012) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. Nature Climate Change, 2, 1–5.

Vanhellemont M, Baeten L, Verheyen K (2014) Relating changes in understorey diversity to environmental drivers in an ancient forest in northern Belgium. Plant Ecology and Evolution, 147, 22–32.

Vellend M (2016) The Theory of Ecological Communities. Monographs in Population Biology, 57, 229.

Vellend M, Brown CD, Kharouba HM, McCune JL, Myers-Smith IH (2013a) Historical ecology: Using unconventional data sources to test for effects of global environmental change. American Journal of Botany, 100, 1294–1305.

Vellend M, Baeten L, Myers-Smith IH et al. (2013b) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proceedings of the National Academy of Sciences, 110, 19456–19459.

Vellend M, Baeten L, Becker-Scarpitta A et al. (2017) Plant biodiversity change across scales during the anthropocene. Annual Review of Plant Biology, 68, 563–586.

Verheyen K, Baeten L, De Frenne P et al. (2012) Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. Journal of Ecology, 100, 352–365.

Verheyen K, De Frenne P, Baeten L et al. (2017) Combining biodiversity resurveys across regions to advance global change research. BioScience, 67, 73–83.

Vild O, Hédl R, Kopecký M, Szabó P, Suchánková S, Zouhar V (2016) The paradox of long-term ungulate impact: increase of plant species richness in a temperate forest. Applied Vegetation Science, 20, 282–292.

Walther G-R, Beißner S, Burga C a. (2005) Trends in the upward shift of alpine plants. Journal of Vegetation Science, 16, 541–548.

Wang Y, Wen S, Farnon Ellwood MD, Miller AD, Chu C (2017) Temporal effects of disturbance on community composition in simulated stage-structured plant communities. Ecology and Evolution, 8, 120–127.

Yagouti A, Boulet G, Vincent L, Vescovi L, Mekis É (2008) Observed changes in daily temperature and precipitation indices for southern Québec, 1960–2005. Atmosphere-Ocean, 46, 243–256.

Zwiener VP, Lira-Noriega A, Grady CJ, Padial AA, Vitule JRS (2017) Climate change as a driver of biotic homogenization of woody plants in the Atlantic Forest. Global Ecology and Biogeography.

3.2.8. Supplementary Materials

- Appendix B-S1 - Climatic trends in three regions of Québec, Canada
- Appendix B-S2 - Taxonomic standardization between surveys
- Appendix B-S3 – Species Temperature Index (STI) database
- Appendix B-S4 - Mean abundance-weighted elevation and number of occurrences per species per survey in Forillon and Mont-Mégantic
- Appendix B-S5 - Species occurrences per survey (number of plots where species were recorded)
- Appendix B-S6 - Results for unweighted Community Temperature Indices (CTIuw)
- Appendix B-S7 - Individual species contributions to Community Temperature Indices (CTIw) for high elevation plots at Mont-Mégantic

4- CHAPITRE 4

CHANGES IN VASCULAR PLANT AND BRYOPHYTE COMMUNITIES ALONG ELEVATIONAL GRADIENTS OVER FOUR DECADES

4.1. Description de l'article et contribution

Dans les chapitres précédents, nous avons établi le lien entre les changements environnementaux et la réponse de la végétation. Le chapitre 2 montre la différence de sensibilité entre les plantes vasculaires et les bryophytes notamment face aux dépositions atmosphériques. Le chapitre 3 établit un lien entre l'intensité du réchauffement de la température et la magnitude de la réponse de la végétation vasculaire. Le chapitre suivant combine ces résultats et explore la différence de sensibilité entre les plantes vasculaires et les bryophytes dans deux sites marqués par différentes intensités de réchauffement de la température. Sur les mêmes sites que le chapitre 3, nous avons combiné des relevés de bryophytes aux données des plantes vasculaires pour le Parc national de Forillon et du Mont-Mégantic. Nous avons testé l'hypothèse que les bryophytes sont moins sensibles que les plantes vasculaires face au réchauffement de la température. Les prédictions centrales sont: les changements temporels de distribution des espèces sur le gradient altitudinal, la diversité, la composition des communautés sont plus grands pour les plantes vasculaires que les bryophytes. L'hypothèse est l'inverse que celle testée dans le chapitre 2, en raison des faibles taux de déposition atmosphérique marqués dans la région étudiée ici. Comme je l'ai développé dans la section *1.4.3.*, les bryophytes ont une plus grande tolérance aux variations de la température que les plantes vasculaires.

Les résultats de ce chapitre sont mitigés. Les conclusions dépendent fortement de la propriété de la communauté. Les changements de distribution des espèces sur le gradient altitudinal, les changements de richesse sont plus importants pour les plantes vasculaires que pour les bryophytes. Cependant, les bryophytes ont subi de plus grands changements de composition.

Les hypothèses testées dans ces chapitres ont été élaborées conjointement avec Mark Vellend. La prise de données sur le terrain a été faiteen collaboration avec Diane Auberson-Lavoie. J'ai mené les analyses et la rédaction du manuscrit avec l'appui de Mark Vellend. Cet article sera soumis avant la soutenance dans *Conservation Biology.*

4.2. Changes in vascular plant and bryophyte communities along elevational gradients over four decades

Antoine Becker Scarpitta*[1], Diane Auberson-Lavoie[1], Mark Vellend[1]

ORCID: Becker-Scarpitta: 0000-0001-9241-091X

1: Université de Sherbrooke, Département de biologie, 2500 boulevard de l'Université, Sherbrooke, J1K 2R1, Québec, Canada.

Contact: *Corresponding author: A. Becker-Scarpitta,

D. Auberson-Lavoie,

M. Vellend,

4.2.1. <u>Introduction</u>

Ecological impacts of global changes have been widely reported in the scientific literature (McGill et al., 2015; Vellend et al., 2017a). Montane ecosystems have received considerable attention due to clear predictions, based on climate warming, of changes in species' distributions and community composition along elevation gradients, although such studies have focused on relatively few taxa, in particular vascular plants and vertebrates (Lenoir et al., 2008; Chen et al., 2011; Pauli et al., 2012; Stockli et al., 2012; Rumpf et al., 2018). Thus, despite many studies showing biodiversity responses to warming, the generality of such responses across taxa remains unclear. For instance, very few studies have reported empirical evidence of bryophyte community responses to climate warming (Hudson & Henry, 2010; He et al., 2016 but see Bergamini et al., 2009; Raabe et al., 2010; Becker-Scarpitta et al., 2017; Vanneste et al., 2017).

Understanding variation among taxa in their responses to environmental change is crucial for identifying priorities in conservation. For example, even if one taxonomic group (e.g., vascular plants) is relatively insensitive to environmental change, other co-occurring taxa (e.g., bryophytes and lichens) might be very sensitive (Hudson & Henry 2010), with potentially important consequences for ecosystem function (Turetsky, 2003; Lindo & Gonzalez, 2010). Thus, our limited knowledge base with which to identify the most relevant set of metrics or the taxonomic groups most sensitive to environmental change constrains our ability to set efficient conservation priorities. We operationally define "sensitivity" here as responsiveness: i.e., the degree to which a given community property changes in the face of environmental change.

To assess long-term responses of ecological communities to warming, "legacy" ecological records can be used as a baseline for comparison with contemporary resurveys (Vellend et al., 2013; Chytrý et al., 2014; Hédl et al., 2017). However, historical botanical studies are strongly biased towards vascular plants, with few data on bryophytes, due in part to the difficulty of identification (Gignac 2001; Möls et al. 2013; He et al. 2016; but see Bergamini et al., 2009; Delgado & Ederra, 2013; Becker-Scarpitta et al., 2017; Vanneste et al., 2017). This is despite the fact that bryophytes are major contributors to diversity and vegetation cover in many temperate and boreal ecosystems, playing an important role in ecosystem functions, such as biomass accumulation, water retention, nutrient cycling, and food web dynamics (Rydin, 2008; Tuba et al., 2011; Turetsky, 2003; Lindo & Gonzalez, 2010).

For several reasons we might expect vascular plants and bryophytes to show different responses to various sources of environmental change (Lee & La Roi, 1979; Möls et al., 2013; Bagella, 2014; Becker-Scarpitta et al., 2017; Vanneste et al., 2017). Compared to vascular plants, bryophytes are distinguished by their small size, high sensitivity to the moisture and chemistry of their immediate microenvironment (i.e., they are poikilohydric), lower temperature optima for growth, absence of roots and an efficient vascular system, type of reproduction and dispersal strategies (Glime, 2007). As such, it is not surprising that these two groups show some contrasted spatial patterns of diversity (Lalanne et al., 2008; Mateo et al., 2016). For instance, vascular plants show a clear latitudinal diversity gradient of decreasing species richness with increasing latitude, while this is not true for bryophytes, for which temperate latitudes are equally diverse as tropical latitudes (Geffert et al., 2013; Mateo et al., 2016). Some studies have also observed different patterns of community β-diversity (Lee & La Roi, 1979; Kraft et al., 2011; Mateo et al., 2016). For example, vascular plant communities often show higher β-diversity along elevation gradients than bryophytes, suggesting a broader tolerance of bryophyte species to temperature (Lee & La Roi, 1979; Vittoz et al., 2010; Glime, 2013; Vanneste et al., 2017). Overall, these considerations lead us to predict that bryophytes should show greater sensitivity than vascular plants to environmental changes such as nutrient deposition (given poikilohydry; see also Chapter 1), but lower sensitivity to climate warming (given broad species' climatic tolerances).

General predictions for the effects of warming on vascular plants include declines in the abundance of cold-adapted species, an upward expansion of elevational range limits for warm-adapted species (Rumpf et al., 2018), and an increase of local species richness (Vellend et al., 2017a). Compared to vascular plants, some studies have suggested that changes in bryophyte communities are more strongly influenced by stochastic processes or by micro-environmental variation than macro-environmental conditions (Pharo & Vitt, 2000; Raabe et al., 2010; Fenton & Bergeron, 2013). Because bryophytes have wider temperature affinities and higher affinity to micro-environment than macro-environment, we might expect bryophytes to show lower sensitivity to global warming than vascular plants. The consequences of warming for β-diversity are more difficult to predict given a paucity of studies on this topic (Socolar et al., 2016, but see Nascimbene & Spitale, 2017). It is though that species with high dispersal capacity will be favoured in areas experiencing strong environmental changes, in which case we might predict a decrease of β-diversity (Mouquet & Loreau, 2003) and thus biotic homogenization (Clavel et al., 2011).

As in many parts of the world, eastern Canada has shown a general warming trend over the past ~50 years, but with a strong east-west gradient in the magnitude of warming in the province of Québec (Yagouti et al. 2008, Appendix B-S1). Chapter 3 showed that the magnitude of temporal changes of vascular plant communities in three protected areas generally increased from east to west in southern Québec, with greater changes in areas of stronger warming in recent decades. For two of these three parks, the historical data also included bryophytes, thus presenting an opportunity to test for differential sensitivity among taxa to warming. Forillon National Park is located at the eastern tip of the province of Québec where warming has been negligible. In contrast, Mont-Mégantic Provincial Park is in central Québec were the warming trend has been steeper (Yagouti et al., 2008; Savage & Vellend, 2015).

Here we report one of the first studies comparing long-term change of bryophytes and vascular plants communities in sites with contrasting warming trends. In each of the two parks, we revisited ~50 legacy vegetation plots initially surveyed in the 1970s, applying the same methods as the original surveys. To minimize potentially confounding factors, plots were selected in mature forest ecosystems that have not experienced major natural or anthropogenic disturbances during the time between surveys. We had two main hypotheses: (**i**) For both taxa, the park with a stronger warming trend (Mont-Mégantic) has experienced greater long-term community changes than the park with a weaker warming trend (Forillon); (**ii**) Vascular plant communities are more sensitive than bryophyte communities to climate warming. For each taxon in each park, we quantified the magnitude of changes in (a) species' distributions along the elevation gradient, (b) species richness, and (c) community composition.

4.2.2. Methods

4.2.2.1. Study site

Our two study sites were Forillon National Park in eastern Québec and Mont-Mégantic Provincial Park in central Québec. Neither park has experienced logging or forest management over the last ~40 years. Forillon National Park is located on the east coast of Canada (48°54′N, 64°21′W), it was created in 1970 and covers 245 km^2; our study plots ranged in elevation from ~50 to 500 m a.s.l. The vegetation at Forillon is dominated by a mixture of northern tree species such as *Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss and *Betula papyrifera* Marsh. at higher elevations, and *Acer saccharum* Marsh. and *Betula alleghaniensis* Britt. at lower elevations (Majcen, 1981). Mont-Mégantic Provincial Park, in the Eastern Townships region of

Québec (45°27′N, 71°9′W), was created in 1994 (logging ceased in the 1960s prior to park planning) and covers ~55 km^2. Our study plots span an elevational gradient from ~460 and 1100 m a.s.l., along which the vegetation transitions from temperate deciduous forests dominated by *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh. and *Betula alleghaniensis* Britt., to boreal forest dominated by *Abies balsamea* (L.) Mill. and *Picea rubens* Sargent, Silva. (Marcotte & Grandtner, 1974).

4.2.2.2. *Data set*

Original vegetation surveys in both parks were conducted using phytosociological methods (Marcotte & Grandtner, 1974; Majcen, 1981). In each plot, authors listed all species in different strata (canopy trees, shrubs, herbs and ground bryophytes) and for each species assigned an abundance coefficient following Braun-Blanquet et al. (1952). For vascular plants, our analyses focused on shrubs and herbs, which were combined into a single "understorey" stratum. All bryophyte species were recorded that were found on the ground (i.e. organic litter and soil surface mineral layers, not including deadwood, tree trunks and rocks); these surveys did not involve intensive searches for individual stems of rare species within moss carpets (i.e., some locally rare species were missed). After consulting with botanists active in Québec in the 1960s and 1970s (C. Ansseau, Z. Majcen, personal communication), we are confident in comparing Braun-Blanquet indices across time for vascular plants (see Chapter 3) but not for bryophytes, given uncertainty in the definition of the area over which percent cover was evaluated (microhabitats vs. entire plots). To maximize comparability across time and taxa, we used presence-absence data for both vascular and bryophyte species in all statistical analyses.

Our approach to plot relocation is described in Chapter 3. In short, original survey plots were not permanently marked, although locations were reported in maps and/or tables, such that plots are considered "semi-permanent". In both parks, original surveyors sampled mature forests where spatial heterogeneity was relatively low, thus minimizing effects of plot relocation uncertainty. We selected plot locations for recent surveys using original plot maps and environmental descriptions (elevation, slope, aspect), and observations in the field to maximize the match of current and historical conditions. In Mont-Mégantic, recent surveys included all plots within the current park boundary. Not all plots in Forillon were accessible, and plot selection for the recent surveys used the following criteria: (i) plots occurred in forest, excluding swamps or bogs; (ii) plots were accessible via <3-4 hours hiking off of established trails; (iii) plots had not obviously experienced major natural disturbances (e.g., storm, fire, or insect outbreak); (iv) in the original survey the plots were sampled in mature stands that have since maintained forest cover (i.e., no early successional dynamics in the intervening period).

Original surveys in Forillon Park were conducted in June-September 1972 in 256 vegetation plots (500 m^2) (Majcen, 1981). We resurveyed 49 plots during July and August of 2015. Original surveys in Mont-Mégantic were conducted in 1970 in 94 plots, roughly half of which fall outside the current park boundaries. Plots were 400 m^2 in coniferous forest and 800 m^2 in broadleaved forests (Marcotte & Grandtner, 1974). We resurveyed the 48 plots falling within the current park limits at Mont-Mégantic for vascular plants in 2012 (see Chapter 3) and for bryophytes during June and July 2014 (reported in the present paper). We harmonized the taxonomy across both parks and periods (see below), so the Mont-Mégantic data are not precisely the same as reported in Savage & Vellend (2015), but they are exactly the same as in Chapter 3 except converted to presence-absence.

4.2.2.3. <u>Taxonomical database</u>

Our taxonomical reference was the Taxonomic Name Resolution Service v4.0 (assessed in Feb 2017: http://tnrs.iplantcollaborative.org) for vascular plants and Flore des bryophytes du Québec-Labrador (Faubert, 2012, 2013, 2014) for bryophytes.

Our data set was collected by four different survey teams: one for each of the two original surveys: Forillon: Majcen (1981); Mont-Mégantic: Marcotte & Grandtner (1974); one for the recent Mont-Mégantic vascular plant survey: Savage & Vellend (2015); and one for the recent Mont-Mégantic bryophyte survey and for the recent survey of both taxa at Forillon (A. Becker-Scarpitta and assistants). Most plants were identified to the species level in the same way across surveys, so for these taxa the only harmonization step was to standardize names. Coarser levels of taxonomic resolution were used in some but not all surveys for certain species (e.g., a pair of similar species not identified to the species level), and for other species (e.g., spring ephemeral plants) the timing of different surveys created doubt about the likelihood of comparable detection. In these situations, comparability was maximized by using the coarser level of resolution applied to all data sets, or by removing species (see Appendix C-S1 for details on taxonomic standardization). All specimens identified at the species level were deposited in the Marie-Victorin herbarium (Université de Montréal, Canada.) and all locations were entered into the GBIF database (GBIF - https://www.gbif.org/).

4.2.2.4. Statistical analysis

All statistical analyses were performed in R v.3.4.2 (R Foundation for Statistical Computing 2017). To test for upward elevational shifts in species distributions at Forillon and Mont-Mégantic, we calculated the mean elevation across all occurrences in each time period. We then conducted linear mixed effect models (LMM, function *lmer*, package 'lme4' v.1.1-14, Bates et al., 2015) testing the effect of time on mean elevation; the models were weighted by the sum species occurrences in each survey, and species was included as a random effect to account for the paired sampling structure of the data (each species observed in each time period).

To test for differences between taxa and parks in terms of the temporal change in plot-level species richness (α-diversity) we first calculated the log ratio, *ln*(original richness / recent richness), for each taxon-park combination, and ran an anova model with each combination of park and taxa as factors. Secondly, we explored separately the temporal trend of α-diversity of both bryophytes and vascular plants within parks using LMMs with time, elevation and the time*elevation interaction (if significant) as fixed effects and with plot ID as a random effect.

We then explored temporal change in β-diversity using two different frameworks. First, we assessed the multivariate homogeneity of group dispersions using an asymmetric binary Jaccard dissimilarity, with significance testing via permutation (PERMDISP, Anderson et al., 2006, function *betadisper*, package 'vegan' v.2.4-4). A decrease in the multivariate distance between plots and the time-specific centroid is interpreted as biotic homogenization, while an increase indicates biotic differentiation. Second, to explore the components of temporal change in species composition, we calculated the temporal pairwise β-diversity as the Jaccard dissimilarity between the recent and original surveys for each plot. Temporal β-diversity was decomposed into two components: turnover due to species replacements (T) and nestedness (N) (function *beta.temp*, package 'betapart'; Baselga 2012; Baselga & Leprieur 2015).

To examine changes in community composition over time, we used permutational analysis of variance (PERMANOVA, Anderson 2001) with Jaccard distances using 999 permutations (function *adonis*, package 'vegan'). We used the R^2 values from the PERMANOVA models as a quantification of the magnitude of temporal change in order to compare among parks. We used non-metric multidimensional scaling (nMDS) with Jaccard distances for visualization (function *metaMDS*, package 'vegan'). Within each park, we identified indicator species for each time period using the IndVal procedure (function *multipatt*, package 'indicspecies', De Cáceres et al., 2010).

4.2.3. Results

4.2.3.1. Species distributions along elevation gradients

Among the four taxa-park combinations, vascular plants at Mont-Mégantic was the only one showing a significant upward shift in mean species elevations over time (Table 4.1, Fig. 4.1). It is important to note that patterns in Fig. 4.1c-d are not exactly the same as those in Fig. 3.2a-b in Chapter 3 (vascular plants in the same two parks), given the use of the presence-absence data in this chapter. The variation among species in mean elevation is lower here (Fig. 4.1c-d) than it was with abundance data (Fig. 4.2a-b in Chapter 3), but the significant upward shift at Mont-Mégantic is qualitatively the same (Table 4.1).

Consistent with our hypothesis, we detected no elevational distribution shift for either vascular plants or bryophytes in Forillon (where the warming trend has weak), nor for bryophytes at

Mont-Mégantic. Despite the lack of trends in average elevation for bryophytes, there was substantial variation among species (less so than for vascular plants) (Table 4.2, Fig. 4.1). This observation is reflected in the strength of correlations between original and recent mean species elevations, which was lower for bryophytes (Forillon = Pearson *r* correlation = 0.327; Mont-Mégantic *r* = 0.577) than for vascular plants (Forillon *r* = 0.518; Mont-Mégantic *r* = 0.729). See Appendix C-S2 for mean elevations and sums of occurrences for each species in each survey.

Table 4.1 - Analyses of temporal changes in (a) average species elevation, (b) plot-level species richness (α-diversity) along elevational gradients, and (c) multivariate β-diversity along elevation gradients.

		Effect	F	df	Pr(>F)	R^2_m	R^2_c
a) Average species elevation (m)							
Forillon							
	Bryophytes	Time	0.12	36	0.73	<0.01	<0.01
	Vascular plants		0.01	31	0.92	<0.01	<0.01
Mégantic							
	Bryophytes	Time	0.16	25	0.69	<0.01	0.09
	Vascular plants		**8.54**	**55**	**0.005**	<0.01	0.18
b) Species richness (α-diversity)							
Forillon							
	Bryophytes						
		Time	2.42	46	0.13	0.04	0.05
		Elevation	1.77	45	0.19		
	Vascular plants						
		Time	3.19	47	0.08	0.04	0.41
		Elevation	1.26	46	0.27		
Mégantic							
	Bryophytes						
		Time	0.01	46	0.92	0.01	0.32
		Elevation	0.85	45	0.36		
	Vascular plants						
		Time	26.77	47	**<0.001**	0.54	0.74
		Elevation	68.14	46	**<0.001**		
c) Heterogeneity (*β*-diversity)							
Forillon							
	Bryophytes						
		Time	7.14	45	**0.002**	0.17	0.26
		Elevation	10.75	46	**0.01**		
	Vascular plants						
		Time	0.92	47	0.27	0.02	0.51
		Elevation	1.25	46	0.34		
Mégantic							
	Bryophytes						
		Time	0.72	45	0.40	0.16	0.39
		Elevation	13.76	46	**<0.001**		
	Vascular plants						
		Time	22.30	46	**<0.001**	0.28	0.63
		Elevation	17.08	47	**<0.001**		

For (a) and (b), results are shown for linear mixed models; in (a) species were weighted by the sum of occurrences across both original and recent surveys. In (c), beta diversity was measured as the distance of plots to time-specific centroids (space defined by Jaccard dissimilarities) and modeled using PERMIDSP. R^2m is the marginal coefficient of determination, measuring the proportion of variance explained by fixed effects; R^2c is the conditional coefficient of determination, giving the proportion of variance explained by both fixed and random effects.

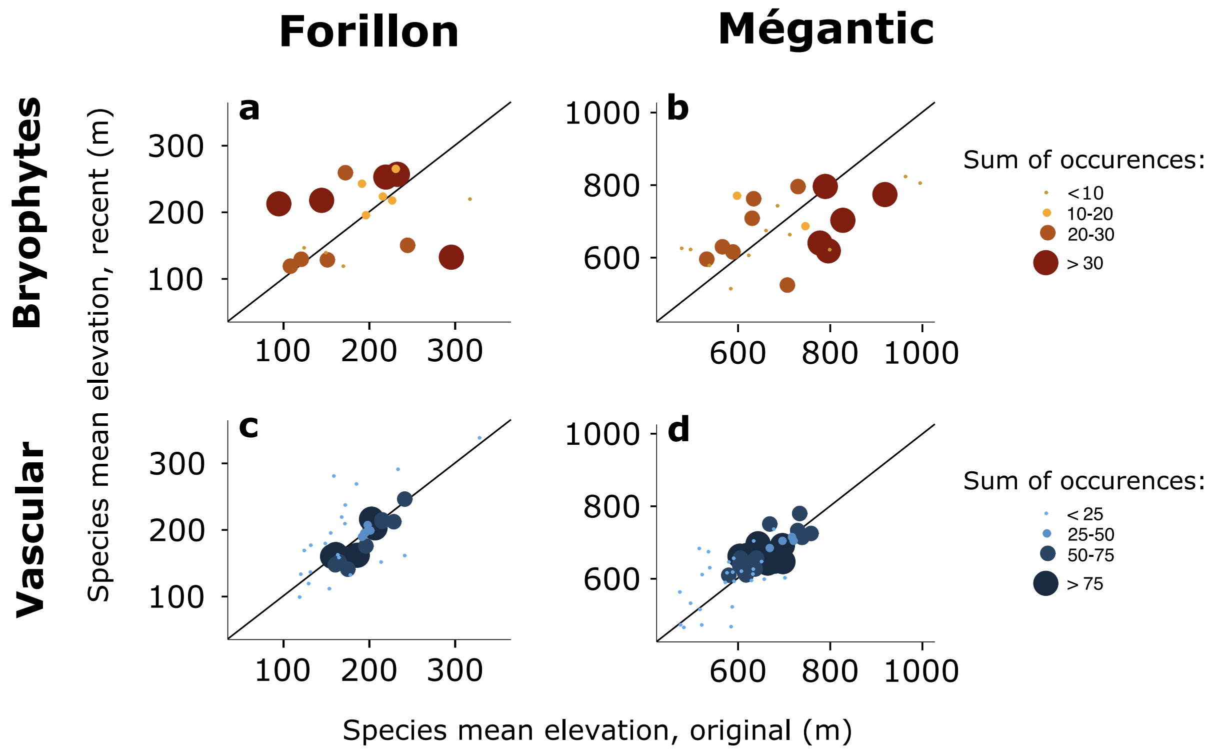


Figure 4.1 - Species distributions along elevation gradients in two-time periods. a) Bryophytes in Park Forillon (n = 19 species); b) Bryophytes at Mont-Mégantic (n = 25 species); c) Vascular plants in Park Forillon (n = 42 species); d) Vascular plants at Mont-Mégantic (n = 64 species).

All species present in both original and recent surveys were included; the size of each point is proportional to the number of occurrences summed across the two survey years for a given species. Diagonals indicate 1:1 lines.

4.2.3.2. Temporal changes in species richness

At Forillon, the total number of bryophyte species across plots was greater in the recent survey (57 species) than in the original survey (42 species); 15 species from the original survey were not found while 30 new species were observed (Table 4.2 and Appendix C-S2 for species occurrences). Conversely, the total number of vascular plants at Forillon declined over time (original survey = 83 vs. recent = 65 species), with 27 original species not found in the recent survey and 9 new species added (Table 4.2).

At Mont-Mégantic we found similar trends between vascular plants and bryophytes. In the recent survey, there was an increase in the overall number of bryophytes species (original survey = 46 vs. recent = 55 species), with 16 species lost and 25 gained. The total number of vascular plant species also increased (from 87 species to 92 species), with 8 species lost and13 gained.

Overall, the only strong significant temporal change detected in mean plot-level species richness was an increase for vascular plants at Mont-Mégantic (mean log ratio of species richness = 0.3; 95% CI [0.16, 0.44]; $t = 4.40$; $df = 47$; $p<0.001$), where richness also declined with elevation (Fig. 4.2d, Table 4.1; see also Chapter 3). For vascular plants at Forillon and for bryophytes in both parks, species richness at the plot level showed neither changes over time nor any relationship with elevation (Table 4.1, Fig. 4.2 a-b-c).

Table 4.2 - Temporal changes in total species numbers, plot-level species richness (α-diversity) and mean species elevation for bryophytes and vascular plants in Forillon Park and Mont-Mégantic Park.

		Total species number					α-diversity			Mean species elevation		
		Original	Recent	Shared	Lost	Gained	Original	Recent	n plot	Original	Recent	n sp
Forillon												
	Bryophytes	42	57	27	15	30	5.4 ± 0.5	6.3 ± 0.4	47	208.8±9.5	204±9.8	19
	Vascular plants	83	65	56	27	9	18.2 ± 1	16.4 ± 1	48	186.3±5.5	186.8±5.6	42
Mégantic												
	Bryophytes	46	55	30	16	25	5.6 ± 0.4	5.5 ± 0.4	47	702.5±21.2	702.5±21.2	25
	Vascular plants	87	92	79	8	13	**21.2 ± 1**	**27 ± 1**	48	**629.2±7.3**	**642.5±7.1**	64

The total number of species observed across all plots is divided into shared, lost, or gained species between the original and recent surveys. For plot-level richness and mean species elevation, mean ± SE are reported. Bold value indicates significant statistical differences ($p < 0.05$, see Table 4.1 for statistical tests). Temporal changes in total species number was not tested statistically.

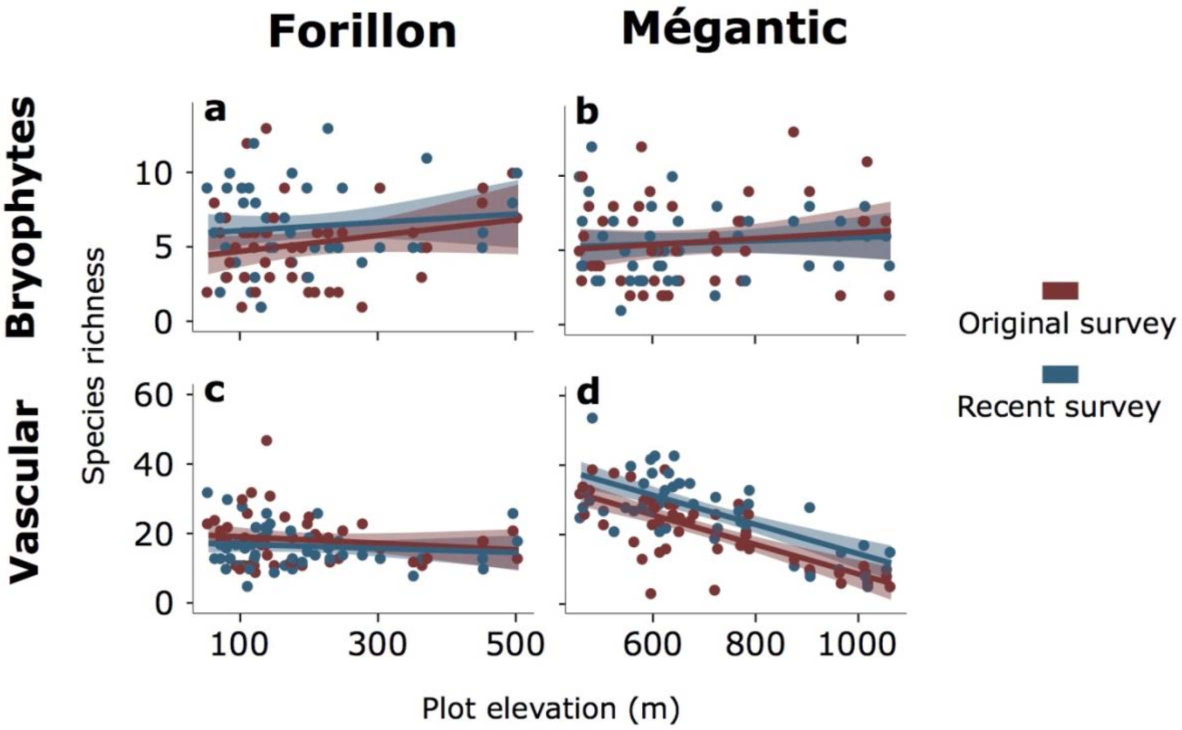


Figure 4.2 - Temporal changes of plot-level species richness (α-diversity) along elevation gradients. The only significant increase of α-diversity over time was for vascular plants in Mont-Mégantic (panel d; see also Table 4.1).

4.2.3.3. Temporal shift in community composition and heterogeneity

Consistent with our hypotheses, we found significant temporal changes in vascular plant β-diversity and community composition at Mont-Mégantic (Figs. 4.3 & 4.4, Table 4.3), where climate warming has been pronounced, as previously reported (Chapter 3). However, we found unexpected results for bryophytes: a significant increase of multivariate dispersion (β-diversity) over the past 40 years at Forillon but not at Mont-Mégantic (Table 4.3, Fig. 4.3). The observed increase in the distance of plots from multivariate centroids at Forillon was consistent along the whole elevation gradient (Table 4.1, Fig. 4.4). The decomposition of the temporal changes in bryophyte community composition showed a greater contribution of turnover (Forillon = 0.7, Mont-Mégantic = 0.86) than nestedness (Forillon = 0.11, Mont-Mégantic = 0.03, Table 4.3).

For vascular plants at Mont-Mégantic but not at Forillon we found a significant decrease of β-diversity over time, consistent along the elevational gradient (Table 4.3, Fig. 4.3 & 4.4). Turnover was also the main driver of temporal community change for vascular plants (Table 4.3).

Table 4.3 - Temporal changes in β-diversity and community composition between original and recent surveys for vascular plants and bryophytes in Forillon Park and Mont-Mégantic Park.

		Multivariate dispersion				β-diversity			Community composition		
		Original	Recent	F	Pr(<F)	βj	T	N	R2	F	Pr(<F)
Forillon											
	Bryophytes	0.54	0.59	4.32	**0.04**	0.81	0.70	0.11	0.07	6.57	**<0.001**
	Vascular plants	0.45	0.44	0.55	0.47	0.52	0.37	0.16	0.02	1.74	0.05
Mégantic											
	Bryophytes	0.62	0.61	0.44	0.52	0.90	0.86	0.03	0.07	7.02	**<0.001**
	Vascular plants	0.50	0.44	9.23	**0.003**	0.54	0.39	0.16	0.04	0.43	**0.002**

Multivariate dispersion was calculated (based on Jaccard's dissimilarity) as the mean distance of plots to time-specific centroids and analyzed using PERMDISP. Temporal β-diversity (βj) was calculated as the pairwise Jaccard's dissimilarity between the recent and original survey and decomposed into components of turnover (T) and nestedness (N). Changes in community composition were analyzed using PERMANOVA. R2 is the proportion of variation in community composition explained by time. Statistical significance levels were calculated with 999 permutations.

In terms of bryophyte indicator species, *Dicranum fuscescens* was associated with original surveys for both parks, while *Dicranum polysetum* was associated with the two recent surveys (Table 4.4). Other indicator bryophytes for either time period were unique to one or the other park. For vascular plants, recent surveys were associated with two of only three non-native species in the data set: *Galeopsis tetrahit* (Mont-Mégantic) and *Epipactis helleborine* (both parks) (Table 4.4). Recent surveys at Mont-Mégantic were also associated with two species of *Carex* and the fern *Dennstaedtia punctilobula.*

For both sites and taxa, we found significant temporal shifts in community composition (Figs. 4.3 & 4.4, Table 4.3), although the effect was substantially weaker for vascular plants at Forillon ($p = 0.05$) than for the other three analyses ($p \leq 0.002$). As predicted, the magnitude of the vascular plant compositional shift was greater for Mont-Mégantic ($R^2 = 4\%$) than Forillon ($R^2 = 2\%$, Table 4.3). However, bryophyte communities experienced an equal magnitude of compositional shift for both Forillon and Mont-Mégantic ($R^2 = 7\%$). Moreover, compositional shifts were greater for bryophytes than for vascular plants at both sites, contrary to our hypothesis (Table 4.3, Fig. 4.3).

Table 4.4 - Indicator species of bryophytes and vascular plants associated with original and recent surveys at Forillon and Mont-Mégantic.

		Bryophytes	Vascular plants
Forillon			
	Original	*Dicranum fuscescens*	*Lycopodium annotinum* *Galium triflorum*
	Recent	*Dicranum montanum* *Dicranum polysetum* *Brachythecium campestre* *Pseudoleskeella tectorum*	*Gymnocarpium disjunctum* *Sambucus racemosa* *Epipactis helleborine*
Mégantic			
	Original	*Brotherella recurvans* *Dicranum fuscescens* *Paraleucobryum longifolium* *Hypnum pallescens* *Bryhnia novae-angliae* *Brachythecium reflexum*	*Osmunda claytoniana* *Botrychium virginianum*
	Recent	*Atrichum altecristatum* *Hylocomiastrum umbratum* *Dicranum polysetum* *Hypnum curvifolium*	*Dennstaedtia punctilobula* *Carex arctata* *Carex deweyana* *Circaea alpina* *Galeopsis tetrahit* *Epipactis helleborine*

Indicator values were considered significant if $p<0.05$ (calculated with 999 permutations).

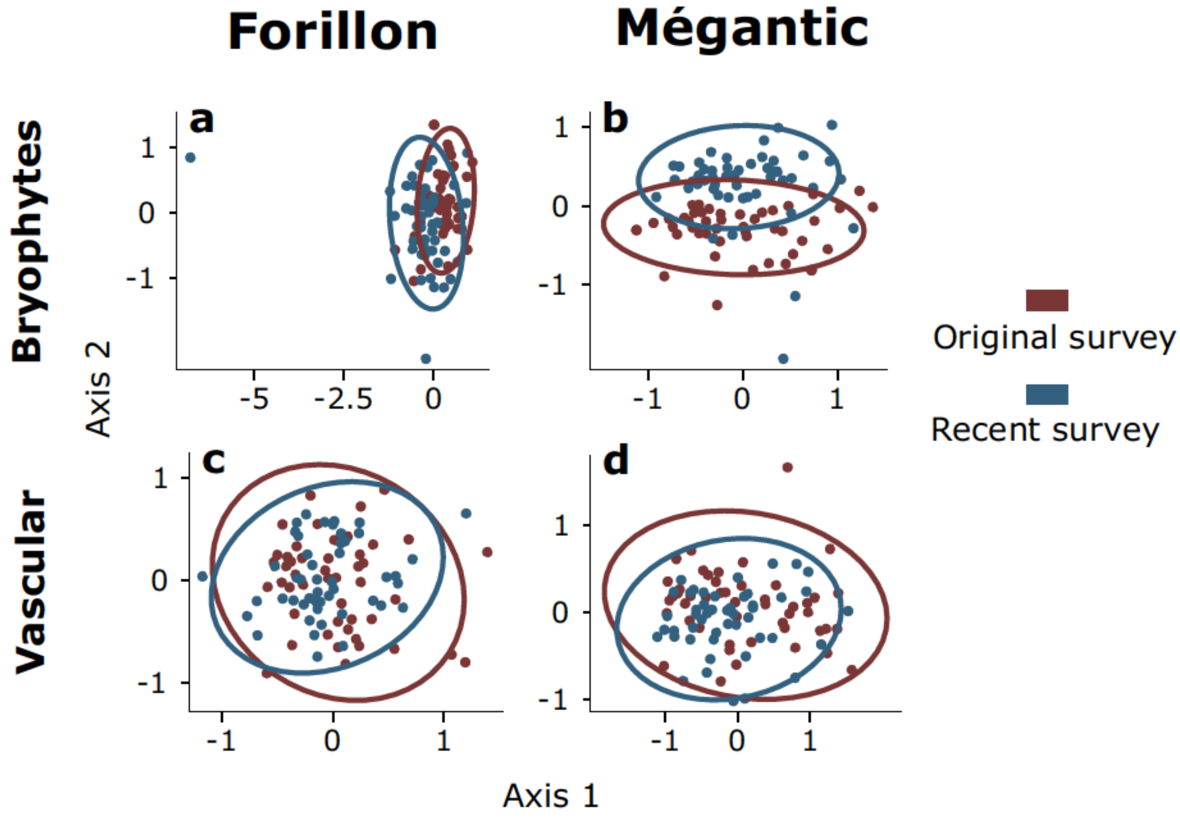


Figure 4.3 - nMDS ordinations (based on Jaccard's dissimilarity) of vascular plant and bryophyte communities across time in Forillon Park and Mont-Mégantic Park.

In panel (a), the left-most plot was composed of a unique species very rare elsewhere; PERMDISP and PERMANOVA results were qualitatively similar with and without this plot.

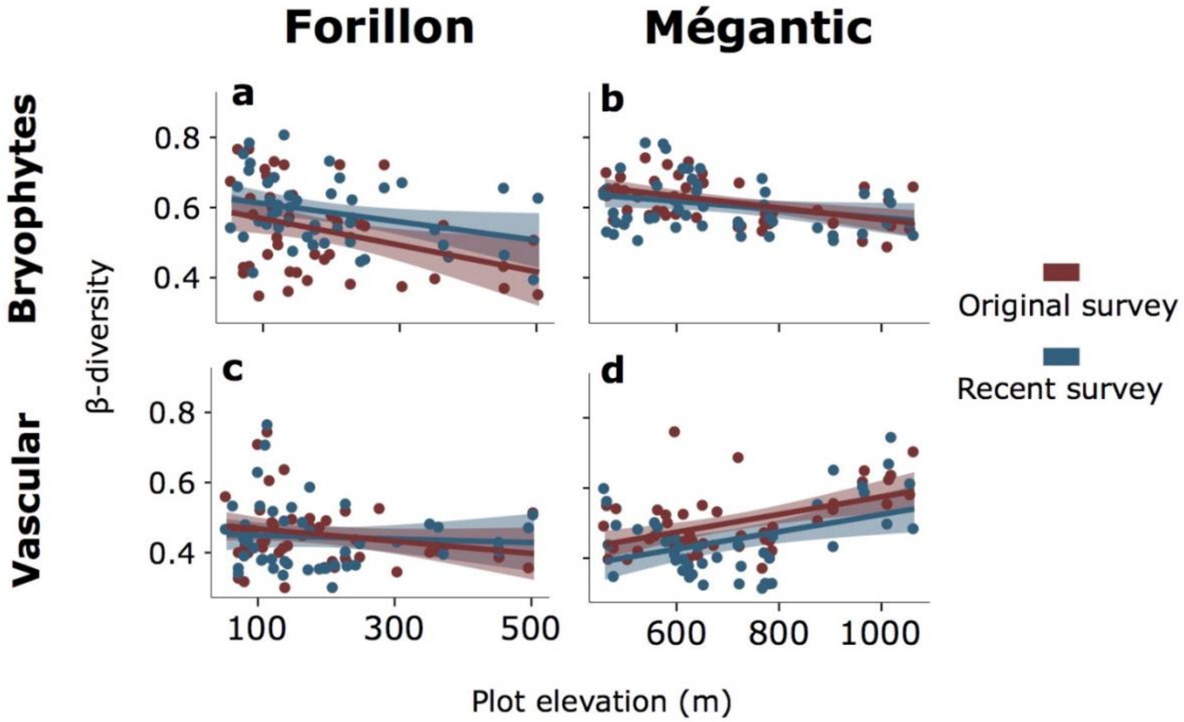


Figure 4.4 - Temporal changes of β-diversity along elevational gradients for bryophytes (a-b) and vascular plant communities (c-d) at Forillon and Mont-Mégantic.

β -diversity is here calculated for each plot as the multivariate distance to time-specific centroibds (Jaccard's dissimilarity; see Table 4.1 for statistical analyses).

4.2.4. Discussion

Most long-term legacy studies have been conducted on vascular plant communities (Verheyen et al., 2017), so it remains unknown whether bryophytes show similar or different responses to the same environmental changes. More broadly, we have limited knowledge of how different taxonomic groups respond to long-term environmental change. Thanks to an extensive resurveying of plots with legacy data we quantified community changes over ~40 years for both bryophytes and vascular plants in two natural protected areas in eastern Canada with contrasting recent warming trends. The vascular plant data for these two parks were reported in Chapter 3 and transformed to presence-absence in the present study to ensure comparability with the bryophyte data over time. Temporal changes in vascular plant communities were consistent with the warming hypothesis, but this was not the case for bryophytes. We also did not find clear support for the hypothesis that vascular plants would show greater sensitivity to environmental change (assumed to be dominated by climate warming at Mont-Mégantic), with results depending on the metric of community change. As predicted for the area with a strong warming trend (Mont-Mégantic), we found a significant upward shift of vascular plant distributions but no change for bryophyte distributions (Table 4.1, Fig. 4.1). However, the higher magnitude of changes in bryophyte community composition at both sites was contrary to our prediction (Table 4.3, Fig. 4.3).

4.2.4.1. Patterns along the gradient of warming trends

Consistent with the abundance-based results in Chapter 3, for vascular plants we found support for the hypothesis that areas with greater warming should experience stronger community changes than areas with weaker warming trends. At Mont-Mégantic, where the warming trend has been strongest, we found a clear pattern for vascular plants of upward shifts in elevational distributions (Table 4.1, Fig. 4.1), a significant increase of α-diversity (Table 4.1 & 4.2, Fig. 4.2), a stronger shift in community composition than in Forillon (Table 4.3, Fig. 4.3) and a significant decrease of β-diversity (Table 4.3, Fig. 4.4). At Forillon, where the warming trend has been weaker, we found neither shifts in elevational distributions nor changes of α-diversity for either vascular plants or bryophytes (Table 4.1 & 4.2, Fig. 4.1 & 4.2). The upward shift in elevation of vascular plants in response to warming is in line with many other studies (Lenoir et al., 2008; Bertrand et al., 2011; Chen et al., 2011). The temporal increase of diversity of vascular plant in Mont-Mégantic is also coherent with the prediction that warming should lead to increased local diversity in areas without severe moisture stress (Vellend et al., 2017a).

Our results suggest that a temperature increase of 1-2 °C does not have as strong an impact on the local diversity and distributions of bryophytes as it does for vascular plants. This interpretation is also supported by the absence of any relationship between bryophyte richness and elevation in the two parks (Table 4.1, Fig. 4.2; Bruun et al., 2006; Grytnes et al., 2006;

Odland et al., 2014, but see Vittoz et al., 2010). The decrease of β-diversity over time for vascular plants at Mont-Mégantic supports the hypothesis that warming might cause biotic homogenization (Urban, 2015; Socolar et al., 2016). Note that this result using presence-absence data was different to the result in Chapter 3 using untransformed abundance data (no homogenization), but similar to the finding of homogenization using fourth-root transformed abundances in Savage and Vellend (2015). These results collectively illustrate that the locally dominant species – whose influence is minimized or eliminated via fourth-root or presence-absence transformation – can mask homogenization created by species of lower abundance.

4.2.4.2. Sensitivity of bryophytes vs. vascular plants

We cannot draw strong conclusions about which of bryophytes or vascular plants is more or less sensitive to environmental change in southern Québec: results depended on which community property was being investigated. Vascular plants showed more prominent upward elevational distribution shifts and richness increases (Table 4.1 & 4.2, Fig. 4.1 & 4.2) while bryophytes experienced stronger shifts in community composition and no difference in the magnitude of compositional changes between the two parks with contrasting warming trends (Table 4.3, Fig. 4.3).

The lack of directional shifts in bryophytes' elevational distributions at either site (Table 4.1, Fig. 4.1) is coherent with other results showing that bryophyte species have broader elevation ranges – and therefore presumably reduced sensitivity to temperature change – compared to vascular plants (Lee & La Roi, 1979; Vittoz et al., 2010; Vanneste et al., 2017). This may be due to the ability of bryophytes to photosynthesize under larger ranges of temperature than vascular plants (Glime, 2013) and their frequent occurrence in microhabitats (e.g., defined by micro-topography) buffered from macro-environmental changes (Raabe et al., 2010). The decrease of bryophyte β-diversity with elevation in both parks (Table 4.1, Fig. 4.4) suggests that bryophyte species found at high elevation (i.e. in boreal forests) tend to be common along the entire gradient, while low elevation sites have some species absent from high elevations (Slack, 1977; Lee & La Roi, 1979).

4.2.4.3. Potential non-climatic drivers of vegetation change

Our sites were chosen specifically due to their contrasting warming trends and lack of other obvious major drivers of vegetation change, but there are certainly other possible drivers of ecological change that might play a role in this region. Among the indicator species of recent surveys, two were non-native: *Galeopsis tetrahit* and *Epipactis helleborine*, the latter of which has increased considerably in recent decades throughout its North American range, even in western Canada (Marie-Victorin, 1997; McCune & Vellend, 2013). As such, some vegetation changes might be due simply to protracted periods of non-native species expansions, regardless of local environmental change. Another potential factor is changes in white-tailed deer browsing, which has increased over the past century in much of North America (Côté et al., 2004). The indicator species of the recent survey at Mont-Mégantic include species known to benefit from high levels of deer browsing: *Dennstaedtia punctilobula* and *Carex* spp. (de la Cretaz & Kelty, 2002; Augustine & Decalesta, 2003; Rooney, 2009; Frerker et al., 2014). Interestingly, at Forillon deer are actually thought to have decreased in abundance due to the expansion of the coyote population in the 1970s (UQCN, 2005), and we found no such species associated with recent surveys in Forillon Park.

Our most difficult result to interpret was the strong species turnover of bryophyte communities at Forillon, which has not experienced strong long-term trends in temperature, precipitation, or atmospheric nutrient deposition (Commission Joint International, 2014; Hember, 2018). We can only speculate and present hypotheses about potential non-climatic drivers of bryophyte community change. First, as in all legacy studies, there is the potential for observer biases due to (i) different sampling effort between original and recent surveys, or (ii) species' identification errors. It seems highly likely that detection probabilities and the potential for identification errors are greater for bryophytes than for vascular plants, although we have no reason to suspect this caused systematic increases or decreases of particular species frequencies (necessary to explain overall compositional shifts). We paid very close attention to repeating the original survey methods, focusing on the visually obvious species in a given microsite (i.e., not examining each individual moss stem closely on the field), and the lack of any difference over time in local richness (Fig. 4.2a-b) suggests comparable species' detection abilities in the two surveys. Although we cannot exclude the possibility that a real richness change was cancelled out by a change in survey effort, we have no reason to suspect this rather unlikely coincidence. Given uncertainty in the comparability of abundance estimates across time for bryophytes, we also decided to use presence-absence data. In short, changes in observer effort seem highly unlikely to account for the temporal change in species composition. Furthermore, our taxonomical homogenization procedure was quite conservative in order to reduce bias due to misidentifications.

One potential hypothesis to explain compositional change over time in bryophyte communities relates to the history of park protection. Forillon Park was established (and so protected) only two years before the original survey was conducted, and parts of the park previously included homesteads (i.e., non-forest land uses). Mont-Mégantic was established as a park more recently (1994), but logging activities (the only prominent land use) ceased ~15 years before the original survey. Although plot selection focused only on non-disturbed forests, metacommunity dynamics involving dispersal of species from sites undergoing rapid succession may have caused local shifts in composition and increased β-diversity. It was previously show that managed forests tend to have a lower β-diversity than protected forests (Kaufmann et al., 2017). The increase in bryophytes β-diversity might partially be due to the recovery of natural forest that occurring in the 1970s.

There is also the possibility that changes in bryophyte communities resulted from interactions with changing vascular plant communities. Studies have shown that bryophyte diversity and abundance can be negatively correlated with total vascular plant biomass (Virtanen et al., 2017), cover (Jiang et al., 2015) or abundances (Jägerbrand et al., 2012). While we have documented an increase of vascular plant species richness at Mont-Mégantic (Table 4.1 & 4.2, Fig. 4.2), we do not have data on vascular plant biomass. If bryophytes are highly sensitive to vascular plant community properties, subtle changes for vascular plants could translate into larger changes in bryophyte communities. This hypothesis is open to testing via observational and experimental studies of the effect of vascular plants on bryophytes communities under warming or other environmental changes. Understanding temporal changes in one component of the community may require more consideration of interactions with other components (Chesson, 2000; HilleRisLambers et al., 2012).

4.2.4.4. *Conservation implications*

Overall, we found a significant temporal shift in the composition of both taxa in both parks but only one significant change in α-diversity. Our results are in accordance with recent meta-analyses and syntheses showing that local diversity can remain unchanged (or increase or decrease with equal likelihood) despite strong changes in composition (Dornelas et al., 2014; Gotelli et al., 2017; Spaak et al., 2017; Vellend et al., 2017b; Magurran et al., 2018). Finally, regardless of whether one taxon is systematically more or less sensitive to environmental change than another, our results suggest that one taxon (e.g., vascular plants) cannot be used as a surrogate for others (e.g., bryophytes) in terms of predicting the nature and magnitude of responses to environmental change (Bagella, 2014; Becker-Scarpitta et al., 2017). In the same plots that experienced the same environmental changes, we found that communities of bryophytes and vascular plants did not predictably change in the same ways (Slack, 1977; Lalanne et al., 2008; Bagella, 2014; Odland et al., 2014; Becker-Scarpitta et al., 2017). Thus, to assess overall biodiversity responses to global change data from different taxonomical groups and community properties need to be synthesized.

4.2.5. References

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26, 32–46.

Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9, 683–693.

Augustine DJ, Decalesta D (2003) Defining deer overabundance and threats to forest communities: From individual plants to landscape structure. Écoscience, 10, 472–486.

Bagella S (2014) Does cross-taxon analysis show similarity in diversity patterns between vascular plants and bryophytes? Some answers from a literature review. Comptes Rendus Biologies, 337, 276–282.

Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography, 21, 1223–1232.

Baselga A, Leprieur F (2015) Comparing methods to separate components of beta diversity. Methods in Ecology and Evolution, 6, 1069–1079.

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67, 1–48.

Becker-Scarpitta A, Bardat J, Lalanne A, Vellend M (2017) Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming. Journal of Vegetation Science, 28, 1220–1229.

Bergamini A, Ungricht S, Hofmann H (2009) An elevational shift of cryophilous bryophytes in the last century - an effect of climate warming? Diversity and Distributions, 15, 871–879.

Bertrand R, Lenoir J, Piedallu C et al. (2011) Changes in plant community composition lag behind climate warming in lowland forests. Nature, 479, 517–520.

Braun-Blanquet J, Roussine N, Nègre R (1952) Les Groupements Végétaux de la France Méditerranéenne, CNRS edn (ed CNRS). Toulouse, 1-297 pp.

Bruun HH, Moen J, Virtanen R, Grytnes J, Oksanen L, Angerbjörn A (2006) Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. Journal of Vegetation Science, 17, 37–46.

De Cáceres M, Legendre P, Moretti M (2010) Improving indicator species analysis by combining groups of sites. Oikos, 119, 1674–1684.

Chen I, Hill JK, Ohlemuller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science, 333, 1024–1026.

Chesson P (2000) Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31, 343–366.

Chytrý M, Tichý L, Hennekens SM, Schaminée JHJ (2014) Assessing vegetation change using vegetation-plot databases: a risky business. Applied Vegetation Science, 17, 32–41.

Clavel J, Julliard R, Devictor V (2011) Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in Ecology and the Environment, 9, 222–228.

Commission Joint International (2014) Canada - United States, Air quality agreement - progress report. 62 pp.

Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM (2004) Ecological impacts of Deer overabundance. Annual Review of Ecology, Evolution, and Systematics, 35, 113–147.

Delgado V, Ederra A (2013) Long-term changes (1982–2010) in the bryodiversity of Spanish beech forests assessed by means of Ellenberg indicator values of temperature, nitrogen, light and pH. Biological Conservation, 157, 99–107.

Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE (2014) Assemblage time series reveal biodiversity change but not systematic loss. Science, 344, 296–299.

Faubert, J (2012) Flore des bryophytes du Québec-Labrador, Vol. 1, Anthocérotes et hépatiques. Société québécoise de bryologie, Saint-Valérien, Québec, 356 pp.

Faubert, J (2013) Flore des bryophytes du Québec-Labrador, Vol. 2, Mousses, première partie. Société québécoise de bryologie, Saint-Valérien, Québec, 402 pp.

Faubert, J (2014) Flore des bryophytes du Québec-Labrador, Vol. 3, Mousses, seconde partie. Société québécoise de bryologie, Saint-Valérien, Québec, 456 pp.

Fenton NJ, Bergeron Y (2013) Stochastic processes dominate during boreal bryophyte community assembly. Ecology, 94, 1993–2006.

Frerker K, Sabo A, Waller D (2014) Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. PLoS ONE, 9, e115843.

Geffert JL, Frahm JP, Barthlott W, Mutke J (2013) Global moss diversity: spatial and taxonomic patterns of species richness. Journal of Bryology, 35, 1–11.

Gignac LD (2001) Bryophytes as indicators of climate change. The Bryologist, 104, 410–420.

Glime JM (2007) Bryophyte Ecology. Volume 1. Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists.

Glime JM (2013) Life cycles: surviving change, Chap 2.2. In Bryophyte Ecology. Vol. 1 Physiology and Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists.

Gotelli NJ, Shimadzu H, Dornelas M, McGill B, Moyes F, Magurran AE (2017) Community-level regulation of temporal trends in biodiversity. Science Advances, 3, e1700315.

Grytnes JA, Heegaard E, Ihlen PG (2006) Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. Acta Oecologica, 29, 241–246.

He X, He KS, Hyvönen J (2016) Will bryophytes survive in a warming world? Perspectives in Plant Ecology, Evolution and Systematics, 19, 49–60.

Hédl R, Bernhardt-Römermann M, Grytnes J-A, Jurasinski G, Ewald J (2017) Resurvey of historical vegetation plots: a tool for understanding long-term dynamics of plant communities. Applied Vegetation Science, 20, 161–163.

Hember RA (2018) Spatially and temporally continuous estimates of annual total nitrogen deposition over North America, 1860–2013. Data in Brief, 17, 134–140.

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics, 43, 227–248.

Hudson JMG, Henry GHR (2010) High Arctic plant community resists 15 years of experimental warming. Journal of Ecology, 98, 1035–1041.

Jägerbrand AK, Kudo G, Alatalo JM, Molau U (2012) Effects of neighboring vascular plants on the abundance of bryophytes in different vegetation types. Polar Science, 6, 200–208.

Jiang Y, Liu X, Song S, Yu Z, Shao X (2015) Diversity and distribution of ground bryophytes in broadleaved forests in Mabian Dafengding National Nature Reserve, Sichuan, China. Acta Ecologica Sinica, 35, 13–19.

Kaufmann S, Hauck M, Leuschner C (2017) Comparing the plant diversity of paired beech primeval and production forests: Management reduces cryptogam, but not vascular plant species richness. Forest Ecology and Management, 400, 58–67.

von Konrat M, Hagborg A, Söderström L et al. (2008) Early land plants today: global patterns of liverwort diversity, distribution, and floristic knowlege. In: Bryology in the New Millennium (eds Mohamed H, Baki B, Nasrulhaq-Boyce A, Pky L), pp. 425–438. University of Malaya, Kuala Lumpur.

Kraft NJB, Comita LS, Chase JM et al. (2011) Disentangling the drivers of diversity along latitudinal and elevational gradients. Science, 333, 1755–1758.

de la Cretaz AL, Kelty MJ (2002) Development of tree regeneration in fern-dominated forest understories after reduction of Deer browsing. Restoration Ecology, 10, 416–426.

Lalanne A, Bardat J, Lalanne-Amara F, Gautrot T, Ponge J-F (2008) Opposite responses of vascular plant and moss communities to changes in humus form, as expressed by the Humus Index. Journal of Vegetation Science, 19, 645–652.

Lee TD, La Roi GH (1979) Bryophyte and understory vascular plant beta diversity in relation to moisture and elevation gradients. Vegetatio, 40, 29–38.

Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science, 320, 1768–1771.

Lindo Z, Gonzalez A (2010) The bryosphere: An integral and influential component of the Earth’s biosphere. Ecosystems, 13, 612–627.

Magurran AE, Deacon AE, Moyes F, Shimadzu H, Dornelas M, Phillip DAT, Ramnarine IW (2018) Divergent biodiversity change within ecosystems. Proceedings of the National Academy of Sciences, 115, 1843–1847.

Majcen Z (1981) Les forets du parc national Forillon, Gaspésie, Québec, étude phytosociologique. Université de Laval, 158 pp.

Marcotte G, Grandtner M (1974) Étude écologique de la végétsation forestière du Mont Mégantic. Université de Laval, 156 pp.

Marie-Victorin F (1997) Flore laurentienne. Troisième édition mise à jour et annotée par L. Brouillet, SG Hay, I. Goulet, M. Blondeau, J. Cayouette et J. Labrecque. Les Presses de l’Université de Montréal, Montréal, Canada, 1030 pp.

Mateo RG, Broennimann O, Normand S et al. (2016) The mossy north: an inverse latitudinal diversity gradient in European bryophytes. Scientific Reports, 6, 25546.

McCune JL, Vellend M (2013) Gains in native species promote biotic homogenization over four decades in a human-dominated landscape. Journal of Ecology, 101, 1542–1551.

McGill BJ, Dornelas M, Gotelli NJ, Magurran AE (2015) Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology & Evolution, 30, 104–113.

Möls T, Vellak K, Vellak A, Ingerpuu N (2013) Global gradients in moss and vascular plant diversity. Biodiversity and Conservation, 22, 1537–1551.

Mouquet N, Loreau M (2003) Community patterns in source-sink metacommunities. The American Naturalist, 162, 544–557.

Nascimbene J, Spitale D (2017) Patterns of beta-diversity along elevational gradients inform epiphyte conservation in alpine forests under a climate change scenario. Biological Conservation, 216, 26–32.

Odland A, Reinhardt S, Pedersen A (2014) Differences in richness of vascular plants, mosses, and liverworts in southern Norwegian alpine vegetation. Plant Ecology & Diversity, 0, 1–11.

Pauli H, Gottfried M, Dullinger S et al. (2012) Recent plant diversity changes on Europe’s mountain summits. Science, 336, 353–355.

Pharo EJ, Vitt DH (2000) Local variation in bryophyte and macro-lichen cover and density in diversity in montane forests of western Canada. The Bryologist, 103, 455–466.

Raabe S, Müller J, Manthey M et al. (2010) Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. Forest Ecology and Management, 260, 1956–1964.

Rooney TP (2009) High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology, 202, 103–111.

Rumpf SB, Hülber K, Klonner G et al. (2018) Range dynamics of mountain plants decrease with elevation. Proceedings of the National Academy of Sciences, 115, 1848–1853.

Rydin H (2008) Population and community ecology of bryophytes. In: Bryophyte Biology, pp. 393–444. Cambridge University Press.

Savage J, Vellend M (2015) Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. Ecography, 38, 546–555.

Slack NG (1977) Species diversity and community structure in bryophytes: New York State studies. New York State Museum, The University of the State of New York, 70 pp.

Socolar J, Gilroy J, Kunin W, Edwards D (2016) How should beta-diversity inform biodiversity conservation? Trends in Ecology & Evolution, 31, 67–80.

Spaak JW, Baert JM, Baird DJ et al. (2017) Shifts of community composition and population density substantially affect ecosystem function despite invariant richness. Ecology Letters, 20, 1315–1324.

Stockli V, Wipf S, Nilsson C, Rixen C (2012) Using historical plant surveys to track biodiversity on mountain summits. Plant Ecology and Diversity, 4, 415–425.

Tuba Z, Slack NG, Stark LR (2011) Bryophyte ecology and climate change. Cambridge University Press., Cambridge, 506 pp.

Turetsky MR (2003) The role of Bryophytes in carbon and nitrogen cycling. The Bryologist, 106, 395–409.

UQCN (2005) Rapport de synthèse - Parc National de Forillon. Importance et impacts des pressions périphériques sur le maintien de l'intégrité écologique des aires protégées au Québec. Québec.

Urban MC (2015) Accelerating extinction risk from climate change. Science, 348, 571–573.

Vanneste T, Michelsen O, Graae BJ, Kyrkjeeide MO, Hassel K, Lindmo S, Frenne P De (2017) Impact of climate change on alpine vegetation of mountain summits in Norway. Ecological Research, 32, 579–593.

Vellend M, Brown CD, Kharouba HM, McCune JL, Myers-Smith IH (2013) Historical ecology: Using unconventional data sources to test for effects of global environmental change. American Journal of Botany, 100, 1294–1305.

Vellend M, Baeten L, Becker-Scarpitta A et al. (2017a) Plant biodiversity change across scales during the anthropocene. Annual Review of Plant Biology, 68, 563–586.

Vellend M, Dornelas M, Baeten L et al. (2017b) Estimates of local biodiversity change over time stand up to scrutiny. Ecology, 98, 583–590.

Verheyen K, De Frenne P, Baeten L et al. (2017) Combining biodiversity resurveys across regions to advance global change research. BioScience, 67, 73–83.

Virtanen R, Eskelinen A, Harrison S (2017) Comparing the responses of bryophytes and short-statured vascular plants to climate shifts and eutrophication. Functional Ecology, 31, 946–954.

Vittoz P, Camenisch M, Mayor R, Miserere L, Vust M, Theurillat J-P (2010) Subalpine-nival gradient of species richness for vascular plants, bryophytes and lichens in the Swiss Inner Alps. Botanica Helvetica, 120, 139–149.

Yagouti A, Boulet G, Vincent L, Vescovi L, Mekis É (2008) Observed changes in daily temperature and precipitation indices for southern Québec, 1960–2005. Atmosphere-Ocean, 46, 243–256.

4.2.6. Supplementary Materials

- Appendix C-S1 - Taxonomic standardization of bryophytes species between surveys
- Appendix C-S2 - Mean species elevation and sum of occurrences for bryophytes for original and recent survey in Forillon and Mont-Mégantic

5- CHAPITRE 5

DISCUSSION GENERALE ET CONCLUSION

La question scientifique qui a structuré ce travail de doctorat est : quel est l’effet des changements environnementaux sur la biodiversité? Les trois projets de recherche que j’ai menés ont permis d’approcher plusieurs aspects de cette grande question :

- Quel est l’effet des changements environnementaux sur la végétation forestière (déposition et réchauffement de la température);
- Comparer la sensibilité de deux grands groupes taxonomiques face aux changements environnementaux (bryophytes et trachéophytes);

L’orientation des hypothèses autour de ces questions offre une articulation très cohérente des trois chapitres. La discussion générale sera donc transversale et recoupera les résultats des différents chapitres. De plus, l’utilisation des méthodes de l’écologie historique dans différents contextes écologiques facilite la discussion transversale des résultats.

Malgré le manque de preuves solides, le groupe des bryophytes est souvent présenté comme un bon indicateur des changements environnementaux. J’ai donc voulu tester la sensibilité comparée des plantes vasculaires et des bryophytes dans deux régions ayant subi des pressions environnementales différentes. Premièrement, le chapitre 2 teste cette sensibilité dans une région du nord-ouest de la France connu pour ses dépositions atmosphériques et son réchauffement de la température. Deuxièmement, le chapitre 4 teste cette même sensibilité, entre bryophytes et plantes vasculaires, sur un gradient d’augmentation de la température dans la province du Québec. La synthèse des résultats indique que les dépositions exercent une plus forte pression sur la structure et la composition des communautés de bryophytes par rapport aux plantes vasculaires. Dans une situation de réchauffement, les résultats sont équivoques. Les tendances temporelles dépendent de la propriété de la communauté ou des indices testés. L’augmentation de la diversité et la migration en altitude des espèces semblent être plus importantes pour les plantes vasculaires. *A contrario,* les bryophytes montrent de plus importants changements de composition. Ces résultats soutiennent trois grandes conclusions : (i) les changements environnementaux sont des moteurs des changements de la biodiversité (ii) les réponses des communautés diffèrent selon le groupe taxonomique et (iii) selon la propriété de la communauté qui est étudiée (i.e. distribution, diversité, composition). Ces trois grandes conclusions répondent directement à mes objectifs de départ.

Les études historiques testant l'effet des changements environnementaux sur la biodiversité sont généralement menées à échelle locale. Il existe quelques rares méta-analyses, mais très peu d'étude sur une échelle régionale (Bertrand et al., 2011; De Frenne et al., 2013; Grabherr et al., 2010; Lenoir et al., 2008; Pauli et al., 2012). Le chapitre 3 est donc une contribution significative dans la compréhension des mécanismes de réponse de la végétation aux changements environnementaux sur une large échelle spatiale.

J'ai montré que les réponses de la biodiversité sont complexes. Un même changement environnemental peut entraîner plusieurs types de réponses des communautés. Ces conclusions supportent l'importance d'analyser plusieurs groupes taxonomiques *via* une multitude de propriétés des communautés pour comprendre l'ensemble des mécanismes à l'œuvre. Dans les prochains paragraphes, je discuterai de manière croisée des différentes conclusions amenées dans cette thèse. Pour finir, je reviendrai sur les avantages, limites et perspective de ce type d'étude.

5.1. Discussion transversale des résultats

La réponse de la biodiversité face aux changements environnementaux est probablement l'enjeu premier de l'écologie scientifique du XXI^{e} siècle. Les activités liées aux développements des sociétés humaines ont des conséquences majeures sur le fonctionnement des écosystèmes et le maintien de la biodiversité. Ces trois projets de recherche sont une contribution à la compréhension de la dynamique de la biodiversité dans l'Anthropocène. La multitude et la divergence des résultats montrent la complexité des mécanismes à l'œuvre. En effet, il n'y a pas une réponse unique de la biodiversité, mais un ensemble de réponses dépendamment du groupe taxonomique (i.e. bryophytes vs plantes vasculaires), des propriétés les décrivant (i.e. diversités, composition, affinité) et du contexte écologique (i.e. déposition atmosphérique, réchauffement…). Comme je l'ai démontré à plusieurs reprises, il peut se produire de profondes transformations dans composition de la végétation sans pour autant être associé à une perte de diversité. Les résultats soutiennent l'importance d'étudier la dynamique de biodiversité avec une approche la plus holistique possible.

5.1.1. Les moteurs des changements écologiques

5.1.1.1. Comparaison de la sensibilité taxonomique

Un des objectifs de ce travail de recherche était la comparaison de la réponse temporelle des bryophytes et des plantes vasculaires. Motiver par un ensemble de différences bio-morpho-écologiques nous avons émis des prédictions diamétralement opposées dans le chapitre 2 et 4. Premièrement, dans une région marquée par les dépositions atmosphériques et le réchauffement de la température, nous avons émis l'hypothèse que les bryophytes étaient plus sensibles que les plantes vasculaires (chapitre 2). Cette hypothèse était principalement soutenue par l'absence de cuticule chez les bryophytes, les rendant hautement sensibles à la composition chimique des précipitations. Le mécanisme prédit était un changement de composition des communautés par le filtrage (i.e. 'sélection') des espèces sensibles au débalancement de la composition chimique des précipitations. Deuxièmement, dans une région touchée principalement par le réchauffement de la température, nous avions émis l'hypothèse que les bryophytes étaient moins sensibles que les plantes vasculaires (chapitre 4). La justification de cette hypothèse était la large gamme de tolérances des bryophytes vis-à-vis de la température et leur plus grande tolérance à la sécheresse par rapport aux plantes vasculaires. Le mécanisme prédit était un changement de composition des communautés de plante vasculaire par le remplacement des espèces de milieux froid par des espèces sudistes sous l'effet de la compétition (i.e. la thermophilisation).

Les résultats concernant la diversité et les affinités écologiques des communautés soutiennent ces deux hypothèses. Premièrement, dans le cas des dépositions les bryophytes ont subi une augmentation de la diversité et des affinités à la température, à l'azote et au pH basique, alors qu'il y a eu une diminution de la diversité des plantes vasculaires sans changements d'affinités des communautés. Deuxièmement, dans le cas du réchauffement de la température il y a eu une augmentation de la diversité et une migration en altitude des plantes vasculaires, mais pas changement pour les bryophytes.

5.1.1.2. *Le découplage entre diversité et composition*

Toutefois, nous avons trouvé un changement systématique de la composition des communautés. Dans chacun des contextes écologiques, la magnitude des changements de composition était toujours plus importante pour les bryophytes que pour les plantes vasculaires. Il y a une double interprétation à ce résultat : (i) dans le cas des dépositions (chapitre 2), les résultats soutiennent l'hypothèse que les dépositions atmosphériques ont un plus grand effet sur les communautés de bryophyte que vasculaire; (ii) dans le cas du gradient de réchauffement (chapitre 4), cela suggère que les bryophytes ont un taux de renouvellement des communautés (*turnover*) plus dynamique que les plantes vasculaires, peu importe qu'il y ait ou non un réchauffement. La similarité des magnitudes des changements de composition observés entre Forillon et Mégantic indique très clairement que des facteurs non climatiques sont impliqués dans la dynamique temporelle des communautés de bryophytes. Les résultats des trois chapitres rejoignent plusieurs études ne montrant aucune perte de diversité à échelle locale malgré d'importants changements de composition (Dornelas et al., 2014; Gotelli et al., 2017; Hillebrand et al., 2018; Magurran et al., 2018; Spaak et al., 2017; Vellend et al., 2017). La crise de biodiversité ne peut que se comprendre comme un phénomène global. Une simple métrique quantitative à échelle locale, telle que le nombre moyen d'espèces par unité de surface, renseigne très peu (et très mal) la crise que traverse la diversité biologique.

5.1.1.3. *Contributions et perspectives*

Mes deux études apportent une importante contribution dans la littérature des cryptogames. Souvent boudés par les botanistes en raison des difficultés d'identification et du nombre très réduit de formations à ce sujet, les cryptogames ne jouissent pas d'une grande popularité. Ainsi, très peu d'études avaient été menées jusqu'à ce jour sur la réponse des bryophytes au réchauffement climatique (notons les récents travaux Bergamini et al., 2009; Delgado et Ederra, 2013; Désamoré et al., 2012; He et al., 2016; Nascimbene et Spitale, 2017; Vanneste et al., 2017 – dont la moitié fût publiée après le début de ce doctorat). Avec ces travaux, j'espère participer à l'élan d'intérêt pour ce groupe qui recèle encore beaucoup de belles découvertes. Pour aller au-delà de la simple comparaison taxonomique, une approche phylogénétique pourrait être envisagée. Il a été montré très récemment par Rafferty et Nabity, (2017) la présence d'un signal phylogénétique dans les réponses phénologiques des plantes aux changements climatiques. Existe-t-il un patron phylogénétique en lien avec les changements climatiques (Lavergne et al., 2010)? Certains clades sont-ils favorisés? Quels attributs fonctionnels caractérisent les clusters de « gagnants » ou « perdants »? Par exemple, comme expliqué dans la section (*1.3.2.5.*) les espèces avec des stratégies de dispersion des propagules - *sensu lato* - à longue distance, seront favorisées par le réchauffement climatique. Il y a-t-il une augmentation des groupes caractérisés par une dispersion anémochore type Graminoïdes, *Composeae, Asteraceae,* etc…

Pour conclure, la comparaison taxonomique a permis de mettre en avant différents mécanismes de réponses aux changements globaux. La littérature manque cruellement d'études sur les dynamiques temporelles des communautés de bryophytes et plus largement des cryptogames. Les chapitres 2 et 4 apportent des réponses et alimentent le questionnement : quels sont les facteurs responsables des changements de composition observés à Forillon alors que la région n'a subi ni déposition ni réchauffement climatique? Pourquoi y a-t-il un si grand *turnover* des communautés de bryophytes? L'approche par trait fonctionnel n'est pas évidente pour le groupe des bryophytes, cependant des initiatives existent (Cornelissen et al., 2007; St. Martin et Azim, 2017; Rice et al., 2008). Une perspective prometteuse serait de tester les mécanismes de réponses des bryophytes *via* l'approche par trait fonctionnel.

5.1.2. Dynamiques temporelles de la diversité des communautés

Les résultats des trois chapitres mettent en avant les différentes tendances que peut prendre la diversité en réponse aux changements environnementaux. Le chapitre 2 montre une augmentation de la diversité-γ (=global) et -α (=locale) pour les bryophytes en réponse aux dépositions sans changement de diversité-β (=hétérogénéité entre communautés). Pour les plantes vasculaires, le chapitre 3 établit un lien entre réchauffement de la température et augmentation de la diversité globale et locale sans changement de l'hétérogénéité entre communautés. Enfin, le chapitre 4 présente des résultats plus contrastés quant à l'effet du réchauffement sur la dynamique de la diversité des deux groupes taxonomiques. Les communautés de bryophytes montrent une augmentation de la diversité globale et de l'hétérogénéité entre communautés sans changement de diversité à échelle locale. Il apparait donc clairement qu'à échelle locale une même perturbation ou une même combinaison de perturbation ne cause pas les mêmes effets sur la diversité.

Rappelons ici que le chapitre 3 et 4 présente les mêmes analyses pour les plantes vasculaires, l'un avec les abondances (chapitre 3), l'autre avec les présences-absences (chapitre 4). Le choix de la métrique utilisé pour l'analyse a une grande influence sur le résultat et son interprétation. Prenons le cas de l'augmentation de la diversité-β observée avec les présences-absences des plantes vasculaires au Mont-Mégantic (chapitre 4) alors qu'aucun changement n'a été constaté avec les abondances (chapitre 3). Cela conduit à deux interprétations écologiques : (i) du point de vue de l'identité des espèces (présence-absence), il y a une diversification des communautés (ii) *a contrario*, lorsque l'on considère la dominance des espèces, la diversité-β n'a pas changé. Autrement dit, les changements de composition observés avec les présences-absences sont grandement influencés par les espèces à faible abondance.

En résumé, les résultats du chapitre 2 sont cohérents avec le faisceau de preuves attestant l'effet néfaste des dépositions atmosphériques (notamment azoté) sur la diversité des plantes vasculaires (Bobbink et al., 2010; de Schrijver et al., 2011; Simkin et al., 2016; Soons et al., 2017; Stevens et al., 2010; Vellend et al., 2017). Les résultats du chapitre 3 soutiennent la prédiction que le réchauffement climatique a un effet positif sur la diversité des plantes vasculaires pour forêts tempérées humides (Pauli et al., 2012; Vellend et al., 2017). Ce patron est principalement expliqué par la plus grande diversité des régions plus chaudes. En revanche, j'ai montré que ce n'est pas le cas pour les bryophytes (chapitre 4), ce qui s'explique en partie par l'absence de gradient latitudinale pour ce groupe indiquant une faible relation au gradient de température (Geffert et al., 2013; von Konrat et al., 2008; Mateo et al., 2016).

En conclusion, les tendances à long terme de la dynamique de la diversité et de la composition sont découplées. La prochaine étape permettant d'affiner notre compréhension des mécanismes de réponse aux changements environnementaux est de tester quels traits fonctionnels expliquent les processus d'assemblages des communautés. Une autre perspective intéressante autour de ces questions serait de tester l'effet de ces changements de structure et composition des communautés sur le fonctionnement de l'écosystème. Le lien entre diversité et fonctionnement a animé une grande réflexion en écologie. Lorsque nous observons un fort changement de composition des communautés, sans changement de diversité, une question émerge : quels sont les effets sur les fonctions écologiques des écosystèmes (e.g. la productivité, stabilité...)? Comment est-ce que le nouvel équilibre affect-il les services écosystémiques?

5.2. Discussion méthodologique

5.2.1. Avantages et limites des affinités écologiques

Les indices d'affinités écologiques permettent de caractériser chaque espèce vis-à-vis d'une variable environnementale (considéré ici comme une des dimensions de la niche écologique cf. Chapitre 1, section *1.1*). D'une manière générale, toutes formes d'indices agrégés à la communauté fournissent un outil puissant pour suivre les mécanismes de réponse directe et indirecte des communautés aux changements environnementaux (Lamarque et al., 2014). Toutefois, il est à noter que ces indices masquent la variabilité intraspécifique (Siefert et al., 2015). Dans le chapitre 2, ces affinités correspondent aux indices d'Ellenberg calculer pour l’Europe et standardisés pour la Grande-Bretagne (Ellenberg et al., 1991; Hill et al., 2004). En revanche, dans le chapitre 4 j’ai calculé des affinités des communautés à la température : le CTI (*Community Temperature Index*). Cette mesure simple de l’enveloppe bioclimatique a été calculée pour les besoins de l’étude suivant la méthodologie décrite dans le *3.2.2.4*. Les résultats non significatifs de cette analyse ont été, pour moi, inattendus. J’avais évidemment connaissance de l’effet *time lag* des communautés - c’est-à-dire un décalage entre l’augmentation de la température et l’affinité des espèces. Malgré cela, l’absence de signal (surtout sur la partie la plus chaude du gradient : Gatineau) a été difficile à comprendre. Après réflexion, et de longues discussions où mon directeur fût surement surpris de me voir insisté sur ces résultats, nous avons identifié plusieurs interprétations écologiques et limitations méthodologiques à ces analyses.

Premièrement, ces indices ont reçu plusieurs critiques du fait de leur simple relation corrélative entre distribution et climat, négligeant bon nombre de processus écologiques (Bilton et al., 2016). Deuxièmement, une affinité à la température est un indice fixe dans le temps et ne renseigne pas la possible acclimatation voire d’adaptation des espèces. Troisièmement, ces indices agrégés à la communauté peuvent être brouillés par des réponses non climatiques. Comme ce fut le cas dans le chapitre 3 : le CTI est sensible à la dynamique de population des espèces, notamment par une modification de la structure d’abondance en réponse à des facteurs non climatiques (e.g. stochasticité, dynamique naturelles…). Enfin, la précision de l’indice dépend de la qualité du modèle de distribution spatiale de l’espèce. Si les données climatiques sont généralement de bonne qualité, ce n’est pas le cas pour les distributions spatiales de certaines espèces. Ainsi une estimation biaisée ou incomplète de la distribution d’une espèce entraîne une imprécision voire une erreur dans l’estimation de son optimum de température. C’est en partie pour cette raison que nous n’avons pas testé les changements de CTI pour les bryophytes dans le Chapitre 4. Grâce au développement récent, ou en cours, de nouvelles approches de modélisation des distributions d’espèces, il est possible de compléter le manque d’occurrences observé par des cartes d’avis d’expert (possiblement une aubaine pour modèle de distribution d’espèces des bryophytes) (Merow et al., 2017).

5.2.2. Intérêt et limites de l’approche historique

L’écologie historique telle que nous l’avons utilisée - i.e. le rééchantillonnage de relevé phytosociologique ancien - possède quelques limitations. En effet, ces méthodes permettent une comparaison de deux états statiques séparés par plusieurs décennies. Il y a deux grandes sources de variations non désirées (i) humaines (Archaux et al., 2012) : biais observateur, différence dans l’effort d’échantillonnage, erreur d’identification, *pseudoturnover* (c’est-à-dire une imprécision dans le replacement des relevés sur le terrain), et (ii) les dynamiques naturelles de l’écosystème forestier (De Frenne et al., 2013, 2015) : dynamique de l’écosystème forestier, événements stochastiques ou tout autre changement non climatique. Ces sources d’erreurs induisent nécessairement du bruit dans m’importe quel type d’étude se basant sur des données récoltées par plusieurs observateurs. Une fois bien identifié il est possible de limiter toutes ces sources de bruit par une méthodologie stricte et clairement transparente.

5.2.2.1. L’identification et le contrôle du bruit

L’important travail d’archive, réalisé en début de projet, a pour objectif de documenter minutieusement les détails de chaque étape de la recherche ancienne. J’ai passé plusieurs mois à préparer les phases de terrain. Chaque point de relevé a été relocalisé en croisant les cartes, les descriptions topographiques et les relevés forestiers. Le protocole de sélection des sites sur le terrain étant le même entre les différents sites (parcs nationaux) sélectionnés afin de permettre la comparabilité.

Une fois le relevé effectué sur le terrain, la phase d’homogénéisation taxonomique a pour but de limiter le bruit provenant d’erreurs d’identification pour les espèces morphologiquement proches et des changements de nomenclature taxonomique. Lorsqu’un doute persistait sur la reproductibilité de la méthode, par exemple l’estimation des abondances des bryophytes, il a été décidé de ne pas les prendre en compte et de conserver uniquement les présences-absences. Ces procédés assurent une grande confiance dans la comparabilité temporelle des relevés.

Cependant, l’ensemble de ces choix a parfois conduit à la perte d’information. Premièrement, le protocole de relocalisation des relevés sur le terrain a éliminé de nombreux relevés potentiels. À titre d’exemple, à Forillon nous avons visité environ 150 relevés potentiels sur lesquels seule une cinquantaine ont été sélectionnés pour faire les inventaires contemporains. Deuxièmement, la phrase d’homogénéisation taxonomique a entraîné une perte information, notamment sur la véritable diversité et la composition des communautés. Par exemple, plusieurs espèces de certaines familles telles que les *Poaceae, Cyperaceae* ou *Asteraceae* ont été regroupées sous des genres voire des familles (ceci prévaut également pour les bryophytes). Finalement, pour les bryophytes, l’utilisation des présences-absences à la place des abondances réduit les informations sur la dominance des espèces.

5.2.2.2. *Perspectives méthodologiques*

Il est nécessaire d’être alerte sur les limitations de la méthodologie utilisée, surtout lorsqu’un demi-siècle nous sépare du « début de l’expérience ». Il est primordial de bien identifier les sources de bruit et de développer des protocoles permettant de les supprimer, du moins de les contrôler. Il existe une multitude d’approches complémentaires permettant de tester des hypothèses à plus fines échelles temporelles. Par exemple, le suivi à long terme des écosystèmes (monitoring) permet de tester des séries temporelles de la diversité et de la composition des communautés. Ces méthodes permettent notamment de comprendre l’importance de la variabilité saisonnière ou annuelle dans la dynamique temporelle des communautés. Néanmoins, l’écologie historique permet aisément de te tester les mécanismes de réponse de la végétation sur de larges échelles temporelles. C’est donc un cadre méthodologique de choix dans l’étude des changements de biodiversité en réponse aux changements environnementaux de l’Anthropocène.

5.3. Le partage des données

La qualité des données historiques est un élément nécessaire dans leur réutilisation des décennies plus tard. Je considère que l'acquisition de données est une contribution au moins aussi importante que la publication d'article scientifique. Voici deux arguments justifiant les longues semaines de mis en page d'un herbier permettant la conservation dès les identifications faites dans ce travail de doctorat. Avec la précieuse aide des assistantes de terrain (Diane, Mélissa et Sarah), nous avons mis sous planche environ 1000 spécimens d'herbier de plantes vasculaires et de bryophytes tous déposés à l'herbier Marie-Victorin (MT) du Centre de le Biodiversité de l'Université de Montréal (quatrième herbier en taille du Canada). En plus du dépôt physique des spécimens dans un herbier national, toutes les occurrences ont été déposées dans la base de données GBIF (*Global Biodiversity Information Facility*). Pour finir, les données temporelles seront déposées dans la base de données spécialisée dans le rééchantillonnage des relevés de végétation en forêt tempérée : *forestReplot*. Cette base de données est une initiative scientifique du ILTER (*International Long-Term Ecological Research*). Par cette démarche je contribue à un large partage des données.

5.4. Conclusion finale

Ce doctorat met une fois de plus en évidence l'effet des changements globaux sur la biodiversité. Les résultats des trois chapitres soutiennent trois grandes conclusions cohérentes avec la littérature :

- (i) les changements environnementaux sont des moteurs des changements de la biodiversité;
- (ii) les réponses des communautés diffèrent selon le groupe taxonomique et;
- (iii) selon la propriété de la communauté qui est étudiée (i.e. distribution, diversité, composition).

Ces travaux empiriques montrent que l'écologie historique est une méthode puissante pour tester les mécanismes de réponses des communautés face aux changements globaux.

ANNEXE A

SUPPLEMENTARY MATERIALS OF CHAPTER 2

Appendix A-S1 - List of bryophyte species and number of occurrences per survey

Supporting information to the paper Becker Scarpitta et al, 2017 - Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming, Journal of Vegetation Science

Species_names	**#Plot 1976**	**#Plot 2012**
Hypnumcupressiforme Hedw.	65	90
Dicranumscoparium Hedw.	46	49
Mniumhornum Hedw.	41	84
Polytrichastrumformosum(Hedw.)G.L.Sm.	41	70
Lophocoleabidentata (L.)Dumort.	33	36
Isotheciummyosuroides Brid.	28	49
Brachytheciumrutabulum (Hedw.)Schimp.	15	63
Thuidiumtamariscinum (Hedw.)Schimp.	14	20
Leucobryumglaucum (Hedw.)Ångstr.	12	7
Dicranellaheteromalla (Hedw.)Schimp.	8	38
Atrichumundulatum (Hedw.)P.Beauv.	8	25
Pleuroziumschreberi (Willd.exBrid.) Mitt.	8	0
Eurhynchiumstriatum (Hedw.)Schimp.	7	8
Pseudoscleropodiumpurum (Hedw.)M.Fleisch.	4	5
Brachytheciumvelutinum (Hedw.)Schimp.	4	0
Rhytidiadelphusloreus (Hedw.)Warnst.	3	1
Lepidoziareptans (L.)Dumort.	2	10
Hylocomiumsplendens (Hedw.)Schimp.	1	0
Kindbergiapraelonga (Hedw.)Ochyra	0	69
Lophocoleaheterophylla (Schrad.)Dumort.	0	52
Plagiotheciumsucculentum (Wilson)Lindb.	0	29
Dicranummontanum Hedw.	0	26
Calypogeiafissa (L.)Raddi	0	13
Pseudotaxiphyllumelegans (Brid.)Z.Iwats.	0	13
Hypnumlacunosum (Brid.)Hoffm.exBrid.	0	11
Leucobryumjuniperoideum (Brid.)Müll.Hal.	0	7
Microlejeuneaulicina (Taylor)A.Evans	0	6
Ulotacrispa (Hedw.)Brid.	0	6

Plagiotheciumnemorale (Mitt.)A.Jaeger	0	5
Calypogeiamuelleriana (Schiffn.)Müll.Frib.	0	4
Calypogeiaarguta Nees&Mont.	0	3
Dicranoweisiacirrata (Hedw.)Lindb.	0	3
Diplophyllumalbicans (L.)Dumort.	0	3
Plagiotheciumcurvifolium Schlieph.exLimpr.	0	3
Dicranummajus Sm.	0	2
Fissidenstaxifolius Hedw.	0	2
Fissidensviridulus (Sw.exanon.)Wahlenb.	0	2
Frullaniadilatata (L.)Dumort.	0	2
Hypnumjutlandicum Holmen&E.Warncke	0	2
Isothecium alopecuroides (Lam.exDubois)Isov.	0	2
Orthotrichumaffine Schrad.exBrid.	0	2
Orthotrichumlyellii Hook.&Taylor	0	2
Pelliaepiphylla (L.)Corda	0	2
Ulotabruchii Hornsch.exBrid.	0	2
Bryumcapillare Hedw.	0	1
Herzogiellaseligeri (Brid.)Z.Iwats.	0	1
Hypnumandoi A.J.E.Sm.	0	1
Metzgeriafruticulosa auct.non (Dicks.)A.Evans	0	1
Metzgeriafurcata (L.)Dumort.	0	1
Orthodontiumlineare Schwägr.	0	1
Plagiomniumundulatum (Hedw.)T.J.Kop.	0	1
Plagiothecium denticulatum (Hedw.)Schimp.	0	1
Pleuridiumacuminatum Lindb.	0	1
Pogonatumaloides (Hedw.)P.Beauv.	0	1
Rhizomniumpunctatum (Hedw.)T.J.Kop.	0	1

Appendix A-S2 - List of vascular plant species and number of occurrences per survey

Supporting information to the paper Becker Scarpitta et al, 2017 - Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming, Journal of Vegetation Science.

Accepted_name_TNRS	**#Plot1976**	**#Plot2009**
Rubusidaeus L.	59	52
Lonicerapericlymenum L.	55	42
Hederahelix L.	55	21
Pteridiumaquilinum (L.)Kuhn	54	52
Deschampsiaflexuosa (L.)Trin.	50	33
Dryopterisfilix -mas (L.)Schott	50	28
Dryopteriscarthusiana (Vill.)H.P.Fuchs	49	41
Holcusmollis L.	44	24
Miliumeffusum L.	39	29
Melicauniflora Retz.	36	28
Oxalisacetosella L.	34	36
Stellariaholostea L.	33	25
Hyacinthoides non-scripta (L.)ChouardexRothm.	30	20
Anemonenemorosa L.	29	20
Carexpilulifera L.	26	9
Luzulapilosa (L.)Willd.	26	8
Dryopterisdilatata (Hoffm.)A.Gray	24	18
Athyriumfilix -femina (L.)Roth	23	12
Lamiumgaleobdolon (L.)L.	23	8
Carex sylvatica Huds.	22	12
Polygonatummultiflorum (L.)All.	20	14
Violareichenbachiana Jord.exBoreau	18	2
Conopodiummajus (Gouan)Loret	18	0
Circaealutetiana L.	17	15
Melampyrumpratense L.	16	6
Carexremota L.	15	23
Galiumodoratum (L.)Scop.	15	7
Poanemoralis L.	15	6
Juncuseffusus L.	14	23
Viciasepium L.	13	1
Arummaculatum L.	13	0
Brachypodiumsylvaticum (Huds.)P.Beauv.	11	12

Poatrivialis L.	11	12
Euphorbiaamygdaloides L.	11	5
Moehringiatrinervia (L.)Clairv.	11	0
Potentillasterilis (L.)Garcke	11	0
Lysimachianemorum L.	10	1
Ajugareptans L.	10	0
Blechnumspicant (L.)Sm.	9	10
Hypericumpulchrum L.	9	9
Digitalispurpurea L.	9	6
Ficariaverna Huds.	9	1
Galiumaparine L.	8	8
Veronicamontana L.	7	1
Violariviniana Rchb.	7	0
Urticadioica L.	6	4
Adoxamoschatellina L.	6	1
Primulaelatior (L.)Hill	6	0
Veronicachamaedrys L.	6	0
Juncusconglomeratus L.	5	8
Geraniumrobertianum L.	5	7
Glechomahederacea L.	5	3
Scrophularianodosa L.	5	3
Luzulaforsteri (Sm.)DC.	5	1
Galiumsaxatile L.	5	0
Geumurbanum L.	4	4
Hypericumandrosaemum L.	4	1
Bromusracemosus L.	4	0
Festucagigantea (L.)Vill.	4	0
Polystichumsetiferum (Forssk.)MooreexWoyn.	4	0
Mercurialisperennis L.	3	3
Stachyssylvatica L.	3	1
Lythrumsalicaria L.	3	0
Primulavulgaris Huds.	3	0
Ranunculusrepens L.	3	0
Epilobiummontanum L.	2	1
Stachysofficinalis (L.)Trevis.	2	1
Agrostiscapillaris L.	2	0
Cardaminepratensis L.	2	0
Chrysospleniumoppositifolium L.	2	0
Fragariavesca L.	2	0
Ranunculusauricomus L.	2	0
Galeopsistetrahit L.	1	5
Moliniacaerulea (L.)Moench	1	3
Callunavulgaris (L.)Hull	1	2

Dactylisglomerata L.	1	2
Hieraciummurorum C.B.Clarke	1	2
Teucriumscorodonia L.	1	1
Alliariapetiolata (M.Bieb.)Cavara&Grande	1	0
Alliumursinum L.	1	0
Cytisusscoparius (L.) Link	1	0
Origanumvulgare L.	1	0
Potentillaerecta (L.)Raeusch.	1	0
Rumexconglomeratus Murray	1	0
Sesleriacaerulea (L.)Ard.	1	0
Dioscoreacommunis (L.)Caddick&Wilkin	1	0
Veronicahederifolia L.	1	0
Veronicaofficinalis L.	0	2
Dryopterisaffinis (Lowe)Fraser -Jen	0	1
Epilobiumangustifolium L.	0	1
Rhamnuscathartica L.	0	1
Brachypodiumpinnatum (L.)P.Beauv.	0	0
Carexstrigosa Huds.	0	0

Appendix A-S3 - Simplified scale of indicator values for bryophytes and vascular plants.

Supporting information to the paper Becker Scarpitta et al, 2017 - Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming, Journal of Vegetation Science.

L,F,R&NareEllenbergindicatorvalues, Climaticmeans:Tjanuarymeans:TJuly are Geographicattributes(speciestemperatureindex).

Bryophytes (Hill et al., 2007)

Light (L)	1: plant in darkness 9: plant in full light, found mostly in full sun
Moisture (F)	1: plant in extreme dryness 12: normally submerged plant
Reaction (R)	1: indicator of extreme acidity, never found on weakly acid or basic substrata 9: On substrata with free calcium carbonate, mainly chalk and limestone
Nitrogen (N)	1: Indicator of extremely infertile sites; almost all are calcifuges 7*: Plant often found in richly fertile places
Climatic means: Tjanuary	min: -2℃ max: 8℃
Climatic means: Tjuly	min: 9.9℃ max: 16.7℃
Climatic means: Average annual temperature *mean (Tjan, Tjul)*	min: 4℃ max: 11.6℃

* The original scale for vascular plants goes up to 9 but there are no bryophytes with value of 8 and 9.

Vascular plants (Hill et al., 2004)

Light (L)	1: plant in deep shade 9: plant in full light, found mostly in full sun
Moisture (F)	1: plant in extreme dryness 12: submerged plant, permanently or almost constantly under water
Reaction (R)	1: indicator of extreme acidity 9: indicator of basic reaction (calcareous soil)
Nitrogen (N)	1: indicator of extreme infertile sites 9: indicator of extremely rich situation
Climatic means: Tjanuary	min: -1.3°C max: 7°C
Climatic means: Tjuly	min: 10.4°C max: 17°C
Climatic means: Average annual temperature *mean (Tjan, Tjul)*	min: 4.6°C max: 11.7°C

References:

Hill,M.O.,Preston,C.D.,Bosanquet,S.D.S.,&Roy,D.B.2007. *Bryoatt - attributesofBritish andIrishmosses,liverwortsandhornworts.* NERC,CentreforEcology&Hydrology *,UK.*

Hill,M.O.,Preston,C.D.,&Roy,D.B.2004. *PlantattatributesofBritishandIrishplants: status,size,lifehistory,geographyandhabitats* .NERC,CentreforEcology&Hydrology, UK.

Appendix A-S4 - Complete model results of linear mixed-effect models

Supporting information to the paper Becker Scarpitta et al, 2017 - Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming, Journal of Vegetation Science.

Temporal changes in species richness were tested using different models for vascular plant and bryophytes, due to the nested sampling design for bryophytes.

- model for vascular plants: lmer (Species.Richness ~ year + (1 | plot))
- model for bryophytes: lmer (Species.Richness ~ year + (1 + plot / subplot))

For ecological indicator values, we ran a separate model for each indicator value in each taxonomical group (5*2 = 10 models). We used the same hierarchical model structure as that for species richness. In all models, the fixed effect is the year (two levels).

- model for vascular plants: lmer (CWM_i ~ year + (1 | plot))
- model for bryophytes: lmer (CMW_i ~ year + (1 + plot / subplot))

where CWM_i is the community aggregated index for variable *i*=L, F, R, N and average annual temperature (AvT).

Table A-S4 - Detailed results of mixed-effect models testing for change over time in five ecological indicator values (community-weighted means, CWM) in bryophytes and vascular plants.

'var.' is the variance of each random effect and %var. is a proportion of the random effects' variance on the sum of the random effects and residuals. The coefficient of determination (R^2, the variance explained by the model) was decomposed in two components: the marginal R^2 describing the proportion of variance explained by the fixed effects (i.e. year) and the conditional R^2 describing the proportion of variance explained by both fixed and random effects (Nakagawa & Schielzeth 2013). Significance levels are: * 0.05; ** 0.01; *** 0.001.

			Bryophytes CWM				
			2.5%	**(50%)**	**97.5%**	**var.**	**%var.**
Affinity to average annual temperature	fixed effects	α : Initial (µ 1976)	8.9	8.90	9.0		
		β : Temporal change (2012-1976)	**0.04**	**0.1*** **	**0.1**		
	Random effects	Intercept$_{\text{subplot:plot}}$				1.09E-07	0.001%
		Intercept$_{\text{plot}}$				1.26E-04	2%
	ε (error)	Residuals				7.30E-03	98%
	fixed effects	R^2 *marginal*	14%				
	fixed + random effects	R^2 *conditional*	16%				
R - affinity to pH	fixed effects	α : Initial (µ 1976)	3.7	3.8	4.0		
		β : Temporal change (2012-1976)	**0.1**	**0.3*** **	**0.4**		
	Random effects	Intercept$_{\text{subplot:plot}}$				0.13	26%
		Intercept$_{\text{plot}}$				0.12	25%
		Residuals				0.24	50%
	fixed effects	R^2 *marginal*	4%				
	fixed + random effects	R^2 *conditional*	52%				
N - affinity to nitrogen	fixed effects	α : Initial (µ 1976)	3.4	3.5	3.6		
		β : Temporal change (2012-1976)	**0.3**	**0.5*** **	**0.6**		
	Random effects	Intercept$_{\text{subplot:plot}}$				0.08	18%
		Intercept$_{\text{plot}}$				0.10	23%
	ε (error)	Residuals				0.26	59%
	fixed effects	R^2 *marginal*	10%				
	fixed + random effects	R^2 *conditional*	47%				
L - affinity to light	fixed effects	α : Initial (µ 1976)	4.8	4.9	5.1		
		β : Temporal change (2012-1976)	**-0.3**	**-0.2*** **	**-0.04**		
	Random effects	Intercept$_{\text{subplot:plot}}$				0.12	26%
		Intercept$_{\text{plot}}$				0.12	26%
	ε (error)	Residuals				0.22	48%
	fixed effects	R^2 *marginal*	2%				
	fixed + random effects	R^2 *conditional*	53%				
F - affinity to moisture	fixed effects	α : Initial (µ 1976)	5.2	5.3	5.4		
		β : Temporal change (2012-1976)	-0.1	0.1	0.2		
	Random effects	Intercept$_{\text{subplot:plot}}$				0.04	18%
		Intercept$_{\text{plot}}$				0.05	21%
	ε (error)	Residuals				0.15	61%
	fixed effects	R^2 *marginal*	0.4%				
	fixed + random effects	R^2 *conditional*	39%				

			Vascular plants CWM				
			2.5%	**(50%)**	**97.5%**	**var.**	**%var.**
Affinity to average annual temperature	fixed effects	α : Initial $_{(\mu\ 1976)}$	9.0	9.0	9.1		
		β : Temporal change $_{(2009\text{-}1976)}$	-0.03	-0.001	0.03		
	Random effects	$\text{Intercept}_{\text{plot}}$				0.01	42%
	ε (error)	Residuals				0.01	58%
	fixed effects	*R^2 marginal*			0.003%		
	fixed + random effects	*R^2 conditional*			42%		
R - affinity to pH	fixed effects	α : Initial $_{(\mu\ 1976)}$	4.2	4.5	4.7		
		β : Temporal change $_{(2009\text{-}1976)}$	-0.2	0.03	0.3		
	Random effects	$\text{Intercept}_{\text{plot}}$				0.60	49%
		Residuals				0.62	51%
	fixed effects	*R^2 marginal*			0.03%		
	fixed + random effects	*R^2 conditional*			50%		
N - affinity to nitrogen	fixed effects	α : Initial $_{(\mu\ 1976)}$	4.1	4.3	4.4		
		β : Temporal change $_{(2009\text{-}1976)}$	-0.1	0.1	0.3		
	Random effects	$\text{Intercept}_{\text{plot}}$				0.27	46%
	ε (error)	Residuals				0.31	54%
	fixed effects	*R^2 marginal*			0.6%		
	fixed + random effects	*R^2 conditional*			47%		
L - affinity to light	fixed effects	α : Initial $_{(\mu\ 1976)}$	5.3	5.4	5.5		
		β : Temporal change $_{(2012\text{-}1976)}$	-0.1	0.04	0.2		
	Random effects	$\text{Intercept}_{\text{plot}}$				0.09	43%
	ε (error)	Residuals				0.12	57%
	fixed effects	*R^2 marginal*			0.2%		
	fixed + random effects	*R^2 conditional*			43%		
F - affinity to moisture	fixed effects	α : Initial $_{(\mu\ 1976)}$	5.4	5.5	5.6		
		β : Temporal change $_{(2009\text{-}1976)}$	-0.1	0.04	0.1		
	Random effects	$\text{Intercept}_{\text{plot}}$				0.001	1%
	ε (error)	Residuals				0.13	99%
	fixed effects	*R^2 marginal*			0.2%		
	fixed + random effects	*R^2 conditional*			1%		

Appendix A-S5 - Temporal change of bryophyte richness per subplot (microhabitat) (mean ± se)

Supporting information to the paper Becker Scarpitta et al, 2017 - Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming, Journal of Vegetation Science.

	1976	2012	Nbr of subplots
Dead wood branches	2.1 ± 0.3	4.9 ± 0.5	15
Dead wood stump	3.7 ± 0.3	7.4 ± 0.5	32
Soil	3.5 ± 0.3	6.9 ± 0.5	44
All	3.3 ± 0.2	6.8 ± 0.3	91

ANNEXE B

SUPPLEMENTARY MATERIALS OF CHAPTER 3

Appendix B-S1 - Climatic trends in three regions of Québec, Canada

For long-lived perennial plants, responses to environmental change inevitably involve temporal lags. For the time span of our empirical data, roughly 1970-2015, we might consider the time period shifted 10 years earlier (1960-2005) to be the most relevant to predicting vegetation changes in our study (Figure B-S1). For a closely corresponding period of time (1960-2003), Yagouti et al. (2008) modeled and interpolated temperature trends across southern Québec. Park Forillon, in eastern Québec, fell in the zone showing 0-0.25 °C warming over this time period; for Mont-Mégantic it was 0.75-1.0 °C, and for Gatineau Park it was 1.0-1.25 °C. In the three parks, there has been no temporal change of mean annual precipitation (Figure B-S2).

Using modeled temperature data for each of our three parks extracted from ANUSPLINE (McKenney et al. 2011), we explored temporal trends for the period 1900-2010. For the full-time period, all three parks show significant warming, but the magnitude of slopes followed the same rank order: Forillon (0.12 ± SE=0.02 °C /decade) < Mégantic (0.14 ± 0.02 °C /decade) < Gatineau (0.18 ± 0.02 °C /decade). For the more relevant period 1960-2005, the differences, and especially the distinction of Forillon, were stronger: Forillon (0.12 ± 0.08 °C /decade) < Mégantic (0.20 ± 0.07 °C /decade) < Gatineau (0.27 ± 0.08 °C /decade). In sum, while the quantitative trends of temperature depend on time periods or methods, the rank order of sites is consistent.

Figure B-S1 - Temporal trends of mean annual temperature for 1900-2015 (a-c) and 1960-2005 (d-e; the period most relevant to our study).

(a) Forillon: F=37.64, $p<0.001$, adjR^2=0.24; (b) Mégantic: F=49.27, $p<0.001$, adjR^2=0.30; (c) Gatineau: F=71.60, $p<0.001$, adjR^2=0.38; (d) Forillon: F=2.35, p=0.132, adjR^2=0.13; (e) Mégantic: F=8.32, p=0.006, adjR^2=0.14 and (f) Gatineau: F=11.51, p=0.001, adjR^2=0.19. Data extracted from ANUSPLINE McKenney et al., (2011).

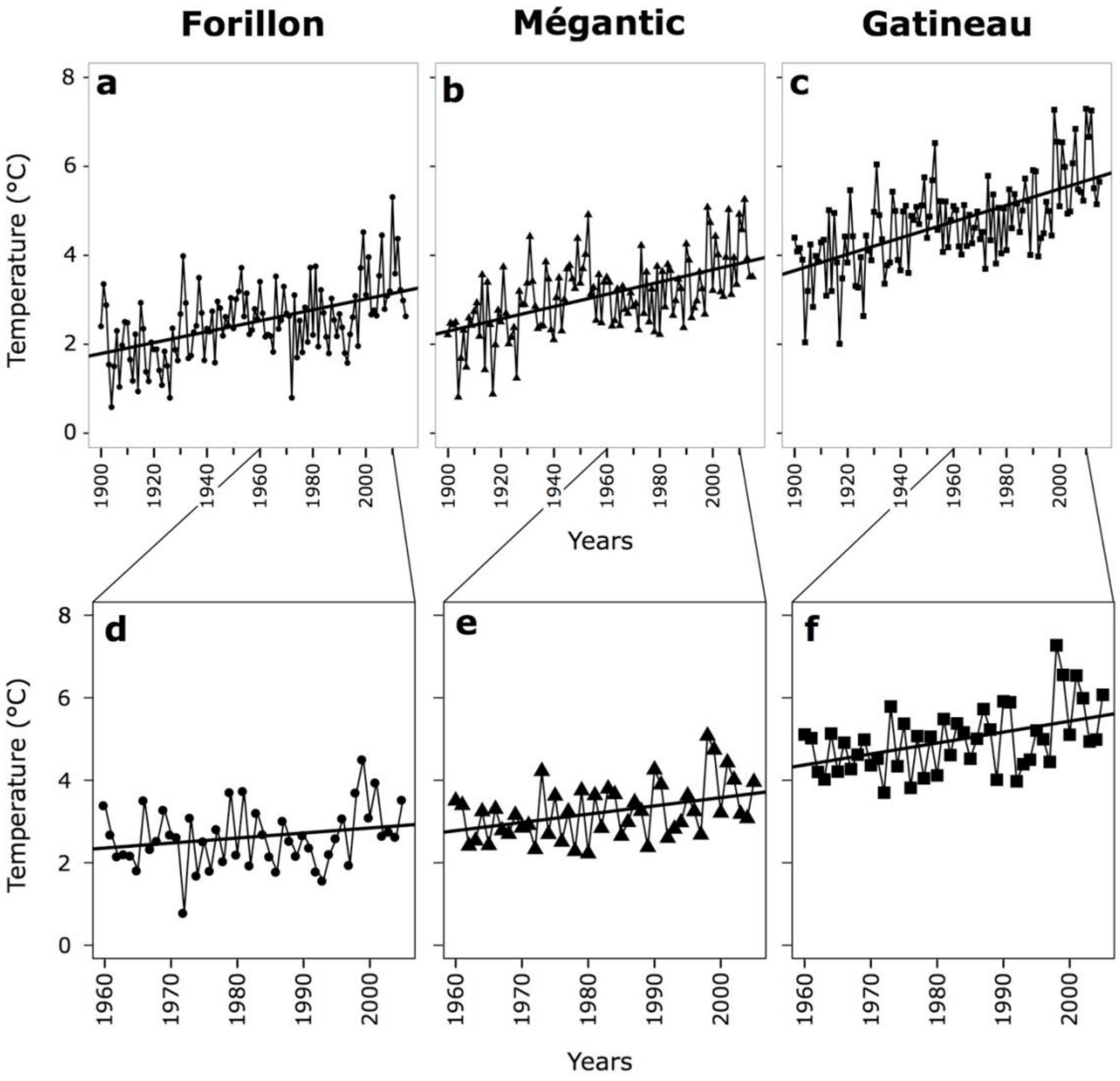
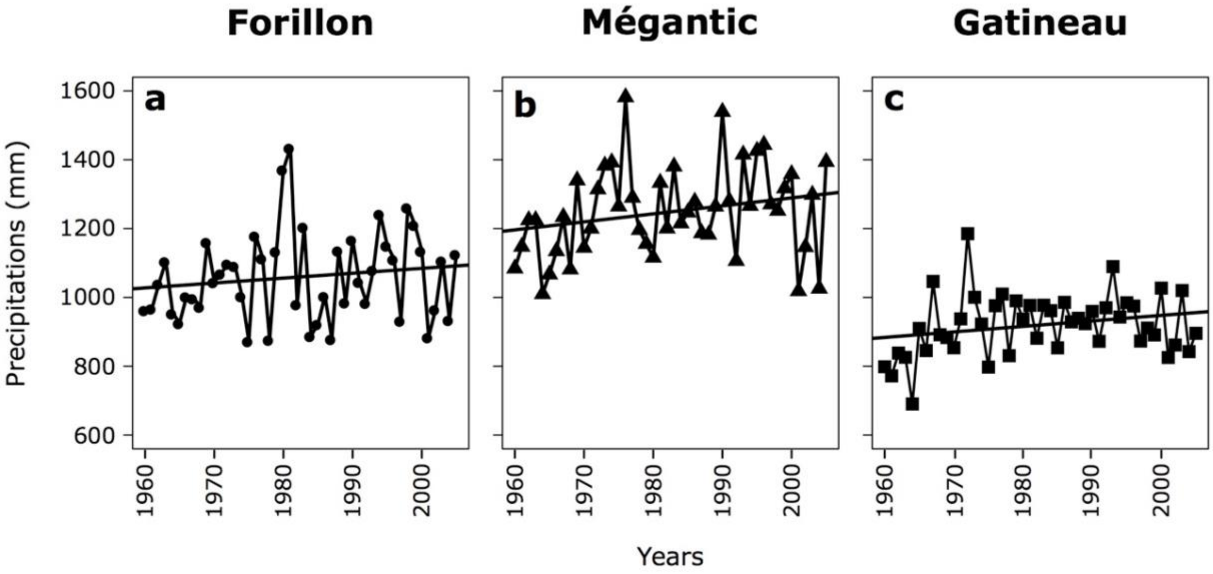


Figure B-S2 - Temporal trends of mean annual precipitation in each park.

We found no significant trends for the period 1960-2005 in (a) Forillon: F=0.99, p=0.33, adjR2=0, (b) Mégantic: F=2.65, p=0.10, adjR2=0.04, and (c) Gatineau: F=2.75, p=0.10, adjR2=0.04. Data extracted from ANUSPLINE McKenney et al., (2011).



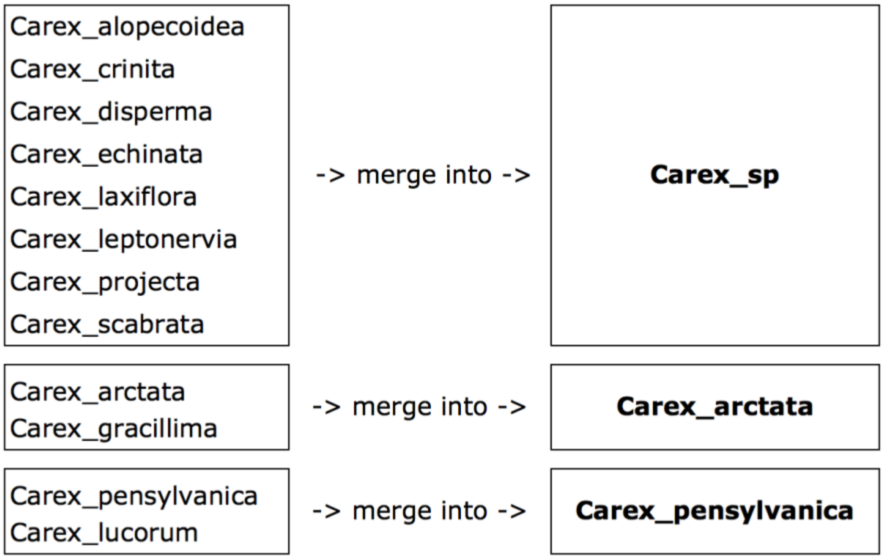
Appendix B-S2 – Taxonomic standardization between surveys

We present here a detailed account of taxonomic standardization across different data sets (six different surveys made by 5 different field teams). As a rule, any decision dictated by a given survey (e.g., removing a species because of high identification uncertainty) was applied to the data for all surveys. Although trees were not included in our analyses, we include them here (*Picea, Pinus…*), effectively as meta-data for the larger data set. Homogenization of data sets involved the following actions:

- Species present aboveground for only a brief period of the growing season were deleted given the strong likelihood that they were missed in some surveys. These species were: *Cardamine diphylla, C. pennsylvanica, Epifagus virginiana, Erythronium americanum, Monotropa uniflora, Corallorhiza maculata*, and *C. trifida*.
- All *Solidago* & *Eurybia* spp were deleted because of doubtful identification in the contemporary survey at Mont Megantic.
- *Oxalis acetosella* and *Oxalis montana* were both lumped to *O. acetosella*.
- Given inconsistent (or absent) identification at the species level (impossible without reproductive structures for some taxa), species were lumped to genus in the following cases: *Actaea* spp., *Amelanchier* spp., *Erigeron* spp., *Habenaria* spp., *Hieracium* spp., *Nabalus* spp., *Picea* spp., *Pyrola* spp., *Ranunculus* spp., *Ribes* spp., *Rubus* spp., *Sorbus* spp., *Thalictrum* spp., *Viola* spp., and some *Carex* spp. (see below for more information on *Carex*). For *Galium*, all species were lumped to the genus level except *Galium trifolium* for which we were confident of the identification by the different observers.
- In cases for which one species in the 1970s has since been split into multiple species, we use the original species name even if it now refers to a complex of species. For example, *Dryopteris spinulosa* and *D. intermedia* (modern species names) are collectively considered as *D. carthusiana*. All *Pinus* species were merged at the genus level.
- All *Poaceae* were merged at the family level for the Mont-Mégantic surveys. For Forillon and Gatineau, we retained easily identifiable species for which we know with

confidence that they do not occur in Mont-Mégantic. Forillon had some northern species that do not occur in the western part of the province, while Gatineau had some southern species absent from the rest of the province. Absence from Mont-Mégantic was confirmed via GBIF species distribution maps and an intensive botanical survey of Mont-Megantic park (Hall, 1998). In sum, the category *Poaceae* has the same meaning across all parks, with some individual species in this family considered at the species level.

- We applied the same methods we used for *Poaceae* to *Carex*: at the species level we retained: *Carex communis, C. deweyana, C. intumescens, C. pedunculata, C. platyphylla, C. arctata, and C. pensylvanica.* We merged species in following cases:



Carex_alopecoidea Carex_crinita Carex_disperma Carex_echinata Carex_laxiflora Carex_leptonervia Carex_projecta Carex_scabrata	-> merge into ->	**Carex_sp**
Carex_arctata Carex_gracillima	-> merge into ->	**Carex_arctata**
Carex_pensylvanica Carex_lucorum	-> merge into ->	**Carex_pensylvanica**

References

Hall, G. 1998. Inventaire floristique du Parc du Mont-Mégantic – Ministère de l'Environnement et de la Faune du Québec. Québec, Canada.

Appendix B-S3 – Species Temperature Index (STI) database

Species	STI
Abies balsamea	4.07
Acer pensylvanicum	5.89
Acer platanoides	9.70
Acer rubrum	12.53
Acer saccharum	5.76
Acer spicatum	4.15
Adiantum pedatum	11.04
Ageratina altissima	10.50
Agrimonia striata	6.21
Allium tricoccum	8.72
Alnus alnobetula	3.36
Alnus incana	6.44
Anaphalis margaritacea	6.18
Apocynum androsaemifolium	8.14
Aralia nudicaulis	6.64
Aralia racemosa	9.65
Arctium minus	9.53
Arisaema triphyllum	10.66
Asplenium viride	2.99
Betula alleghaniensis	4.58
Betula papyrifera	4.49
Betula populifolia	5.97
Botrychium virginianum	11.50
Brotherella recurvans	8.23
Caltha palustris	8.31
Carex arctata	5.17
Carex communis	8.61
Carex deweyana	6.17
Carex intumescens	10.01
Carex pedunculata	6.65
Carex pensylvanica	10.20
Carex platyphylla	10.24
Caulophyllum thalictroides	10.09
Chelone glabra	9.64
Chimaphila umbellata	7.42
Chrysosplenium americanum	8.82
Circaea alpina	6.93
Circaea canadensis	11.54
Clematis virginiana	10.48
Climacium dendroides	6.07
Clintonia borealis	6.04
Conioselinum chinense	2.00
Coptis trifolia	6.20
Cornus alternifolia	10.09
Cornus canadensis	4.55
Cornus rugosa	6.64
Cornus sericea	6.21
Corylus cornuta	8.91
Cystopteris bulbifera	8.82
Cystopteris fragilis	4.96
Dennstaedtia punctilobula	9.96
Deparia acrostichoides	10.34
Diervilla lonicera	6.64
Dirca palustris	9.47
Dryopteris carthusiana	7.63
Dryopteris goldiana	10.33
Dryopteris marginalis	10.49
Epigaea repens	10.95
Epilobium angustifolium	6.81
Epilobium ciliatum	6.32
Epilobium palustre	1.55
Equisetum pratense	3.68
Equisetum sylvaticum	4.55
Eupatorium maculatum	7.20
Fagus grandifolia	7.06
Fallopia cilinodis	6.42
Fragaria virginiana	8.82
Frangula alnus	8.74

Species	STI	Species	STI
Fraxinus americana	9.11	*Nemopanthus mucronatus*	6.36
Fraxinus nigra	5.39	*Oclemena acuminata*	9.11
Galeopsis tetrahit	5.66	*Oncophorus wahlenbergii*	4.98
Galium aparine	11.37	*Onoclea sensibilis*	10.27
Galium kamtschaticum	4.33	*Osmunda claytoniana*	8.55
Galium triflorum	10.37	*Osmundastrum cinnamomeum*	10.71
Gaultheria hispidula	5.35	*Ostrya virginiana*	9.73
Gaultheria procumbens	8.59	*Oxalis acetosella*	8.51
Geocalyx graveolens	7.94	*Oxalis stricta*	10.30
Geranium robertianum	7.13	*Panax trifolius*	8.28
Geum rivale	6.32	*Petasites frigidus*	5.13
Gymnocarpium disjunctum	2.11	*Phegopteris connectilis*	5.71
Heracleum maximum	5.90	*Pilosella caespitosa*	9.24
Huperzia lucidula	6.97	*Pinus strobus*	7.45
Hydrocotyle americana	8.10	*Polygonatum pubescens*	9.31
Impatiens capensis	10.14	*Polypodium virginianum*	9.35
Juncus tenuis	10.18	*Polystichum acrostichoides*	11.91
Juniperus communis	6.05	*Polystichum braunii*	4.59
Laportea canadensis	10.36	*Populus balsamifera*	4.83
Larix laricina	4.61	*Populus grandidentata*	5.85
Linnaea borealis	3.32	*Populus tremuloides*	4.82
Lonicera canadensis	6.08	*Prunella vulgaris*	10.55
Lycopodium annotinum	3.27	*Prunus pensylvanica*	5.70
Lycopodium clavatum	4.77	*Prunus serotina*	10.62
Lycopodium complanatum	5.60	*Prunus virginiana*	6.62
Lycopodium obscurum	5.67	*Pteridium aquilinum*	12.23
Lycopus uniflorus	7.06	*Quercus rubra*	9.83
Maianthemum canadense	6.64	*Rhamnus cathartica*	8.61
Maianthemum racemosum	11.25	*Salix discolor*	6.64
Maianthemum trifolium	6.00	*Sambucus racemosa*	7.66
Matteuccia struthiopteris	6.30	*Sanguinaria canadensis*	10.95
Medeola virginiana	10.33	*Sanicula marilandica*	6.40
Melampyrum lineare	8.83	*Scutellaria lateriflora*	9.53
Mitchella repens	12.50	*Solanum dulcamara*	8.82
Mitella diphylla	9.44	*Solidago caesia*	12.44
Mitella nuda	3.27	*Streptopus amplexifolius*	3.91
Moneses uniflora	4.95	*Streptopus lanceolatus*	5.49

Species	**STI**
Symphyotrichum cordifolium	10.37
Symphyotrichum puniceum	9.18
Taraxacum campylodes	9.88
Taxus canadensis	6.03
Thelypteris confluens	10.13
Thelypteris noveboracensis	10.94
Thuja occidentalis	4.87
Tiarella cordifolia	10.33
Tilia americana	7.21
Tortella tortuosa	5.63
Trientalis borealis	6.36
Trillium cernuum	6.26
Trillium erectum	9.31
Trillium grandiflorum	9.48
Trillium undulatum	9.08
Tsuga canadensis	6.54
Ulmus americana	9.64
Uvularia grandiflora	10.22
Vaccinium angustifolium	6.36
Vaccinium myrtilloides	5.85
Vaccinium ovalifolium	-1.56
Veratrum viride	9.34
Veronica officinalis	8.93
Viburnum acerifolium	11.45
Viburnum edule	1.39
Viburnum lantanoides	8.93
Viburnum lentago	8.63
Viburnum nudum	14.93
Viburnum opulus	7.18
Vicia cracca	6.46

Appendix B-S4 – Mean abundance-weighted elevation and number of occurrences per species per survey in Forillon and Mont-Mégantic

		Elevation		Occurrences	
Species	**Park**	**Original**	**Recent**	**Original**	**Recent**
Acer spicatum	Forillon	205	209	44	44
Actaea sp	Forillon	165	383	7	6
Amelanchier sp	Forillon	345	291	23	19
Aralia nudicaulis	Forillon	151	193	46	43
Athyrium filix femina	Forillon	146	258	9	6
Chimaphila umbellata	Forillon	182	168	22	17
Clintonia borealis	Forillon	211	215	44	40
Coptis trifolia	Forillon	279	342	14	8
Cornus alternifolia	Forillon	172	126	10	14
Cornus canadensis	Forillon	222	243	38	38
Cornus sericea	Forillon	102	139	8	10
Corylus cornuta	Forillon	153	170	30	35
Diervilla lonicera	Forillon	88	117	5	7
Dryopteris carthusiana	Forillon	300	259	34	36
Galium triflorum	Forillon	154	369	15	4
Gymnocarpium disjunctum	Forillon	199	149	15	20
Linnaea borealis	Forillon	260	177	25	21
Lonicera canadensis	Forillon	151	154	27	30
Maianthemum canadense	Forillon	199	167	33	33
Mitella nuda	Forillon	150	241	16	4
Nabalus sp	Forillon	148	180	12	12
Osmundastrum cinnamomeum	Forillon	343	115	14	10
Oxalis acetosella	Forillon	363	274	19	22
Phegopteris connectilis	Forillon	184	141	11	12
Pilosella caespitosa	Forillon	112	116	5	6
Pteridium aquilinum	Forillon	138	150	13	11
Pyrola sp	Forillon	184	136	32	23
Ribes sp	Forillon	284	317	21	22
Rubus sp	Forillon	138	136	24	16
Sambucus racemosa	Forillon	155	263	4	14

		Elevation		Occurrences	
Species	**Park**	**Original**	**Recent**	**Original**	**Recent**
Sorbus sp	Forillon	265	272	43	46
Streptopus lanceolatus	Forillon	159	132	30	29
Taxus canadensis	Forillon	142	175	20	27
Trientalis borealis	Forillon	178	176	44	43
Viburnum edule	Forillon	194	279	8	10
Acer spicatum	Megantic	681	717	43	38
Actaea sp	Megantic	656	597	12	10
Aralia nudicaulis	Megantic	613	692	28	36
Arisaema triphyllum	Megantic	632	611	6	13
Athyrium filix femina	Megantic	616	623	22	36
Carex arctata	Megantic	611	639	5	21
Carex intumescens	Megantic	587	656	19	30
Carex sp	Megantic	557	711	20	39
Circaea alpina	Megantic	590	655	4	14
Clintonia borealis	Megantic	706	870	41	44
Coptis trifolia	Megantic	650	774	18	22
Cornus alternifolia	Megantic	603	608	19	11
Cornus canadensis	Megantic	803	897	16	19
Corylus cornuta	Megantic	571	619	11	10
Deparia acrostichoides	Megantic	605	584	12	11
Dryopteris carthusiana	Megantic	673	716	47	48
Galium triflorum	Megantic	528	655	16	11
Gymnocarpium disjunctum	Megantic	482	673	5	4
Huperzia lucidula	Megantic	652	678	22	34
Impatiens capensis	Megantic	494	604	15	13
Lonicera canadensis	Megantic	578	607	19	24
Lycopodium obscurum	Megantic	467	561	4	7
Maianthemum canadense	Megantic	589	639	21	36
Maianthemum racemosum	Megantic	637	624	19	22
Medeola virginiana	Megantic	568	520	5	6
Mitchella repens	Megantic	575	615	4	6
Nabalus sp	Megantic	549	632	12	17
Oclemena acuminata	Megantic	699	680	32	42

		Elevation		Occurrences	
Species	**Park**	**Original**	**Recent**	**Original**	**Recent**
Osmorhiza claytonii	Megantic	588	617	11	12
Oxalis acetosella	Megantic	823	733	40	48
Phegopteris connectilis	Megantic	643	660	22	36
Poaceae	Megantic	535	640	27	33
Polygonatum pubescens	Megantic	629	648	13	21
Polypodium virginianum	Megantic	643	669	4	4
Polystichum acrostichoides	Megantic	592	591	4	5
Pyrola sp	Megantic	579	645	5	5
Ribes sp	Megantic	688	773	20	28
Rubus sp	Megantic	742	670	26	31
Sambucus racemosa	Megantic	622	640	27	25
Sorbus sp	Megantic	732	784	18	23
Streptopus amplexifolius	Megantic	728	731	14	17
Streptopus lanceolatus	Megantic	637	684	24	37
Thelypteris noveboracensis	Megantic	572	573	19	18
Tiarella cordifolia	Megantic	616	635	22	22
Trientalis borealis	Megantic	635	696	23	27
Trillium erectum	Megantic	652	672	27	38
Trillium undulatum	Megantic	618	620	17	23
Veratrum viride	Megantic	628	646	5	7
Viburnum lantanoides	Megantic	624	649	32	34
Viola sp	Megantic	605	615	28	18

Appendix B-S5 – Species occurrences per survey (number of plots where species were recorded)

	Forillon		Mont-Mégantic		Gatineau	
Species	**Original**	**Recent**	**Original**	**Recent**	**Original**	**Recent**
Acer spicatum	44	44	43	38	-	-
Actaea sp	7	6	12	10	4	4
Adiantum pedatum	-	-	-	-	-	2
Ageratina altissima	-	-	7	2	-	-
Agrimonia striata	-	-	-	-	1	-
Allium tricoccum	-	-	1	-	-	3
Amelanchier sp	23	19	-	-	1	6
Amphicarpaea bracteatae	-	-	-	-	-	1
Anaphalis margaritacea	1	2	-	-	-	-
Antennaria howellii	-	-	-	-	1	-
Apocynum androsaemifolium	2	-	-	-	-	-
Aralia nudicaulis	46	43	28	36	16	18
Aralia racemosa	-	-	2	3	-	-
Arctium minus	-	-	-	-	-	1
Arisaema triphyllum	-	-	6	13	-	1
Asplenium viride	-	1	-	-	-	-
Athyrium filix femina	9	6	22	36	-	2
Botrychium virginianum	2	-	8	1	1	2
Caltha palustris	2	-	-	-	-	-
Carex arctata	8	1	5	21	17	10
Carex communis	-	-	-	2	-	6
Carex deweyana	-	-	1	13	1	7
Carex intumescens	-	-	19	30	-	2
Carex pedunculata	-	-	-	-	1	-
Carex pensylvanica	-	-	-	-	1	1
Carex platyphylla	-	-	-	-	-	1
Carex sp	2	7	20	39	4	18
Caulophyllum thalictroides	-	-	-	1	2	3
Chelone glabra	-	-	2	1	-	-
Chimaphila umbellata	22	17	-	-	1	2
Chrysosplenium americanum	1	-	2	4	-	-
Circaea alpina	3	2	4	14	1	1

	Forillon		Mont-Mégantic		Gatineau	
Species	**Original**	**Recent**	**Original**	**Recent**	**Original**	**Recent**
Circaea canadensis	-	-	-	-	1	-
Clematis virginiana	-	-	-	-	-	1
Clintonia borealis	44	40	41	44	4	4
Conioselinum chinense	1	-	-	-	-	-
Coptis trifolia	14	8	18	22	-	2
Cornus alternifolia	10	14	19	11	1	2
Cornus canadensis	38	38	16	19	-	-
Cornus sericea	8	10	-	-	-	-
Corylus cornuta	30	35	11	10	1	1
Cypripedium acaule	-	-	2	5	-	1
Cystopteris bulbifera	-	1	-	-	-	-
Cystopteris fragilis	-	1	-	-	2	3
Dennstaedtia punctilobula	-	-	-	22	-	-
Deparia acrostichoides	-	-	12	11	1	-
Diervilla lonicera	5	7	4	1	3	4
Dirca palustris	-	-	-	-	2	5
Dryopteris carthusiana	34	36	47	48	14	18
Dryopteris goldiana	-	-	1	-	-	-
Dryopteris marginalis	-	-	-	-	9	9
Epigaea repens	1	-	-	-	-	-
Epilobium angustifolium	6	1	3	-	-	-
Epilobium ciliatum	-	-	1	4	-	-
Epilobium palustre	1	-	-	-	-	-
Epipactis helleborine	-	9	1	8	2	11
Equisetum pratense	2	1	-	-	-	-
Equisetum sylvaticum	5	1	3	3	-	-
Erigeron sp	-	-	1	-	-	1
Eupatorium maculatum	1	-	1	-	-	-
Fallopia cilinodis	-	-	-	-	-	1
Fragaria virginiana	3	1	2	1	-	-
Frangula alnus	-	-	-	-	-	1
Galeopsis tetrahit	-	-	-	8	-	2
Galium aparine	-	-	-	-	1	1
Galium brevipes	-	-	-	-	-	1
Galium kamtschaticum	1	-	3	7	-	-

	Forillon		**Mont-Mégantic**		**Gatineau**	
Species	**Original**	**Recent**	**Original**	**Recent**	**Original**	**Recent**
Galium triflorum	15	4	16	11	3	4
Gaultheria hispidula	2	5	1	2	-	-
Gaultheria procumbens	-	-	-	1	3	4
Geranium robertianum	-	-	-	-	-	1
Geum rivale	2	-	-	-	-	-
Goodyera oblongifolia	2	-	-	-	-	-
Goodyera repens	-	-	2	-	-	-
Gymnocarpium disjunctum	15	20	5	4	4	-
Habenaria sp	-	-	1	6	-	-
Heracleum maximum	1	1	-	-	-	-
Hieracium sp	-	-	-	-	1	-
Huperzia lucidula	5	-	22	34	1	4
Hydrocotyle americana	-	-	-	1	-	-
Hypericum perforatum	1	1	-	-	-	-
Impatiens capensis	2	-	15	13	-	-
Juncus tenuis	-	-	-	1	-	-
Juniperus communis	-	-	-	-	-	1
Laportea canadensis	-	-	-	-	-	1
Linnaea borealis	25	21	1	-	1	1
Lonicera canadensis	27	30	19	24	10	15
Lycopodium annotinum	11	-	1	6	-	1
Lycopodium clavatum	-	-	-	1	-	-
Lycopodium complanatum	-	-	-	-	1	1
Lycopodium obscurum	4	1	4	7	3	4
Lycopus uniflorus	-	-	-	1	-	-
Maianthemum canadense	33	33	21	36	18	22
Maianthemum racemosum	2	4	19	22	5	11
Maianthemum trifolium	1	-	-	-	-	-
Matteuccia struthiopteris	2	1	1	2	-	-
Medeola virginiana	-	-	5	6	6	6
Melampyrum lineare	-	-	-	-	-	2
Mitchella repens	1	-	4	6	4	7
Mitella diphylla	-	-	-	-	1	-
Mitella nuda	16	4	-	-	-	-
Moneses uniflora	12	3	-	1	-	-

	Forillon		**Mont-Mégantic**		**Gatineau**	
Species	**Original**	**Recent**	**Original**	**Recent**	**Original**	**Recent**
Nabalus sp	12	12	12	17	7	6
Nemopanthus mucronatus	1	-	3	3	-	-
Neottia convallarioides	2	-	-	-	-	-
Neottia cordata	-	-	-	1	-	-
Oclemena acuminata	-	-	32	42	10	2
Onoclea sensibilis	-	1	2	4	1	-
Osmorhiza chilensis	4	-	-	-	-	-
Osmorhiza claytonii	-	-	11	12	7	3
Osmunda claytoniana	-	-	9	-	-	-
Osmundastrum cinnamomeum	14	10	3	11	1	-
Ostrya virginiana	-	-	1	1	19	21
Oxalis acetosella	19	22	40	48	-	-
Oxalis stricta	-	-	-	-	1	1
Panax quinquefolius	-	-	-	2	-	-
Panax trifolius	-	-	-	-	-	1
Patis racemosae	-	-	-	-	4	2
Petasites frigidus	1	-	-	-	-	-
Phegopteris connectilis	11	12	22	36	1	-
Pilosella caespitosa	5	6	-	-	-	-
Platanthera obtusata	1	-	-	-	-	-
Poaceae	3	1	27	33	13	21
Polygonatum pubescens	-	-	13	21	17	25
Polypodium virginianum	-	1	4	4	3	3
Polystichum acrostichoides	-	-	4	5	-	-
Polystichum braunii	-	1	2	3	-	-
Prunella vulgaris	1	-	-	-	1	1
Pteridium aquilinum	13	11	2	2	5	6
Pyrola sp	32	23	5	5	2	3
Ranunculus sp	3	1	1	1	1	2
Rhamnus cathartica	-	-	-	-	-	1
Ribes sp	21	22	20	28	4	6
Rubus sp	24	16	26	31	1	3
Sambucus racemosa	4	14	27	25	4	9
Sanguinaria canadensis	-	-	-	-	-	1
Sanicula marilandica	1	-	-	-	-	1

	Forillon		**Mont-Mégantic**		**Gatineau**	
Species	**Original**	**Recent**	**Original**	**Recent**	**Original**	**Recent**
Scutellaria lateriflora	-	1	-	-	-	-
Solanum dulcamara	-	-	-	-	-	1
Solidago caesia	-	-	-	-	-	9
Sorbus sp	43	46	18	23	-	-
Streptopus amplexifolius	1	-	14	17	-	-
Streptopus lanceolatus	30	29	24	37	12	7
Symphyotrichum cordifolium	-	-	-	-	2	3
Symphyotrichum puniceum	3	-	1	3	-	-
Taraxacum campylodes	-	-	-	5	-	-
Taxus canadensis	20	27	2	1	-	-
Thalictrum sp	-	-	2	6	-	1
Thelypteris noveboracensis	-	-	19	18	-	-
Tiarella cordifolia	-	-	22	22	3	-
Trientalis borealis	44	43	23	27	8	9
Trillium cernuum	3	3	-	-	-	-
Trillium erectum	-	-	27	38	10	15
Trillium grandiflorum	-	-	-	-	6	5
Trillium undulatum	-	-	17	23	3	2
Uvularia grandiflora	-	-	-	-	9	6
Vaccinium angustifolium	1	-	-	-	2	3
Vaccinium myrtilloides	1	-	3	4	-	-
Vaccinium ovalifolium	6	3	-	-	-	-
Veratrum viride	-	-	5	7	-	-
Veronica officinalis	-	-	-	-	-	1
Viburnum acerifolium	-	-	-	-	-	3
Viburnum edule	8	10	-	-	-	-
Viburnum lantanoides	-	-	32	34	4	10
Viburnum lentago	-	-	-	-	-	1
Viburnum nudum	-	-	9	3	-	-
Viburnum opulus	2	1	-	-	-	-
Vicia cracca	-	1	-	-	-	-
Viola sp	5	1	28	18	8	8

Appendix B-S6 – Results for unweighted Community Temperature Indices (CTIuw)

In the main text we report results for abundance-weighted Community Temperate Indices (CTIw). The unweighted version, CTIuw, is the raw median STI across species in a given community, and thus differences among plots or over time are influenced only by which species are present or absent, not their abundances. Table B-S6 and Figure B-S6 report results for CTIuw.

Table B-S6 - Parameter estimates from linear mixed models for CTIuw.

	Effect	Fvalue	df	Pr(>|t|)	R^2m	R^2c
Forillon						
	Time	0.06	48	0.8	0.02	0.41
	Elevation	1.08	47	0.31		
Megantic						
	Time	1.31	47	0.26	0.21	0.61
	Elevation	**16.52**	**47**	**<0.001**		
Gatineau						
	Time	0.47	27	0.5	0.004	0.49

R^2m is the marginal R^2, measuring the proportion of variance explained by fixed effects; R^2c is conditional R^2, the proportion of variance explained by both fixed and random effects.

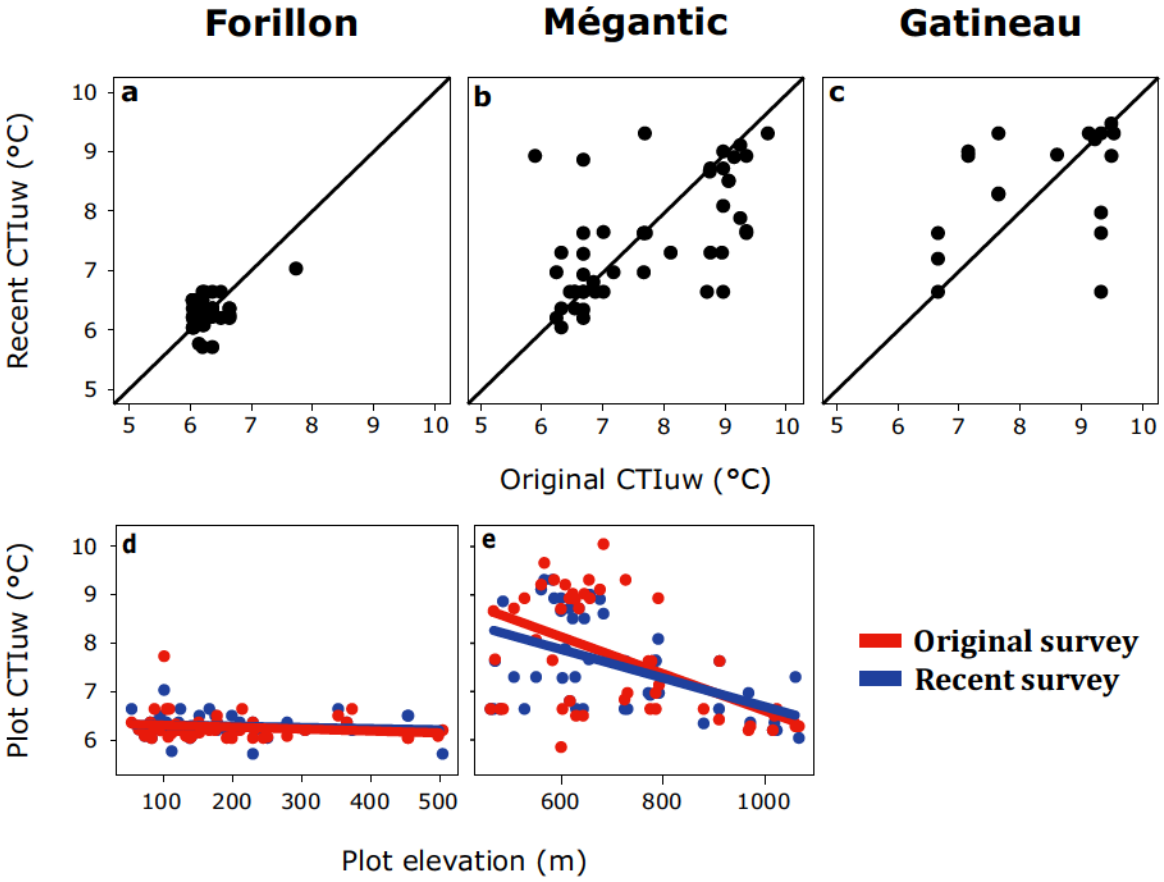


Figure B-S6 - Unweighted community Temperature Indices (CTIuw) during the two-time periods and across the elevational gradient.

(a-c) CTIuw at Forillon, Mont-Mégantic, and Gatineau, with the 1:1 line indicating no temporal change between two times. (d-e) Relationships between CTIuw and elevation for each time period at Forillon and Mont-Mégantic. Red and blue illustrate original and recent surveys, respectively. Each point is a plot in all panels.

Appendix B-S7 – Individual species contributions to Community Temperature Indices (CTIw) for high elevation plots at Mont-Mégantic

Temporal changes in abundance of two dominant species made major contributions to the unexpected decline of CTIw at high elevations (i.e. plots >800m) at Mont-Mégantic. *Oxalis acetosella* showed a marked decline in abundance, and therefore contribution to CTIw, while the opposite was true for *Dryopteris carthusiana*. In Table B-S7, we report for each plot at high elevation the CTIw, the STI weighted by the relative abundance of the species in the given plot (i.e. STI*RA) and the species contribution to the plot CTIw, which the simple percentage of the total CTIw that the species represent (e.g. *Dryopteris* contributed about 13% of the total CTIw of the original survey of plot 38).

Table B-S7 – Local contribution of *O. acetosella* and *D. carthusiana* to CTIw in high elevation (>800 m) plots at Mont-Mégantic.

Plot	Year	CTI_w	STI*RA - Oxalis	%ofCTI $_w$	STI*RA - Dryopteris	%ofCTI $_w$
38	Original	8.3	6.9	83	1.1	13
38	Recent	6.3	0.2	4	1.3	20
6	Original	7.4	3.8	51	1.4	18
6	Recent	7.5	0.1	1	6.7	90
65	Original	7.9	5.3	67	1.2	15
65	Recent	7.0	0.7	9	3.5	50
67	Original	8.3	7.5	91	0.3	4
67	Recent	7.4	0.2	3	5.6	75
68	Original	8.1	5.1	63	2.8	34
68	Recent	6.6	1.7	26	1.5	23
7	Original	8.3	7.9	95	0.1	1
7	Recent	7.1	0.5	7	2.5	36
81	Original	8.0	6.4	81	0.3	3
81	Recent	7.3	0.7	10	3.8	52
82	Original	8.3	7.3	89	0.1	1
82	Recent	7.3	0.9	12	4.6	63
91	Original	6.8	2.1	31	0.0	0
91	Recent	6.8	0.1	1	3.6	53
92	Original	8.2	7.1	87	0.5	6
92	Recent	5.7	0.3	5	0.3	5

For O acetosella, STI = 8.6; for D. carthusiana, STI = 7.6. STI*RA is the Species Temperature Index multiplied by the relative abundance (RA) of species in the community and % of CTIw is the species contribution of total CTIw for original and recent survey.

ANNEXE C

SUPPLEMENTARY MATERIALS OF CHAPTER 4

Appendix C-S1 - Taxonomic standardization of bryophytes species between surveys

We present here a detailed account of taxonomic standardization of bryophytes species across different data sets (four surveys made by 3 different field teams). As a rule, any decision made by a given survey (e.g., merging species because of high morphological resemblances) was applied to all surveys. Homogenization of data sets involved the following merging procedure:

In cases for which one species in the 1970s has since been split into multiple species, we use the original species name even if it now refers to a complex of species.

Species with very close morphologically sharing the same ecological requirements were merge under a single name.

	Doubtfull species	**Merge into**
Forillon original		
	Hypnum lindbergii *Hypnum pratense*	*Hypnum lindbergii*
	Hylocomium pyrenaicum *Hylocomium umbratum*	*Hylocomiastrum umbratum*
Forillon recent		
	Plagiothecium cavifolium *Plagiothecium latebricola*	*Plagiothecium cavifolium*
	Brachythecium curtum *Brachythecium rivulare* *Brachythecium starkei* *Kinbergia praelonga*	*Brachythecium curtum*
	Brachythecium campestre *Brachythecium falcatum* *Brachythecium rutabulum*	*Brachythecium campestre*
	Barbilophozia barbata *Barbilophozia hatcheri* *Barbilophozia lycopodioides*	*Barbilophozia hatcheri*
	Dicranum brevifolium *Dicranum fuscescens*	*Dicranum fuscescens*
	Herzogiella striatella *Herzogiella turfacea*	*Herzogiella striatella*
	Thuidium delicatum *Thuidium recognitum*	*Thuidium delicatum*

Mégantic original		
	Amblystegium varium	*Hygroamblystegium varium*
	Atrichum oerstedianum	*Atrichum crispulum*
	Brachythecium rutabulum	*Brachythecium campestre*
	Brachythecium salebrosum	*Brachythecium acutum*
	Brachythecium starkei	*Brachythecium curtum*
	Eurhynchium pulchellum	*Eurhynchiastrum pulchellum*
	Hylocomium umbratum	*Hylocomiastrum umbratum*
	Hypnum pratense	*Hypnum lindbergii*
	Hypnum reptile	*Hypnum pallescens*
	Isopterygium distichaceum	*Pseudotaxiphyllum distichaceum*
	Jungermannia lanceolata	*Jungermania leiantha*
	Lophozia attenuata	*Barbilophozia attenuata*
	Mnium ciliare	*Plagiomnium ciliare*
	Mnium cusidatum	*Plagiomnium cuspidatum*
	Mnium medium	*Plagiomnium medium*
	Mnium ponctuatum	*Rhizomnium punctatum*
	Polytrichum gracile	*Polytrichum longisetum*
	Polytrichum ohioense	*Polytrichastrum pallidisetum*
	Porella platyphylloïdea	*Porella platyphylla*
	Sphagnum centrale *Sphagnum girgensohnii* *Sphagnum recurvum* *Sphagnum robustum* *Sphagnum squarrosum* *Sphagnum warnstorfianum*	*Sphagnum sp*
Mégantic recent		
	Brachythecium curtum *Brachythecium rivulare* *Kinbergia praelonga*	*Brachythecium curtum*
	Brachythecium rutabulum	*Brachythecium campestre*
	Calypogeia neesiana *Calypogeia mulleriana*	*Calypogeia neesiana*
	Dicranum ontariense *Dicranum polysetum*	*Dicranum polysetum*
	Hylocomiastrum pyrenaicum *Hylocomiastrum umbratum*	*Hylocomiastrum umbratum*
	Polytrichastrum ohioense *Polytrichastrum pallidisetum*	*Polytrichastrum pallidisetum*
	Fissidens dubius	*Fissidens osmundoides*

Appendix C-S2 - Mean species elevation and sum of occurrences for bryophytes for original and recent survey in Forillon and Mont-Mégantic

			Elevation		Occurrences	
Species	**Strate**	**Park**	**Original**	**Rencent**	**Original**	**Recent**
Atrichum altecristatum	bryophytes	PN_Forillon	0	83	0	1
Aulacomnium palustre	bryophytes	PN_Forillon	0	105	0	1
Barbilophozia hatcheri	bryophytes	PN_Forillon	317	220	3	5
Bazzania trilobata	bryophytes	PN_Forillon	107	118	5	5
Blepharostoma trichophyllum	bryophytes	PN_Forillon	112	128	1	2
Brachythecium campestre	bryophytes	PN_Forillon	0	115	0	11
Brachythecium curtum	bryophytes	PN_Forillon	215	223	24	17
Brachythecium erytrorhizon	bryophytes	PN_Forillon	81	0	1	0
Brachythecium reflexum	bryophytes	PN_Forillon	171	259	7	4
Brachythecium velutinum	bryophytes	PN_Forillon	65	0	1	0
Brotherella recurvans	bryophytes	PN_Forillon	0	305	0	1
Bryhnia novae-angliae	bryophytes	PN_Forillon	118	0	1	0
Bryum creberrimum	bryophytes	PN_Forillon	0	199	0	1
Callicladium haldanianum	bryophytes	PN_Forillon	120	129	3	8
Calypogeia integristipula	bryophytes	PN_Forillon	0	185	0	3
Campyliadelphus chrysophyllus	bryophytes	PN_Forillon	0	132	0	2
Campylophyllum hispidulum	bryophytes	PN_Forillon	65	0	1	0
Cephalozia media	bryophytes	PN_Forillon	498	0	1	0
Chiloscyphus polyanthos	bryophytes	PN_Forillon	0	214	0	1
Climacium dendroides	bryophytes	PN_Forillon	118	69	1	2
Dicranella heteromalla	bryophytes	PN_Forillon	0	232	0	1
Dicranum fuscescens	bryophytes	PN_Forillon	230	265	30	5
Dicranum majus	bryophytes	PN_Forillon	219	253	12	11
Dicranum montanum	bryophytes	PN_Forillon	144	218	3	21
Dicranum polysetum	bryophytes	PN_Forillon	95	213	3	17
Dicranum scoparium	bryophytes	PN_Forillon	196	195	32	32
Dicranum viride	bryophytes	PN_Forillon	0	151	0	1
Eurhynchiastrum pulchellum	bryophytes	PN_Forillon	110	0	2	0
Fissidens bryoides	bryophytes	PN_Forillon	0	199	0	1
Geocalyx graveolens	bryophytes	PN_Forillon	124	0	1	0
Herzogiella striatella	bryophytes	PN_Forillon	0	170	0	2
Hylocomiastrum umbratum	bryophytes	PN_Forillon	191	243	27	14

			Elevation		Occurrences	
Species	**Strate**	**Park**	**Original**	**Rencent**	**Original**	**Recent**
Hypnum lindbergii	bryophytes	PN_Forillon	134	54	3	1
Hypnum pallescens	bryophytes	PN_Forillon	341	0	3	0
Hypnum plicatulum	bryophytes	PN_Forillon	0	230	0	1
Jamesoniella autumnalis	bryophytes	PN_Forillon	0	201	0	2
Jungermannia leiantha	bryophytes	PN_Forillon	498	82	1	1
Lepidozia reptans	bryophytes	PN_Forillon	244	150	8	2
Lophozia bicrenata	bryophytes	PN_Forillon	0	367	0	2
Marchantia polymorpha	bryophytes	PN_Forillon	118	0	1	0
Mnium lycopodioides	bryophytes	PN_Forillon	0	153	0	2
Mnium spinulosum	bryophytes	PN_Forillon	0	305	0	1
Paraleucobryum longifolium	bryophytes	PN_Forillon	81	0	1	0
Plagiochila porelloides	bryophytes	PN_Forillon	118	129	1	6
Plagiomnium ciliare	bryophytes	PN_Forillon	0	82	0	1
Plagiomnium cuspidatum	bryophytes	PN_Forillon	124	147	2	4
Plagiomnium medium	bryophytes	PN_Forillon	0	112	0	2
Plagiothecium cavifolium	bryophytes	PN_Forillon	0	165	0	3
Plagiothecium denticulatum	bryophytes	PN_Forillon	81	0	1	0
Plagiothecium laetum	bryophytes	PN_Forillon	0	364	0	5
Pleurozium schreberi	bryophytes	PN_Forillon	226	217	24	32
Pohlia nutans	bryophytes	PN_Forillon	0	150	0	2
Polytrichastrum alpinum	bryophytes	PN_Forillon	0	157	0	4
Polytrichastrum formosum	bryophytes	PN_Forillon	0	369	0	5
Polytrichastrum pallidisetum	bryophytes	PN_Forillon	0	205	0	2
Polytrichum commune	bryophytes	PN_Forillon	178	0	1	0
Polytrichum juniperinum	bryophytes	PN_Forillon	296	133	12	12
Pseudocalliergon brevifolium	bryophytes	PN_Forillon	0	167	0	1
Pseudoleskeella tectorum	bryophytes	PN_Forillon	0	120	0	8
Ptilidium ciliare	bryophytes	PN_Forillon	0	504	0	1
Ptilium crista-castrensis	bryophytes	PN_Forillon	233	257	15	10
Rhizomnium magnifolium	bryophytes	PN_Forillon	129	0	2	0
Rhynchostegium serrulatum	bryophytes	PN_Forillon	0	109	0	1
Rhytidiadelphus squarrosus	bryophytes	PN_Forillon	118	0	1	0
Rhytidiadelphus triquetrus	bryophytes	PN_Forillon	150	128	6	6
Sanionia uncinata	bryophytes	PN_Forillon	115	115	1	1
Sphagnum sp	bryophytes	PN_Forillon	118	376	1	3
Tetraphis pellucida	bryophytes	PN_Forillon	139	139	2	1

			Elevation		Occurrences	
Species	**Strate**	**Park**	**Original**	**Rencent**	**Original**	**Recent**
Tortella tortuosa	bryophytes	PN_Forillon	0	65	0	1
Trichocolea tomentella	bryophytes	PN_Forillon	129	0	2	0
Atrichum altecristatum	bryophytes	PN_Megantic	493	597	1	17
Atrichum crispulum	bryophytes	PN_Megantic	583	514	4	2
Barbilophozia attenuata	bryophytes	PN_Megantic	1016	0	1	0
Barbilophozia hatcheri	bryophytes	PN_Megantic	1016	0	1	0
Bazzania trilobata	bryophytes	PN_Megantic	778	640	9	12
Brachythecium acutum	bryophytes	PN_Megantic	0	493	0	1
Brachythecium campestre	bryophytes	PN_Megantic	0	753	0	4
Brachythecium curtum	bryophytes	PN_Megantic	632	761	7	9
Brachythecium populeum	bryophytes	PN_Megantic	612	0	2	0
Brachythecium reflexum	bryophytes	PN_Megantic	617	784	7	1
Brachythecium rotaeanum	bryophytes	PN_Megantic	0	614	0	1
Brotherella recurvans	bryophytes	PN_Megantic	753	0	25	0
Bryhnia novae-angliae	bryophytes	PN_Megantic	587	615	12	4
Caliergonella cuspidata	bryophytes	PN_Megantic	0	607	0	3
Callicladium haldanianum	bryophytes	PN_Megantic	564	629	9	9
Calligeron cordifolium	bryophytes	PN_Megantic	466	0	1	0
Calypogeia neesiana	bryophytes	PN_Megantic	0	783	0	2
Cephalozia media	bryophytes	PN_Megantic	877	0	1	0
Climacium dendroides	bryophytes	PN_Megantic	466	0	1	0
Conocephalum salebrosum	bryophytes	PN_Megantic	0	576	0	1
Dicranella heteromalla	bryophytes	PN_Megantic	0	626	0	2
Dicranowiesia crispula	bryophytes	PN_Megantic	0	460	0	1
Dicranum flagellare	bryophytes	PN_Megantic	589	460	3	1
Dicranum fulvum	bryophytes	PN_Megantic	541	0	1	0
Dicranum fuscescens	bryophytes	PN_Megantic	796	619	21	2
Dicranum montanum	bryophytes	PN_Megantic	827	703	8	16
Dicranum polysetum	bryophytes	PN_Megantic	0	589	0	10
Dicranum scoparium	bryophytes	PN_Megantic	597	770	11	21
Dicranum viride	bryophytes	PN_Megantic	0	577	0	2
Diphyscium foliosum	bryophytes	PN_Megantic	0	598	0	1
Fissidens osmundoides	bryophytes	PN_Megantic	0	606	0	1
Herzogiella striatella	bryophytes	PN_Megantic	0	626	0	1
Hygroamblystegium varium	bryophytes	PN_Megantic	598	0	1	0
Hygrohypnum eurygium	bryophytes	PN_Megantic	0	722	0	1

			Elevation		Occurrences	
Species	**Strate**	**Park**	**Original**	**Rencent**	**Original**	**Recent**
Hylocomiastrum umbratum	bryophytes	PN_Megantic	789	796	4	18
Hylocomium splendens	bryophytes	PN_Megantic	685	743	4	4
Hypnum cupressiforme	bryophytes	PN_Megantic	0	799	0	4
Hypnum curvifolium	bryophytes	PN_Megantic	0	750	0	10
Hypnum pallescens	bryophytes	PN_Megantic	619	0	11	0
Jungermannia leiantha	bryophytes	PN_Megantic	801	0	2	0
Lepidozia reptans	bryophytes	PN_Megantic	963	823	3	2
Mnium spinulosum	bryophytes	PN_Megantic	581	0	1	0
Oncophorus wahlenbergii	bryophytes	PN_Megantic	0	775	0	1
Paraleucobryum longifolium	bryophytes	PN_Megantic	705	523	15	2
Pellia epiphylla	bryophytes	PN_Megantic	0	708	0	2
Plagiochila porelloides	bryophytes	PN_Megantic	0	641	0	1
Plagiomnium ciliare	bryophytes	PN_Megantic	530	595	9	5
Plagiomnium cuspidatum	bryophytes	PN_Megantic	623	606	7	2
Plagiomnium medium	bryophytes	PN_Megantic	496	622	2	4
Plagiothecium curvifolium	bryophytes	PN_Megantic	460	654	1	1
Plagiothecium denticulatum	bryophytes	PN_Megantic	477	626	3	1
Plagiothecium laetum	bryophytes	PN_Megantic	712	663	6	3
Pleurozium schreberi	bryophytes	PN_Megantic	919	774	11	13
Pohlia nutans	bryophytes	PN_Megantic	995	805	3	2
Polytrichastrum alpinum	bryophytes	PN_Megantic	0	576	0	1
Polytrichastrum formosum	bryophytes	PN_Megantic	0	993	0	2
Polytrichastrum longisetum	bryophytes	PN_Megantic	0	553	0	2
Polytrichastrum pallidisetum	bryophytes	PN_Megantic	745	686	22	33
Polytrichum commune	bryophytes	PN_Megantic	0	564	0	3
Porella platyphylla	bryophytes	PN_Megantic	598	0	1	0
Pseudotaxiphyllum distichaceum	bryophytes	PN_Megantic	877	581	1	1
Ptilidium pulcherrimum	bryophytes	PN_Megantic	877	0	1	0
Ptilium crista-castrensis	bryophytes	PN_Megantic	729	795	5	7
Rhizomnium appalachianum	bryophytes	PN_Megantic	0	550	0	2
Rhizomnium pseudopunctatum	bryophytes	PN_Megantic	0	773	0	1
Rhizomnium punctatum	bryophytes	PN_Megantic	660	675	5	3
Rhytidiadelphus squarrosus	bryophytes	PN_Megantic	466	0	1	0
Rhytidiadelphus triquetrus	bryophytes	PN_Megantic	466	0	1	0
Sphagnum sp	bryophytes	PN_Megantic	629	707	6	8
Tetraphis pellucida	bryophytes	PN_Megantic	799	622	7	2
Thuidium delicatum	bryophytes	PN_Megantic	537	578	3	4

ANNEXE D

PLANT BIODIVERSITY CHANGE ACROSS SCALES DURING THE ANTHROPOCENE

Cet article est une revue de la littérature menée par Mark Vellend dans laquelle j'ai participé en parallèle de mes recherches principales.

Vellend M, Baeten L, Becker-Scarpitta A, Boucher-Lalonde V, McCune JL, et al. 2017. Plant biodiversity change across scales during the Anthropocene. *Annual Review of Plant Biology*. 68 (1): 563–86

Mark Vellend[1], Lander Baeten[2], Antoine Becker-Scarpitta[1], Véronique Boucher-Lalonde[1], Jenny L. McCune[3], Julie Messier[1], Isla H. Myers-Smith[4], and Dov F. Sax[5]

[1] Département de biologie, Université de Sherbrooke, 2500 boulevard de l'Université, Sherbrooke, QC, J1K 2R1, Canada

[2] Department of Forest and Water Management, Forest & Nature Lab, Ghent University, BE-9090 Melle-Gontrode, Belgium

[3] Department of Integrative Biology, University of Guelph, Science Complex, Guelph, Ontario, N1G 2W1, Canada

[4] School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, UK

[5] Department of Ecology and Evolutionary Biology, Brown University, Box G-W, 80 Waterman Street, Providence, RI 02912, USA

Keywords: biodiversity, climate change, habitat fragmentation, land use, nitrogen deposition, scale

ABSTRACT

Plant communities have undergone dramatic changes in recent centuries, although not all such changes fit with the dominant biodiversity-crisis narrative used to describe them. At the global scale, future declines in plant species diversity are highly likely given habitat conversion in the tropics, although few extinctions have been documented for the Anthropocene to date (<0.1%). Non-native species introductions have greatly increased plant species richness in many regions of the world, at the same time that they prompt the creation of new hybrid polyploid species by bringing previously isolated congeners into close contact. At the local scale, conversion of primary vegetation to agriculture has decreased plant diversity, while other drivers of change – e.g., climate warming, habitat fragmentation, nitrogen deposition – have highly context-dependent effects, resulting in a distribution of temporal trends with a mean close to zero. These results prompt a reassessment of how conservation goals are defined and justified.

CONTENTS

- THE REGIONAL SCALE
    - Observed richness changes at the regional scale
    - Functional and phylogenetic diversity
    - Underlying causes and the future of regional-scale plant diversity
    - Regional-scale conclusions
- THE LOCAL SCALE
    - Temporal plant biodiversity trends in re-survey studies
    - Effects of land use
    - Effects of habitat fragmentation
    - Effects of climate warming
    - Effects of nitrogen input
    - Local-scale conclusions
- PLANT BIODIVERSITY CHANGE ACROSS SCALES
- IMPLICATIONS FOR CONSERVATION
- FROM CURRENT KNOWLEDGE TO FUTURE RESEARCH

INTRODUCTION

Over the past 30 years, ecology, evolution, and conservation biology have coalesced around the concept of biodiversity. At the same time, driven by the sense of a current or pending crisis, innumerable international agreements, national policies, and research organizations have adopted biodiversity as their central focus. There is thus tremendous interest among scientists, policy makers, land managers, and the general public in understanding patterns and causes of biodiversity across space and time. This interest stems both from a desire to conserve biodiversity as an end in itself, and from the potential for biodiversity changes to have an impact on the benefits people derive from nature, such as food, fiber and clean air and water (63).

Human domination of the biosphere in recent centuries – a period of time often referred to as the Anthropocene (91) – is widely considered to have elevated species' extinction rates to the point of a global-scale biodiversity crisis (7; 66). However, for plants, extinction-rate estimates are highly uncertain, and human activities, such as species introductions that bring close relatives into geographic proximity, may have actually increased the rate of plant speciation (98). At sub-global scales of observation – from local study plots of a few m^2 to entire continents – recent research points to immense variability in temporal biodiversity trends (25; 65; 82; 106). For example, non-native species cause declines in some native species, at the same time that they have greatly enriched regional floras (82; 119). By understanding how plant biodiversity has changed in recent centuries and why, we can hope to improve predictions how it will change in the future.

A huge literature concerns patterns of plant species diversity over space and time and their underlying causes. Studies range from those addressing how factors such as productivity or land use influence diversity at small spatial scales (65; 112), to those addressing the effects of non-native species on regional-scale diversity (82; 119), and the quantification of global extinction and speciation rates (44; 73; 98). Here we review this literature and present a synthesis of knowledge of patterns and causes of plant biodiversity change during the Anthropocene across spatial scales.

Our review integrates multiple lines of evidence. First, at each spatial scale – global, regional, and local – we describe observed or estimated temporal trends of plant diversity in nature, which ultimately represent the phenomena in need of explanation. Second, at regional and local scales, we assess spatial correlations between plant diversity and potential causal factors (e.g., climate, land use), which provide the basis for making space-for-time predictions. If, for example, sites with higher temperature harbour greater plant diversity, warming might be expected to cause an increase in plant diversity over time (89). Third, when possible, we evaluate manipulative experiments in which the response of plant diversity to particular factors (e.g., temperature increase) was quantified. In addition to drawing on many individual case studies, we draw on the rich body of existing reviews and meta-analyses on particular drivers of biodiversity change.

We begin by briefly reviewing some basic concepts in the characterization and study of biodiversity.

WHAT IS BIODIVERSITY AND WHY DO WE CARE ABOUT IT?

Definitions and metrics of biodiversity

The term biodiversity means many things to many people. By its broadest definition, biodiversity is synonymous with all life on earth, but this definition is scientifically unusable. Here we adopt the scientifically operational definition of biodiversity as the variety of organisms found in a given place and time and we focus this paper more narrowly on species diversity: any measure of variety that begins by determining the taxonomic identity of each organism in a community. The vast majority of studies documenting spatial and temporal patterns of biodiversity concern species diversity, with by far the most common metric of diversity being species richness – the number of species found in a given place and time. Most of the studies on which this review is based are about species richness.

In some instances, we also draw on studies using one of the great many indices that incorporate data on species relative abundances, traits, or phylogenetic relationships (59). Indices of species diversity incorporating abundance data (e.g., the commonly-used Shannon or Simpson indices) aim to capture differences in the evenness of abundances: a community with two species at equal abundance is considered more diverse than a community in which one of the two species is far more abundant than the other. Indices of functional and phylogenetic diversity capture the variety of trait values represented by species in the community or the amount of evolutionary history (i.e., portion of the tree of life) those species represent, respectively (50; 107). For both functional diversity (e.g., based on leaf traits) and phylogenetic diversity, a community of conifers and angiosperms is typically more diverse than a community of only conifers or of only angiosperms. At present, studies have been too few and too heterogeneous to permit generalizations about functional or phylogenetic diversity, but we note selected cases where these measures appear to behave differently than species richness.

Why people care about biodiversity

Patterns of biodiversity across space and time are among the most striking features of nature, and they beg for scientific explanation. Why are there so many more plant species in the tropics than in temperate and polar regions? How do dozens or even hundreds of plant species coexist in small areas despite similar requirements for a small number of resources? These questions and many others motivate scientists to care about biodiversity as a fundamental property of the natural world.

When we hear the word biodiversity, the word conservation is rarely far behind. Many people care deeply about biodiversity for its own sake: we attribute great moral and cultural value to the variety of living organisms. This presents biodiversity scientists with the considerable challenge of separating our deep passion for biodiversity conservation from the need for an impartial approach to credible science (64; 96). We have tried to make this separation, presenting and interpreting the data as it appears in the literature, returning to conservation questions during the discussion.

People also care about biodiversity because of its potential to provide ecosystem services that benefit human well-being (14). By the broad definition of biodiversity as life on earth, this argument is true by definition: people rely on other organisms and ecosystems directly or indirectly for every facet of our lives. By the narrower, scientifically viable definition of biodiversity as variety per se in particular places and times, there is vigorous debate as to whether empirical results on biodiversity-ecosystem service links provide a general justification for biodiversity conservation (60; 106; 113). We revisit this issue in the discussion.

METHODS OF STUDYING TEMPORAL BIODIVERSITY CHANGE

Various methods can be used to infer patterns and causes of temporal biodiversity change, each of which comes with advantages and disadvantages. First and foremost, we can directly observe changes over time in particular places. Plants stand still, so at the local scale we can count species and estimate abundance with good accuracy. By conducting long-term vegetation monitoring, or by revisiting plots surveyed in the past, many studies have quantified temporal changes in plant biodiversity at the local scale (e.g., up to hundreds of m^2). However, such studies rarely cover more than ~50 years of time, and they cover only a subset of situations of interest.

In some cases, temporal observational studies provide some scope for inferring causes, via two methods. First, one can test *a priori* predictions about the direction of long-term trends based on cause-effect hypotheses, such as a positive effect of climate warming on alpine species diversity due to colonization of species from lower elevations (70). Second, one can test for temporal correspondence between fluctuations in diversity and of a given hypothesized driver of change (e.g., precipitation, 36).

At larger spatial and temporal scales, one can combine data on the extant flora, notes of early explorers, fossils (in some cases), and information on species' biogeographic origins to reconstruct the pre-Anthropocene flora as a basis for characterizing changes through to the present (e.g., 82; 83; 119). An advantage here is the ability to cover the full-time period of interest, although historical data include more uncertainty than local-scale observations and are unavailable in many regions.

The environmental correlates of plant biodiversity patterns across space provide insights into possible causes of temporal change. For example, if we assume that an unlogged forest represents the historical state of a logged forest, the difference between the two is an estimate of the change in plant diversity over time due to logging. Similar space-for-time inferences have been applied to many potential drivers of change, such as nitrogen deposition (86; 92) and climate change (89). An advantage of the space-for-time approach is the massive amount of applicable data. The main limitation is considerable uncertainty in the assumption that temporal change will mirror spatial gradients. Potential confounding variables limit our confidence in the causal inference: e.g., people cut down trees in places with particular soil conditions, and soil differences rather and logging might be the cause of an observed spatial pattern. In addition, reference sites themselves may have undergone major temporal changes (3; 9).

Finally, manipulative experiments provide the most direct means, in principle, of controlling potentially confounding factors, although applying experimental results to nature is difficult. For example, variables such as temperature or anthropogenic nutrient input change gradually in nature, but they are typically changed instantaneously in experiments, with potentially important consequences (46; 88; 120), such as limited opportunities for colonization of new species that might offsite rapid declines of residents. The magnitude of experimentally imposed environmental change also often greatly exceeds the change observed or expected in nature (8).

SPATIAL AND TEMPORAL SCALES

Patterns of biodiversity frequently depend on the spatial and temporal scale of observations. While it is possible for patterns and processes to interact across scales (e.g., local diversity can depend on regional diversity, 78; 105), species diversity at different scales can behave independently (62). For example, non-native species introductions across continents can cause large increases in regional species richness at the same time that extinctions cause a global decrease.

We recognize three spatial scales in this paper. The global scale includes the entirety of planet earth. The local scale refers to study plots used in field-based studies – typically 1-1000m^2. The regional scale is almost anything between local and global, but most often refers to areas of thousands of km^2, such as most countries, states, or provinces. One could add additional levels (e.g., the landscape scale between local and regional), but most studies fall cleanly into one of these categories.

Plant biodiversity can fluctuate up and down, so the observed temporal trend in a given place will depend on when and for how long data were collected. The focus of this paper is the Anthropocene, defined broadly as the era during which humans have had a profound impact on the earth, although considerable debate surrounds the exact timing of the onset (87). Here we loosely define the Anthropocene as applying to the past 300-500 years or so.

THE GLOBAL SCALE

Roughly 350,000 plant species on earth have been named, representing an estimated 80-90% of the true total (44; 73). Since the first vascular plants evolved >400 million years ago, global plant diversity has increased markedly. Surprisingly, the periodic mass extinctions observed for animals do not appear to apply to plants (115; 117). This is one clue that plants might be comparatively resistant to extinction. Still, plant extinctions have occurred throughout this history and can be characterized by “background” rates, which help to put the Anthropocene in context. That said, using the fossil record and/or molecular phylogenies to generate extinction and speciation estimates is fraught with uncertainties, and all estimates should be interpreted as very rough approximations. In addition, the types of Anthropocene extinction and speciation events we have been able to observe (rare island endemics and hybrid polyploids during the first decades of their existence, respectively) are exactly of the type not represented in the fossil record (39; 75). Nonetheless, the central tendencies of background plant extinction rates mostly fall in the range 0.05-0.15 S/MSY (Species per Million Species Years; see **Table D-1**), while background speciation rates (based on the same data sources) mostly fall in the range of 0.1-1.0 S/MSY (**Table D-1**).

Table D-1 - Estimated rates of plant extinction and speciation in the distant past (background), the recent past (Anthropocene) and the future (projected).

Median/mean rate (S/MSY[a])	**Data source(s)**	**Data type**
Extinction: background		
0.05	De Vos et al (22)	Phylogenetic

0.07[b]	Levin and Wilson (54)	Species durations, fossil record
0.13	Stanley (90)	Species durations, fossil record
Extinction: Anthropocene, to date		
0.98	IUCN Red List (extinct or extinct in the wild, July 2016) (41)	142 extinctions from 1600-2016
4.1	World Conservation Monitoring Center (122)	592 extinctions from 1600-2016
5.2	Regan et al (76)	Australia: 33 extinctions out of 16,000 species over 400 years[c]
Extinction: Anthropocene, conservative projection		
50	Reid (77), van Vuuren et al (104)	5% extinction spread over 1000 years[d]
Speciation: background		
0.65[b]	Levin and Wilson (54)	Age of genera and number of species in each genus

0.14	De Vos et al (22)	Phylogenetic (net diversification + extinction)
Speciation: Anthropocene, to date		
6.3	Thomas (98)	6 new species (in a region with ~3000) from 1700-2015; only for the UK
Speciation: Anthropocene, projected		
No estimates available		

[a] S/MSY: units are species / species / million years or species / million species / year; for example, an estimate of 1.0 means that each species is likely to give rise to one additional species every million years, or equivalently, that for every million species, one new species will arise each year.

[b] weighted average for herbs, shrubs, and hardwoods, assuming that 45% of species are woody (evenly split between shrubs and hardwoods) and the rest are herbaceous (32).

[c] these are rough mid-points from a range of possibilities reported in Regan et al (76)

[d] the low-end of projected percentages of species committed to extinction in Reid (77) is 4% by 2040 and 7% by 2050, but we have no estimate of the time course over which these extinctions will occur; here we consider 1000 years a conservative guess.

Anthropocene extinction

Estimates of Anthropocene extinction are usually made by estimating the proportion of species “committed to extinction” within a specified time frame given habitat loss or other anthropogenic factors such as climate change. Alternatively, one can also estimate the Anthropocene extinction rate based on species whose extinction has already been observed (or inferred). Given huge discrepancies between observed and projected extinction rates (93) we treat them separately here, followed by a treatment of Anthropocene speciation.

A report in the early 1990s listed 592 plant species as having gone extinct either in the wild or completely from the earth since 1600 (122). The current International Union for Conservation of Nature (IUCN) Red List includes 142 extinct plant species (41). The IUCN evaluated 86 taxa from the initial list of 592 and found that 36 had been rediscovered in the wild, 42 remained classified as extinct, 4 lacked sufficient data to make a determination, and 4 were no longer recognized as distinct taxa. The majority of the 142 IUCN-listed species were not included in the WCWC list of 592. There is thus massive uncertainty with respect to undocumented extinctions and unknown extant populations of rare species. Nonetheless, if we take 142 and 592 as somewhere in the ballpark of extinctions that have occurred between 1600 and 2016, we get extinction rates of 0.98-4.1 (**Table D-1**; see also 76), 1-2 orders of magnitude higher than the background rate.

The future extinction rate in the face of habitat loss and climate change is even more uncertain. Future risks from habitat loss, often referred to as "commitment to extinction", are typically calculated using species-area relationships. As the area of habitat (A) declines, the number of species (S) declines in concert, often following (at least approximately) the relationship $S = cA^z$, in which c is a constant and z the slope of $\log S$ vs. $\log A$. This approach involves many questionable assumptions, the details of which are beyond the scope of this paper. However, even if one takes at face value a prediction such as 7-25% of species committed to extinction by 2050 (104), it is not possible to calculate an extinction rate without an estimate of the time course over which those extinctions will actually happen. A key point for our purposes here is that even if we take low-end estimate of 5% extinction (77) and assume a 1000-year period over which these extinctions occur, the estimated extinction rate (50 S/MSY) is upwards of 1000× the background rate (see Table 1). The time course of extinctions may well exceed 1000 years (24), but so might other factors, such as climate change, push extinction rates even higher (43; 102).

Anthropocene speciation

Until recently, analyses of Anthropocene biodiversity change have assumed that speciation is a negligible part of the equation. However, human activities during the Anthropocene include some of the key ingredients in the recipe for speciation, such as the establishment of new populations isolated from the species' native range (109). For plants, hybridization plus a change in chromosome number is an especially efficient and historically common route to the rapid creation of new species (11; 121). Many such Anthropocene hybrid-polyploid plant species have been documented, but we sorely lack a global compilation. Based on data just for Britain, Thomas (98) estimated an Anthropocene speciation rate of 6.3 S/MSY, comparable to the Anthropocene extinction rate to date. We do not know whether the future plant speciation rate will be higher or lower. With human-mediated species introductions showing no sign of deceleration (83), we might expect at least maintenance of the current Anthropocene rate of plant speciation.

Global-scale conclusions

- Both extinction and speciation rates have likely increased due to human activities during the Anthropocene.
- We cannot conclude definitively that the number of plant species on earth has decreased or increased since the onset of the Anthropocene.
- Extinctions during the coming centuries have the potential to greatly outnumber speciation events, causing a decline in global plant species richness.

THE REGIONAL SCALE

At the regional and local scale, immigration joins speciation as an important input term in the biodiversity equation. By far the largest contribution to regional-scale Anthropocene immigration comes from deliberate or accidental human-mediated species introductions among continents, with geographic range shifts within continents playing a comparatively minor role. Considerable effort has been invested in documenting non-native plant establishment across the globe (103). Regional-scale extinctions have been quantified in far fewer regions, although the existing studies provide consistent results on positive net diversity change during the Anthropocene.

Observed richness changes at the regional scale

For 11 islands or archipelagos largely in the Pacific and Indian oceans, Sax et al (84) documented both extinctions and introductions, with the net effect being an average two-fold increase in regional plant species richness during the Anthropocene (see also 83). The sample included the Hawaiian Islands (>15,000 km^2) and New Zealand (>250,000 km^2), and the proportional increase over time was consistent across archipelagoes (see **Figure D-1a**). Islands typically experienced <5% extinction and the establishment of roughly as many non-native species as the original number of native species. The qualitative pattern observed for islands also applies to continental regions of Europe (119) and the United States (82), where the net increase in richness has been roughly 20-25% on average (**Figure D-1b**).

With regard to regional-scale changes in plant diversity, the biggest unknown is the number of extinctions in continental tropical regions. In terms of introductions, van Kleunen et al (103) compiled data on non-native plant species in 481 mainlands and 362 island regions across the globe, including many tropical countries. Continental tropical regions were typically found to be home to dozens to hundreds of non-native species. In order to gain a rough sense of the proportion of non-native species in tropical floras, we looked up the total number of plant species in five haphazardly selected African countries (Burundi, Chad, Gabon, Namibia, Uganda). The proportion of non-native species varied from 1.4% in Uganda (68/4900; 1) to 12.1% in Chad (278/2288; 13), with all five below the average of ~20% in European regions and the United States. At present, it is unknown how these numbers compare to numbers of plant extinctions in the same regions, although upwards of 10% extinction (i.e., to match invasions in a country like Chad) would be quite high even for tropical islands, where species are thought to be particularly prone to extinction (83).

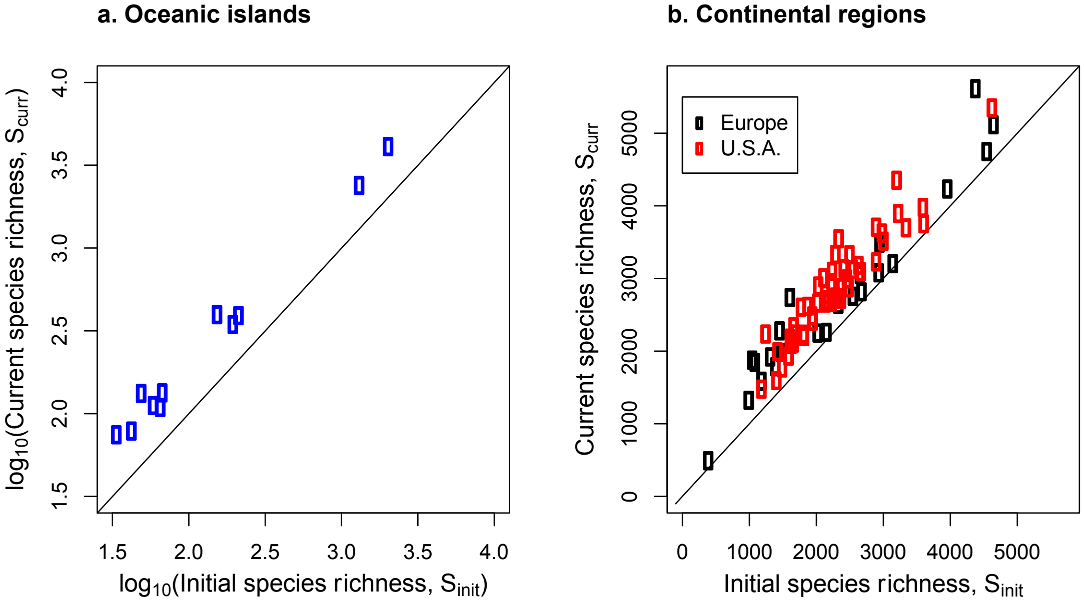


Figure D-1 - Estimated current species richness (S_{curr}) versus pre-Anthropocene initial species richness (S_{init}) for (a) 11 oceanic islands (data updated from 88) and (b) 23 countries or regions of Europe (data from 124) and the 50 states in the United States [data collated from NatureServe (http://www.natureserve.org); see also 87].

Points above the diagonal 1:1 lines show net increases in richness. A log scale was used for the islands for ease of presentation, given the large range in richness among archipelagos.

Functional and phylogenetic diversity

To our knowledge, Winter et al (119) is the only study to address regional-scale changes in plant functional or phylogenetic diversity (PD). At the scale of Europe, phylogenetic diversity (average phylogenetic distance between pairs of species) showed a statistically significant but very small increase: a randomly chosen pair of species is now ~1% more distantly related than in the year 1500. Within regions (mostly countries), phylogenetic diversity showed a statistically significant 0.3% decline over the same period. However, it is important to note that a small change in the average phylogenetic distance between pairs of species does not imply a change in total phylogenetic diversity – originally quantified in conservation biology as the sum of branch lengths connecting the set of co-occurring species (30). With the addition of so many species, total PD may well increase even as average pairwise PD declines, given the tendency for non-native species to have one or more close relatives in the native flora. This requires caution when interpreting results of phylogenetic or functional diversity metrics designed to statistically control for correlation with species richness (50; 107).

Underlying causes and the future of regional-scale plant diversity

The dominant cause of regional-scale plant diversity changes is clearly the establishment of non-native species, which in turn depends on both introduction pressure and the suitability of biotic and abiotic conditions (57). Net increases in diversity may be due in part to increased environmental heterogeneity, with a mix of disturbed and undisturbed habitats permitting the persistence of non-native and native species alike (20; 97). Interestingly, the same economic activities that prompt introductions (agriculture, horticulture, and urbanization) also result in the creation of suitable habitat for many non-native species, and the modification of habitat to the detriment of many native species (37; 74). It is thus difficult to predict future net changes in plant diversity at the regional scale, especially in tropical areas, where increasing international trade and habitat disturbance should promote both non-native species invasions and native extinctions.

From a theoretical point of view, an elevated rate of immigration via non-native introductions is expected to increase diversity (79; 105), and for places that have been repeatedly surveyed over time, there is no sign of a recent decline in the rate of new species establishment (83). In general, increasing human activity and anthropogenic habitat modification should accelerate the establishment of non-native species (55), a process that might be especially important in developing tropical nations. Shifting geographic ranges due to climate warming are also expected to bring new species to particular regions (68; 89), and time lags involved in such range shifts create an "immigration credit" for future regional diversity (42).

Much more uncertainty is involved in predicting future extinctions. On one hand, many species might already be "committed" to regional extinction, e.g., for those populations that are on a continual decline, with such populations representing an "extinction debt" (42; 100; 110). The huge number of endemic plant species in tropical biodiversity hotspots, which have experienced massive forest loss, points to the likelihood of a great many regional (and global) extinctions (51). However, the fact that observed large-scale extinctions to date have been far fewer than predicted (17; 93), and the suggestion from paleobotanical data (115; 117) and more recent extinction data (82) that plants are less extinction prone than other taxonomic groups, encourage caution in making predictions of future extinctions.

Regional-scale conclusions

So far, the number of non-native plant species established in a given region is typically far greater than the number of species that have gone regionally extinct.

The resulting net increase in regional richness has been greater on islands than in mainland regions.

Very little is known about net plant biodiversity changes during the Anthropocene in tropical continental areas, particularly with respect to extinctions.

Continued regional increases in plant species richness seem likely, but the magnitude is highly uncertain, especially for tropical continental areas.

THE LOCAL SCALE

Our knowledge of biodiversity change at the local scale is in some senses better and in some senses worse than our knowledge at global and regional scales. Local-scale vegetation plots are by definition small (most often ≤1000m^2, 106), such that there is far less uncertainty involved in estimating species presence or abundance. There have been hundreds of studies following local-scale temporal vegetation change in a wide range of habitat types and geographic regions. However, local studies are typically of short duration (rarely >50 years), and essentially none cover the entire Anthropocene. In this section we first summarize a recent meta-analysis focusing on observed trends in repeated vegetation surveys. Subsequent sub-sections review the major hypothesized drivers of biodiversity change (not an exhaustive treatment), in each case drawing on both "space-for-time" and experimental studies.

Temporal plant biodiversity trends in re-survey studies

Vellend et al (106) systematically searched the literature for studies reporting estimates of plant diversity in one or more local-scale plots (≤5ha for trees, ≤1ha otherwise) surveyed at least twice over a period of at least five years. The dataset (updated to the end of 2014, 108) includes studies from all continents except Antarctica, but with an underrepresentation of tropical regions. The main result across 212 studies is that the distribution of temporal trends is centered on zero, regardless of habitat type or geographic region (**Figure D-2**). Some individual studies report substantial increases in plant richness over time: e.g., +38% in forests and grasslands of Vancouver Island between 1968 and 2009 (61), while other studies report substantial decreases in richness over time: e.g., -70% in the Siskyou mountains of Oregon between 1950 and 2007 (18). Most studies reported very little temporal change in either direction (<10%).

The observational data in Vellend et al (106) provide limited scope for assessing underlying causes and they cover almost exclusively the 20th and 21st centuries. All of the individual studies concerned sites that had not undergone major land-use transitions during the period of study. However, many studies were conducted in anthropogenically altered habitats (e.g., pastures or urban areas) or had been subject to disturbances of various kinds – climate change, species invasions, etc. In other words, while this was not a sample of "pristine" sites, the sites remained the same habitat type during the period of study, consistent with the original motivation to combine the results with experimental studies of how biodiversity influences ecosystem function, essentially all of which share this same feature (38). As described below, major land use transitions often cause major losses to local scale plant diversity (65). What the results of Vellend et al (106) suggest is that in the absence of major land use transitions, local-scale plant diversity in any given ecosystem has been just as likely to increase as it has been to decrease over the past century or so, with many places showing no significant temporal trend at all. Exceedingly few local-scale data are available to assess changes prior to the 20th century, with relatively few for even the first part of the 20th century.

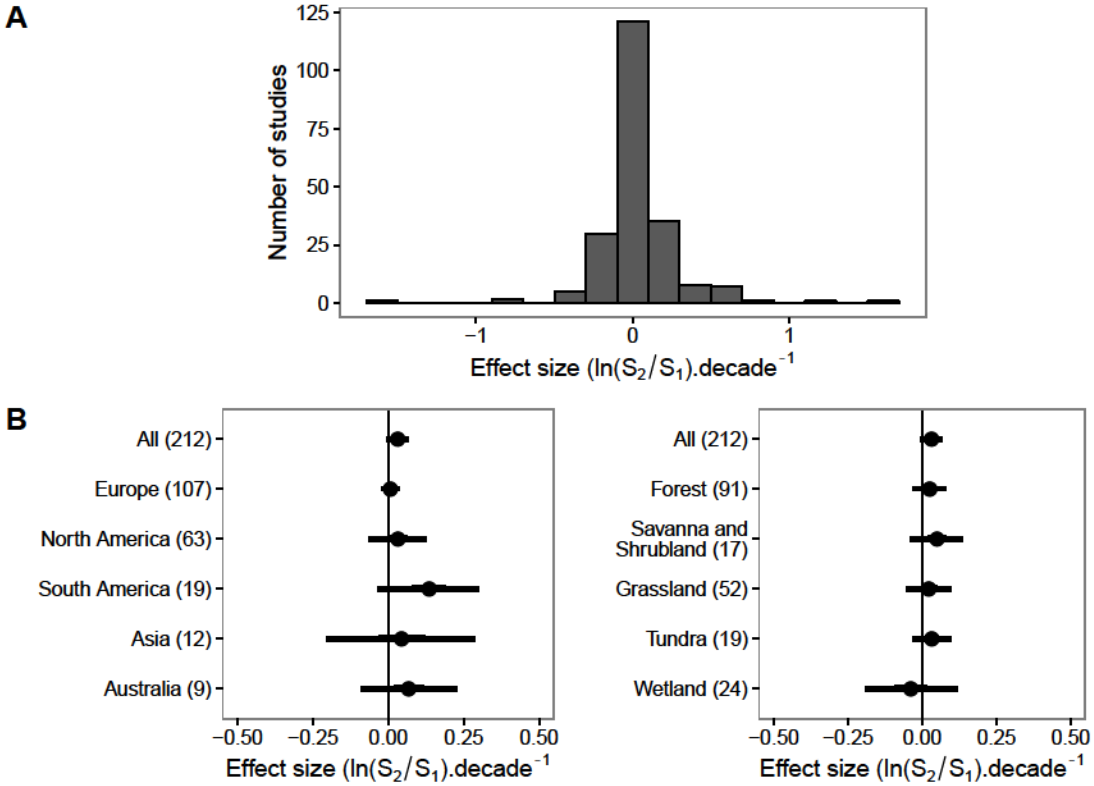


Figure D-2 - Local-scale temporal change in plant species richness in 212 studies of 5–261 years' duration.

Temporal change is expressed as the log ratio of species richness for the last year of surveys (S2) and the first year (S1) per decade. (a) Histogram of all studies. (b) Mean ± 95% credible intervals for different geographic regions and habitat types, with the number of studies shown in parentheses. Not shown in this panel are two studies from Africa with a raw mean effect size of 0.165. Data were compiled from the published literature as reported in References 106 and 108.

<u>Effects of land use</u>

Huge areas of the earth's surface have been converted from primary vegetation to anthropogenic habitats. Newbold et al (65) compiled data from >250 space-for-time studies to assess the local-scale consequences of land use for biodiversity in a range of animal and plant taxa. Here we focus on results that apply to plants (Tim Newbold, personal communication), of which the clearest was that local species richness was ~30% lower on agricultural lands (by far the dominant human land use) than in minimally disturbed primary vegetation.

Urban areas occupy a very small portion of the earth's surface, but roughly half of the human population lives in them. Suburban yards or urban areas devoid of green spaces typically have lower species richness than primary vegetation, but larger, managed urban green spaces have average species richness similar to that in primary vegetation (65). Consistent with these results, a negative correlation between the magnitude of human presence in cities (e.g., population density) and plant species richness has been observed for small study plots, but in units of observation >1km^2 species richness actually increases as a function of human impact (71). The latter result could be due to humans tending to settle in areas already high in biodiversity, or to positive effects of human-caused environmental heterogeneity and species introductions. The latter conclusion is supported by increases in city-wide plant species richness in recent centuries due specifically to introduced "neophytes" (47).

In primary vegetation and successional sites no longer under intense land use, anthropogenic activities such as logging and bush-meat hunting did not have a significant impact on local species richness (65). Similarly, a meta-analysis aimed specifically at assessing the effect of logging of various intensities on local plant biodiversity in temperate forests found no significant effect on average (26). For plants, species richness was not significantly lower in secondary vegetation (of any age) than primary vegetation, although the qualitative trend was of reduced diversity (T. Newbold, personal communication).

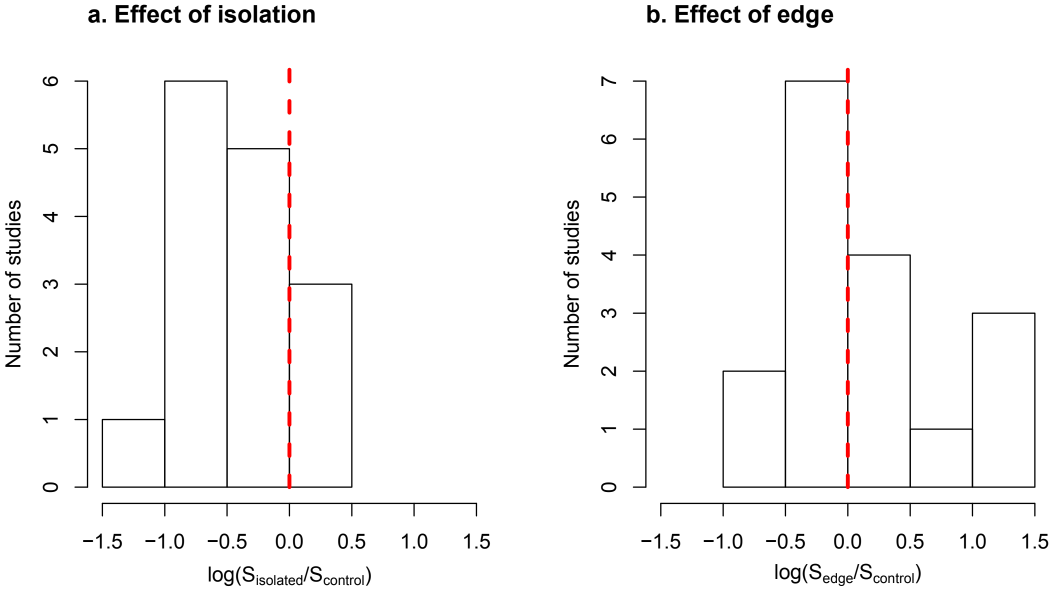
In sum, when people destroy primary vegetation to make way for agriculture and urbanization, local-scale plant biodiversity declines. Less intensive land uses, such as logging, might have positive or negative effects in any given case. Upon abandonment from agricultural use, local biodiversity tends to increase, ultimately to similar levels observed in primary vegetation.

Effects of habitat fragmentation

Studies of fragmentation focus not on the areas converted to a new land use but on the smaller habitat patches left behind. Distinguishing an effect of fragmentation per se from an effect of habitat loss requires comparing habitat fragments to equal-area portions of larger habitats (29). Two kinds of alteration to habitat patches that can be unambiguously attributed to fragmentation per se are increased spatial isolation from other similar habitats and the creation of edges between a focal habitat (e.g., forest) and an anthropogenic habitat (e.g., crop field).

The most famous study of habitat fragmentation involved the experimental creation of forest fragments of 1ha, 10ha, and 100ha in the Amazon rainforest, and measurement of many ecological variables over the subsequent 30+ years (52). When ensuring equal sample effort or plot area, small fragment size led to sharp declines in the diversity of several taxa – most dramatically birds (95) – but not generally for plants. The smallest fragments showed greatly increased tree mortality and rapid community turnover, but species richness of trees in 1ha plots was not influenced by fragment size (53). There was also no significant decline in the diversity of palms (85) or ant-dispersed understorey plants (12), but a significant decline for epiphyllous bryophytes (124). Other studies of tropical forest fragments have focused on functional or phylogenetic plant diversity, finding increases, decreases, or no change with fragment size, depending on the metric used or the specific context (2; 58; 80).

There is considerable variation among studies testing the effects of fragmentation on plants (40). Fragment isolation is most often found to have a negative effect on species richness (**Figure D-3a**), while edges have strong positive effects more often than strong negative effects (**Figure D-3b**). Ibáñez et al (40) began their meta-analysis by classifying effects as positive or negative, regardless of effect size, but looking at the underlying data shows that many effects are quite close to zero (**Figure D-3**). This result is consistent with other cross-taxon reviews of the habitat fragmentation (23; 29).


a. Effect of isolation

b. Effect of edge

Figure D-3 - Distributions of effect sizes of (a) patch isolation and (b) proximity to patch edges on plant species richness (data from 41).

<u>Effects of climate warming</u>

Climate is the primary determinant of global vegetation patterns (114) and changing climatic conditions can cause extinctions of some species (102) at the same time that it creates suitable conditions for others (70). Across many studies, spatial variation in regional- and local-scale plant species richness is best predicted by variables calculated from climate data, such as potential evapotranspiration (31). The effect of temperature on regional-scale plant species richness varies from strongly positive in mesic or humid portions of the earth, to strongly negative in severely water-limited areas (89). Therefore, the regional "capacity" for plant species richness will likely increase with climate warming in temperate and polar regions, while it decreases in dry tropical regions by the year 2100 (89).

Climate-richness relationships at local scales tend to be similar to those at larger scales (35; 48; 81; see **Figure D-4**), if somewhat weaker in magnitude (31). Using space-for-time substitution, we can thus make a prediction that climate warming should increase local plant diversity in cool and mesic or humid regions and decrease diversity in drier regions. This is consistent with some explicitly temporal observational studies, which have found local richness increases in temperate mountainous areas, and diversity declines with reduced rainfall or increased temperature in water-limited grasslands (15; 36; 67; 70; 81; 99, see **Figure D-4b**).

Many field experiments have manipulated temperature and/or precipitation, although multi-habitat meta-analyses have not included species diversity as a response variable (5; 56; 123). Our qualitative review of experimental warming studies suggests that effects on species diversity are highly variable and context-dependent from study to study. We focus largely on temperature manipulations, given the near ubiquity of predicted temperature increases across the globe.

Experimental warming, typically of ~1-2C, seems most often to have no effect on species richness or diversity (e.g., 28; 72; 125), although some studies report warming-induced declines (e.g., 45). In six shrubland sites in Europe, Peñuelas et al (72) experimentally imposed both warming and drought, finding no significant effects on plant species richness after seven years, except at one site where there was a negative effect of drought (in Spain). Elmendorf et al (28) reported no overall effect of experimental warming on species diversity (Simpson's index) over up to 20 years in 61 tundra sites. In contrast, reduced species richness or diversity due to experimental warming was found in Tibetan grassland and shrubland (45) and in a New England salt marsh (34).

Space-for-time and experimental studies both predict effects of warming that are highly variable from site to site. However, the space-for-time prediction of increased local diversity due to warming in mesic or humid sites has not generally been borne out in experiments, despite some support for this prediction from observational studies (67; 70; 81). One possible explanation is that instantaneous environmental change imposed by experiments might not mimic the effects of more gradual warming in nature (46; 88), and might cause declines in some species more rapidly than can be offset by colonization of new species during a short-term study. More generally, the space-for-time prediction represents a long-term expectation, and for perennial plant communities (i.e., most plant communities) the lag time of response may well be on the order of many decades or even centuries (42). Given the very general and strong spatial relationships between climate and plant diversity, it seems reasonable to expect climate warming to cause local plant diversity to decline, on average, in water-limited regions, at the same time that it increases elsewhere.

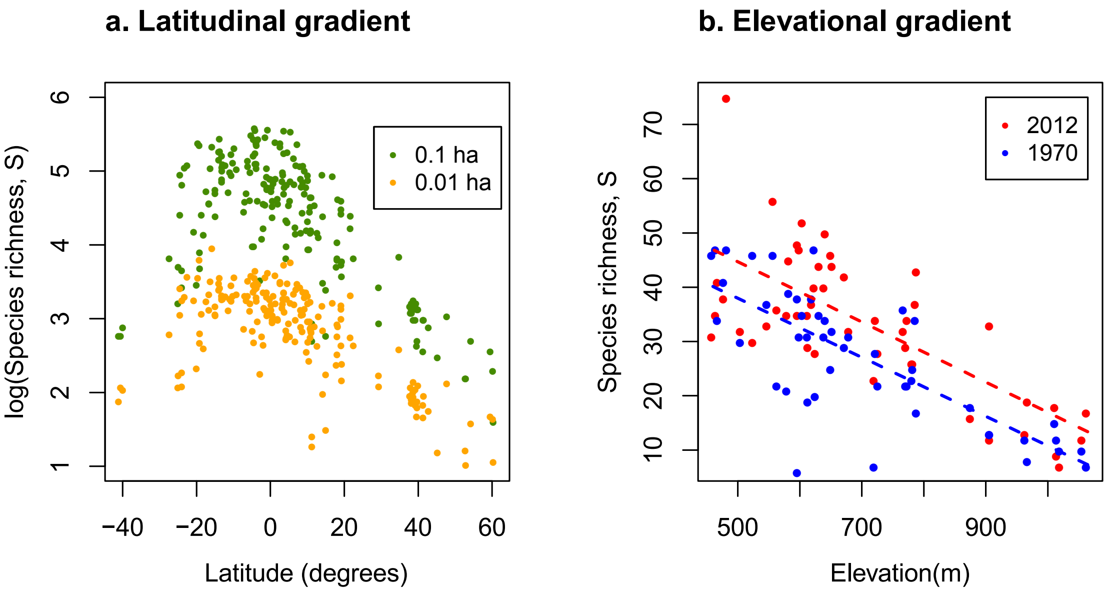


Figure D-4 - Patterns of local-scale forest plant diversity along putative climatic gradients showing increased diversity at relatively warm places and times.

The trend with latitude (a) is shown for trees as the average in individual 0.01 ha plots (orange points) or the sum across 10 such nearby plots (green data points; data from ref. 35 as reported in ref. 48). The elevational data (b, with linear regression lines) include all vascular plants and come from 20×20m or 20×40m plots on Mont-Mégantic in southern Québec, Canada, both before (blue points) and after (red points) a period of ~1.5C climatic warming (81).

Effects of nitrogen input

Nitrogen (N) is a key limiting nutrient for plant growth, and anthropogenic N additions to the biosphere via the burning of fossil fuels and fertilizer production have increased dramatically during the Anthropocene (33). The effects of nitrogen addition are especially amenable to manipulative experiments, although many experiments apply a high N input over a short period of time, with uncertain implications for understanding the consequences of long-term inputs of lower magnitude (8).

Many N-addition experiments have led to clear declines in local-scale plant richness and diversity, with the most striking and consistent results in temperate grasslands (8; 16; 21). Outside of temperate grasslands, N addition almost always causes shifts in species composition (e.g., favouring nitrophilous species), and most often causes increased biomass production, but effects on species diversity and richness are highly variable, with increases in diversity possible, if quite rare (10). The main mechanisms underlying diversity loss appears to be dominance achieved by one or a few species that are strongly favoured by increased N availability, leading to the competitive exclusion of others, as well as soil acidification (8).

Space-for-time studies of N deposition have been conducted less often than experimental N additions. In European grasslands, Stevens et al (92) found a sharp decline in local-scale plant species richness with increasing N deposition. Across a broad range of vegetation types in the United States, Simkin et al (86) found strong context dependence of N deposition effects. Simkin et al (86) confirmed the generally negative effect of N deposition in grasslands and other open habitats, especially on acidic soils. However, when looking within particular vegetation types (most relevant to making space-for-time inferences), 36.5% showed a negative effect of N deposition on plant richness, 45.5% showed no effect, and 18% showed a positive effect. Local plant species richness is expected to increase with N deposition in relatively cool habitats, on soils with high pH, and where current N deposition is relatively low (86).

Overall, the evidence indicates that N deposition has caused and will likely continue to cause loss of local plant diversity in temperate grasslands and possibly other habitats, although across the globe the effects of N deposition are highly variable, often with no effect on local plant diversity, or even positive effects in some cases.

Local-scale conclusions

Conversion of primary vegetation to intense agricultural or urban use tends to cause a decline in plant biodiversity.

The effects of other major drivers of plant community change – resource extraction, habitat fragmentation, climate warming, and nitrogen deposition – are all highly context dependent.

Outside of wholesale agricultural or urban habitat conversion, high context-dependence and potentially counteracting forces create massive variation from place to place in temporal plant biodiversity trends, with many places showing increases, decreases, or little if any change at all.

Substantial uncertainty about long-term changes of diversity at local scales remains because of a lack of local-scale studies that span the Anthropocene.

PLANT BIODIVERSITY CHANGE ACROSS SCALES

Synthesizing the results presented thus far, plant biodiversity changes during the Anthropocene show clear scale-dependence (**Figure D-5**). At the global scale, the Anthropocene has seen relatively few documented plant extinctions to date, and a non-trivial number of speciation events, with the future long-term net trend likely to be negative. At the regional scale, non-native species establishment has far outweighed extinction in those regions studied, although weaker or even negative regional trends are possible for poorly studied tropical continental areas. Both the magnitude and direction of local-scale plant biodiversity change has varied tremendously from place to place (**Figure D-5**).

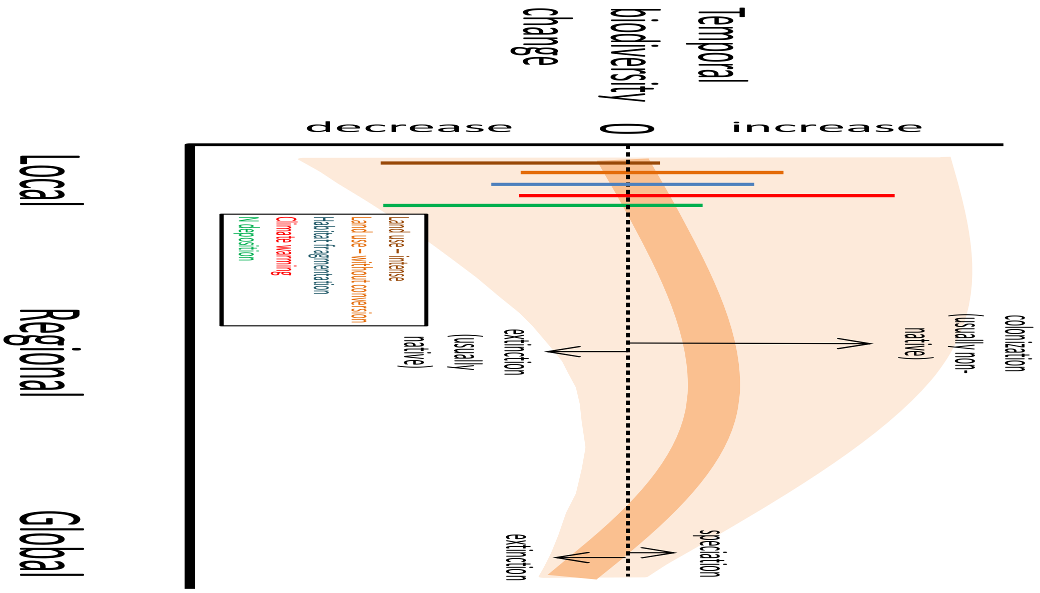


Figure D-5 - Schematic illustrating the key empirical results concerning plant biodiversity change during the Anthropocene at different spatial scales.

The large shaded polygon represents the range of possible outcomes, with the central tendency indicated by the thick, darker curve. Colored bars represent the range of local-scale outcomes of different drivers of change; context dependence creates wide variation for each driver, and combinations of drivers might push diversity change further than any one driver, in either direction. The height of each arrow represents the relative direction and strength of the process indicated.

The combination of extinctions of species native to particular continents or islands, and the widespread colonization of many non-native species, suggests that distant regions (e.g., different continents) must be getting more similar in species composition. This phenomenon has been dubbed "biotic homogenization", and indeed many studies show evidence of this (6). When comparing continents such as North America vs. Europe, for example, non-native plant species have caused homogenization (118). Within continents or at smaller spatial scales, changes in compositional similarity have been highly variable from study to study. For example, non-native species have caused regions (typically countries) within Europe to actually diverge in species composition, while regions of North America have shown homogenization (118). Temperate urban areas share many cosmopolitan plant species, and thus have shown clear biotic homogenization (49), while in any particular landscape in Europe, forests have sometimes shown homogenization, sometimes differentiation, and sometimes no change in compositional similarity in recent decades (4). Species composition varies tremendously among different land uses (65), such that within a typical mixed landscape of primary vegetation, secondary vegetation, and various forms of agriculture, spatial variation in species composition is almost certainly far higher than it would have been in a pre-Anthropocene landscape dominated by primary vegetation. In short, the Anthropocene has seen both biotic homogenization and differentiation, depending on scale and context, with the only likely generalization being that intense human land use and non-native species introductions have caused species composition to converge across continents and to diverge among different land uses within landscapes.

IMPLICATIONS FOR CONSERVATION

The concept of biodiversity is tightly linked both historically and thematically with conservation biology (60; 96; 116), and the results of this review speak to several important conservation questions.

First, counter to the biodiversity-crisis narrative, many regions of the earth have actually seen a net gain in plant biodiversity during the Anthropocene, largely due to the establishment of non-native species. Such increases in biodiversity are still considered a problem if a conservation goal is to prevent declines of native species specifically. On the surface, it is paradoxical that an increase in biodiversity would not be welcomed by a discipline whose aim is the protection and maintenance of biodiversity. The resolution of this paradox comes from the fact that the perceived problem is not actually one of biodiversity per se, but of the species composition of the flora. Focusing on native species is a normative judgement, not one based on science, and it is crucial to make this distinction clear when articulating the rationale behind conservation philosophies and actions (19). Both observational and experimental studies almost universally find shifts in species composition in response to various drivers of change, but the response of biodiversity per se is far less predictable or consistent.

In recent years, an additional major focus of ecologists and conservation biologists has been ecosystem services – benefits that humans derive from nature – as a target of conservation efforts, and the possibility that ecosystem services depend on biodiversity. The argument that ecosystem functions or services depend on biodiversity has a scientific basis, largely in the form of experimental studies manipulating plant species richness in small study plots (38). However, there are some important nuances and context-dependencies that restrict the application of this argument to justify biodiversity conservation. First, because biodiversity is generally increasing for plants at regional scales, concerns about declines (at least of total biodiversity) at these scales are not applicable. Second, the primary scenario in which we see consistent and predictable declines in local diversity – and therefore where this argument should be most applicable – is the conversion of land to agricultural use. But the reduction of plant diversity in crop fields is not an incidental consequence of land use. Rather, people aim to maximize one ecosystem service – food production – by deliberately creating simplified ecosystems with one or a few crop species (27). Intensive agriculture can certainly come at a cost to other ecosystem services, such as carbon storage and water quality (63), but even here it is doubtful that the underlying cause is decreased biodiversity, rather than yearly harvesting and ploughing, or habitat conversion (i.e., replacing a forest with an annual-dominated system).

Outside of agricultural fields, major declines in plant biodiversity are not especially common (**Figure D-2**), so arguments about compromised ecosystem function based on biodiversity loss pertain only to some sites. That being said, the importance of native species diversity specifically for ecosystem function is still not well understood. There is experimental evidence to suggest that interacting plant species can evolve rapidly in ways that promote ecosystem function (e.g., 126), but it is unclear how important hundreds, thousands or millions of years might be in shaping how native assemblages function. One fairly restricted domain in which specific management actions are clearly justified by a link between biodiversity and ecosystem function involves habitats such as tree plantations or restoration projects, where people directly control local biodiversity (101; 111). An important and rarely asked question concerns the impact of increasing local biodiversity for the many systems where this has occurred.

Overall, the tendency for regional-scale plant biodiversity increases and highly variable local-scale trends during the Anthropocene challenge conservation biologists to specify more clearly the precise goals of conservation actions (e.g., diversity vs. composition), whether these goals stem from normative judgements or scientific evidence, and the degree to which scientific evidence relates directly to particular conservation actions.

FROM CURRENT KNOWLEDGE TO FUTURE RESEARCH

At all scales, our knowledge of plant biodiversity changes during the Anthropocene is especially poor in tropical continental regions. Compiling and exploiting any and all available historical data on plant communities in the tropics is an important research priority. Our ability to study the past is limited by the availability of historical data, but forward-looking biodiversity monitoring studies are straightforward to implement, if extremely challenging to generate funding for. Long-term monitoring of plant communities in all habitat types is needed in order to understand the causes and consequences of Anthropocene plant biodiversity change. Biodiversity change in response to a given driver is subject to time lags, both for extinction and colonization (42), and only by following communities over the long term can we assess the time course of such changes.

This paper focuses on roughly the past 500 years, but ecological impacts of human land use extend back in time thousands of years, with important consequences for interpreting more recent human impacts. The pre-Anthropocene scale of human impacts was likely localized compared to the present day, although perhaps covering a broader swath of terrestrial ecosystems than is generally appreciated (9). For example, human land use upwards of 1000 years ago may well be the cause of relatively high contemporary plant biodiversity in systems such as European heathlands and grasslands (69), where modern land use intensification is causing declines (69; 94). Better integration of studies from the Holocene and the Anthropocene can help contextualize and provide important nuance to site-specific conservation implications of recent biodiversity trends.

Predicting future biodiversity change presents massive challenges, especially for regions undergoing rapid economic development. At regional scales, conversion of primary vegetation to anthropogenic uses is clearly one of the main drivers of extinctions (73). However, as we have seen for the temperate zone, expansion of agriculture and resource extraction also increase environmental heterogeneity and is typically associated with non-native species introductions, both of which can contribute to increasing regional diversity. Predicting the net result of these forces in both temperate and tropical regions will require the integration of many lines of evidence: studies of the potential pool of non-native colonists to a given region, estimates of their probability of arrival and establishment, the development of robust projections of future land use, improved understanding of likely changes in climate, and more reliable estimates of future extinctions, including models that can account for the small number of extinctions observed to date. Filling these needs presents a daunting task but developing such models and confronting them with data in the future will provide an improved basis for predicting the future of plant life on Earth.

SUMMARY POINTS

1. At the global scale, the rate of plant extinctions has increased during the Anthropocene relative to background levels, but the total number of these extinctions has been far fewer than predicted by some models, while plant speciation may have accelerated.
2. The available data support, but do not conclusively demonstrate, the assertion that that the number of plant species globally has declined during the Anthropocene, but future declines seem likely given current and pending threats.
3. At the regional scale, the number of nonnative plant species established exceeds the number of native species that have gone extinct, often by a large margin, especially on islands.
4. At the local scale, conversion of primary vegetation to crop fields or urban development typically causes plant biodiversity to decline.

5. Outside of situations of wholesale habitat conversion for human use, recent temporal trends in local plant biodiversity are highly variable, sometimes positive, sometimes neg- ative, and often of negligible magnitude.
6. Major drivers of global environmental change, such as habitat fragmentation, climate change, and nitrogen deposition, have effects on local plant biodiversity that are highly context dependent, both in magnitude and in direction.
7. Thekinds of local or regional biotic changes that often concern conservation biologists— e.g., declines in native species and increases in nonnative species—do not necessarily involve declines in biodiversity per se, but rather represent changes in species composition.

ACKNOWLEDGMENTS

We thank Ines Ibáñez, Nathan Kraft and Tim Newbold for kindly sharing data or unpublished results, and Mark van Kleunen and Marten Winter for clarifying aspects of their studies. M.V. was supported by the Natural Sciences and Engineering Research Council, Canada.

LITERATURE CITED

1. African Plants Database, version 3.4.0. 2016. http://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an
2. Arroyo-Rodríguez V, Cavender-Bares J, Escobar F, Melo FP, Tabarelli M, Santos BA. 2012. Maintenance of tree phylogenetic diversity in a highly fragmented rain forest. *Journal of Ecology* 100:702-11
3. Baeten L, Hermy M, Van Daele S, Verheyen K. 2010. Unexpected understorey community development after 30 years in ancient and post-agricultural forests. *Journal of Ecology* 98:1447-53

4. Baeten L, Warton DI, Van Calster H, De Frenne P, Verstraeten G, et al. 2014. A model-based approach to studying changes in compositional heterogeneity. *Methods in Ecology and Evolution* 5:156-64

5. Bai E, Li S, Xu W, Li W, Dai W, Jiang P. 2013. A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytologist* 199:441-51

6. Baiser B, Olden JD, Record S, Lockwood JL, McKinney ML. 2012. Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society of London B: Biological Sciences* 279:4772-7

7. Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471:51-7

8. Bobbink R, Hicks K, Galloway J, Spranger T, Alkemade R, et al. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological applications* 20:30-59

9. Boivin NL, Zeder MA, Fuller DQ, Crowther A, Larson G, et al. 2016. Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences*:201525200

10. Bowman WD, Gartner JR, Holland K, Wiedermann M. 2006. Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: are we there yet? *Ecological applications* 16:1183-93

11. Brennan AC, Woodward G, Seehausen O, Muñoz-Fuentes V, Moritz C, et al. 2015. Hybridization due to changing species distributions: adding problems or solutions to conservation of biodiversity during global change? *Evolutionary Ecology Research* 16:475-91

12. Bruna EM, Vasconcelos HL, Heredia S. 2005. The effect of habitat fragmentation on communities of mutualists: Amazonian ants and their host plants. *Biological Conservation* 124:209-16

13. Brundu G, Camarda I. 2013. The flora of Chad: a checklist and brief analysis. *PhytoKeys* 12:1-18

14. Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, et al. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59-67

15. Cleland EE, Collins SL, Dickson TL, Farrer EC, Gross KL, et al. 2013. Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology* 94:1687-96

16. Cleland EE, Harpole WS. 2010. Nitrogen enrichment and plant communities. *Annals of the New York Academy of Sciences* 1195:46-61

17. Cronk Q. 2016. Plant extinctions take time. *Science* 353:446-7

18. Damschen EI, Harrison S, Grace JB. 2010. Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). *Ecology* 91:3609-19

19. Davis MA, Chew MK, Hobbs RJ, Lugo AE, Ewel JJ, et al. 2011. Don't judge species on their origins. *Nature* 474:153-4

20. De Camargo RX, Currie DJ. 2015. An empirical investigation of why species–area relationships overestimate species losses. *Ecology* 96:1253-63

21. De Schrijver A, De Frenne P, Ampoorter E, Van Nevel L, Demey A, et al. 2011. Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Global Ecology and Biogeography* 20:803-16

22. De Vos JM, Joppa LN, Gittleman JL, Stephens PR, Pimm SL. 2015. Estimating the normal background rate of species extinction. *Conservation Biology* 29:452-62

23. Debinski DM, Holt RD. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14:342-55

24. Diamond JM. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. *Proceedings of the National Academy of Sciences* 69:3199-203

25. Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, et al. 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344:296-9

26. Duguid MC, Ashton MS. 2013. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. *Forest Ecology and Management* 303:81-90

27. Ellis EC. 2015. Ecology in an anthropogenic biosphere. *Ecological Monographs* 85:287-331

28. Elmendorf SC, Henry GH, Hollister RD, Björk RG, Bjorkman AD, et al. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters* 15:164-75

29. Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487-515

30. Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61:1-10

31. Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JAF, et al. 2009. Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography* 36:132-47

32. FitzJohn RG, Pennell MW, Zanne AE, Stevens PF, Tank DC, Cornwell WK. 2014. How much of the world is woody? *Journal of Ecology* 102:1266-72

33. Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, et al. 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70:153-226

34. Gedan KB, Bertness MD. 2009. Experimental warming causes rapid loss of plant diversity in New England salt marshes. *Ecology Letters* 12:842-8

35. Gentry AH. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*:1-34

36. Harrison SP, Gornish ES, Copeland S. 2015. Climate-driven diversity loss in a grassland community. *Proceedings of the National Academy of Sciences* 112:8672-7

37. Hobbs RJ, Huenneke LF. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324-37

38. Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105-8

39. Hulme PE, Bernard-Verdier M, Bufford JL, Godsoe W. 2015. Rapid Anthropocene speciation reveals pull of the recent: a response to Thomas. *Trends in Ecology & Évolution* 30:635-6

40. Ibáñez I, Katz DS, Peltier D, Wolf SM, Barrie C, Benjamin T. 2014. Assessing the integrated effects of landscape fragmentation on plants and plant communities: The challenge of multiprocess–multiresponse dynamics. *Journal of Ecology* 102:882-95

41. IUCN. 2016. *The IUCN Red List of Threatened Species. Version 2016-1.* http://www.iucnredlist.org

42. Jackson ST, Sax DF. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution* 25:153-60

43. Javeline D, Hellmann JJ, McLachlan JS, Sax DF, Schwartz MW, Cornejo RC. 2015. Expert opinion on extinction risk and climate change adaptation for biodiversity. *Elementa: Science of the Anthropocene* 3:000057

44. Joppa LN, Roberts DL, Pimm SL. 2010. How many species of flowering plants are there? *Proceedings of the Royal Society of London B: Biological Sciences* 278:554-9

45. Klein JA, Harte J, Zhao XQ. 2004. Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters* 7:1170-9

46. Klironomos JN, Allen MF, Rillig MC, Piotrowski J, Makvandi-Nejad S, et al. 2005. Abrupt rise in atmospheric CO2 overestimates community response in a model plant–soil system. *Nature* 433:621-4

47. Knapp S, Kühn I, Stolle J, Klotz S. 2010. Changes in the functional composition of a Central European urban flora over three centuries. *Perspectives in Plant Ecology, Evolution and Systematics* 12:235-44

48. Kraft NJ, Comita LS, Chase JM, Sanders NJ, Swenson NG, et al. 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science* 333:1755-8

49. La Sorte FA, McKinney ML, Pyšek P. 2007. Compositional similarity among urban floras within and across continents: biogeographical consequences of human-mediated biotic interchange. *Global Change Biology* 13:913-21

50. Laliberté E, Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305

51. Laurance WF. 2007. Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Évolution* 22:65-70

52. Laurance WF, Camargo JL, Luizão RC, Laurance SG, Pimm SL, et al. 2011. The fate of Amazonian forest fragments: a 32-year investigation. *Biological Conservation* 144:56-67

53. Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ribeiro JELS, et al. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences* 103:19010-4

54. Levin D, Wilson A. 1976. Rates of evolution in seed plants: Net increase in diversity of chromosome numbers and species numbers through time. *Proceedings of the National Academy of Sciences* 73:2086-90

55. Levine JM, D'Antonio CM. 2003. Forecasting biological invasions with increasing international trade. *Conservation Biology* 17:322-6

56. Lin D, Xia J, Wan S. 2010. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. *New Phytologist* 188:187-98

57. Lockwood JL, Hoopes MF, Marchetti MP. 2013. *Invasion Ecology*. London: Wiley-Blackwell

58. Magnago LFS, Edwards DP, Edwards FA, Magrach A, Martins SV, Laurance WF. 2014. Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. *Journal of Ecology* 102:475-85

59. Magurran AE. 2003. *Measuring Biological Diversity*. London: Wiley-Blackwell

60. Maier DS. 2012. *What's So Good About Biodiversity?: A Call for Better Reasoning About Nature's Value*. Springer Netherlands

61. McCune JL, Vellend M. 2013. Gains in native species promote biotic homogenization over four decades in a human-dominated landscape. *Journal of Ecology* 101:1542-51

62. McGill BJ, Dornelas M, Gotelli NJ, Magurran AE. 2015. Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Évolution* 30:104-13

63. Millenium Ecosystem Assessment. 2005. *Ecosystems and Human Well-Being*. Island Press Washington, DC

64. Morar N, Toadvine T, Bohannan BJM. 2015. Biodiversity at twenty-five years: revolution or red herring? *Ethics, Policy & Environment* 18:16-29

65. Newbold T, Hudson LN, Hill SL, Contu S, Lysenko I, et al. 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520:45-50

66. Novacek MJ. 2001. *The Biodiversity Crisis: Losing What Counts*. New York: New Press, American Museum of Natural History

67. Odland A, Høitomt T, Olsen SL. 2010. Increasing vascular plant richness on 13 high mountain summits in southern Norway since the early 1970s. *Arctic, Antarctic, and Alpine Research* 42:458-70

68. Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42

69. Pärtel M, Helm A, Reitalu T, Liira J, Zobel M. 2007. Grassland diversity related to the Late Iron Age human population density. *Journal of Ecology* 95:574-82

70. Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, et al. 2012. Recent plant diversity changes on Europe’s mountain summits. *Science* 336:353-5

71. Pautasso M. 2007. Scale dependence of the correlation between human population presence and vertebrate and plant species richness. *Ecology letters* 10:16-24

72. Peñuelas J, Prieto P, Beier C, Cesaraccio C, De Angelis P, et al. 2007. Response of plant species richness and primary productivity in shrublands along a north–south gradient in Europe to seven

years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. *Global Change Biology* 13:2563-81

73. Pimm SL, Joppa LN. 2015. How many plant species are there, where are they, and at what rate are they going extinct? *Annals of the Missouri Botanical Garden* 100:170-6

74. Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, et al. 2010. Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences* 107:12157-62

75. Rabosky DL. 2016. Reproductive isolation and the causes of speciation rate variation in nature. *Biological Journal of the Linnean Society* 118:13-25

76. Regan HM, Lupia R, Drinnan AN, Burgman MA. 2001. The currency and tempo of extinction. *The American Naturalist* 157:1-10

77. Reid WV. 1992. How many species will there be? In *Tropical Deforestation and Species Extinction*, ed. TC Whitmore, JA Sayer:55-71. London: Chapman & Hall. Number of 55-71 pp.

78. Ricklefs RE. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167-71

79. Rosenzweig ML. 2001. The four questions: what does the introduction of exotic species do to diversity? *Evolutionary Ecology Research* 3:361-7

80. Santos BA, Arroyo-Rodríguez V, Moreno CE, Tabarelli M. 2010. Edge-related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. *PloS One* 5:e12625

81. Savage J, Vellend M. 2015. Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography* 38:546-55

82. Sax DF, Gaines SD. 2003. Species diversity: from global decreases to local increases. *Trends in Ecology & Évolution* 18:561-6

83. Sax DF, Gaines SD. 2008. Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences* 105:11490-7

84. Sax DF, Gaines SD, Brown JH. 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist* 160:766-83

85. Scariot A. 1999. Forest fragmentation effects on palm diversity in central Amazonia. *Journal of Ecology* 87:66-76

86. Simkin SM, Allen EB, Bowman WD, Clark CM, Belnap J, et al. 2016. Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. *Proceedings of the National Academy of Sciences* 113:4086-91

87. Smith BD, Zeder MA. 2013. The onset of the Anthropocene. *Anthropocene* 4:8-13

88. Smith MD, Knapp AK, Collins SL. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90:3279-89

89. Sommer JH, Kreft H, Kier G, Jetz W, Mutke J, Barthlott W. 2010. Projected impacts of climate change on regional capacities for global plant species richness. *Proceedings of the Royal Society of London B: Biological Sciences* 277:2271-80

90. Stanley SM. 1985. Rates of evolution. *Paleobiology* 11:13-26

91. Steffen W, Grinevald J, Crutzen P, McNeill J. 2011. The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* 369:842-67

92. Stevens CJ, Duprè C, Dorland E, Gaudnik C, Gowing DJ, et al. 2010. Nitrogen deposition threatens species richness of grasslands across Europe. *Environmental Pollution* 158:2940-5

93. Stork NE. 2010. Re-assessing current extinction rates. *Biodivers Conserv* 19:357-71

94. Storkey J, Macdonald A, Poulton P, Scott T, Köhler I, et al. 2015. Grassland biodiversity bounces back from long-term nitrogen addition. *Nature* 528:401-4

95. Stouffer PC, Johnson EI, Bierregaard Jr RO, Lovejoy TE. 2011. Understory bird communities in Amazonian rainforest fragments: species turnover through 25 years post-isolation in recovering landscapes. *PloS One* 6:e20543

96. Takacs D. 1996. *The Idea of Biodiversity: Philosophies of Paradise*. Johns Hopkins University Press

97. Thomas CD. 2013. The Anthropocene could raise biological diversity. *Nature* 502:7

98. Thomas CD. 2015. Rapid acceleration of plant speciation during the Anthropocene. *Trends in Ecology & Évolution* 30:448-55

99. Tilman D, El Haddi A. 1992. Drought and biodiversity in grasslands. *Oecologia* 89:257-64

100. Tilman D, May RM, Lehman CL, Nowak MA. 1994. Habitat destruction and the extinction debt. *Nature* 371:65-6

101. Tilman D, Reich PB, Isbell F. 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences* 109:10394-7

102. Urban MC. 2015. Accelerating extinction risk from climate change. *Science* 348:571-3

103. van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, et al. 2015. Global exchange and accumulation of non-native plants. *Nature*

104. van Vuuren DP, Sala OE, Pereira HM. 2006. The future of vascular plant diversity under four global scenarios. *Ecology and Society* 11:25

105. Vellend M. 2016. *The theory of ecological communities*. Princeton NJ: Princeton University Press

106. Vellend M, Baeten L, Myers-Smith IH, Elmendorf SC, Beauséjour R, et al. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences* 110:19456-9

107. Vellend M, Cornwell WK, Magnuson-Ford K, Mooers AO. 2010. Measuring phylogenetic biodiversity. In *Biological Diversity: Frontiers in Measurement and Assessment*, ed. AE Magurran, B McGill. New York: Oxford University Press.

108. Vellend M, Dornelas M, Baeten L, Beausejour R, Brown C, et al. 2016. Estimates of local biodiversity change over time stand up to scrutiny. *bioRxiv*:062133

109. Vellend M, Harmon LJ, Lockwood JL, Mayfield MM, Hughes AR, et al. 2007. Effects of exotic species on evolutionary diversification. *Trends in Ecology & Évolution* 22:481-8

110. Vellend M, Verheyen K, Jacquemyn H, Kolb A, Van Calster H, et al. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87:542-8

111. Verheyen K, Vanhellemont M, Auge H, Baeten L, Baraloto C, et al. 2016. Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio* 45:29-41

112. Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, et al. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30:257-300

113. Wardle DA. 2016. Do experiments exploring plant diversity–ecosystem functioning relationships inform how biodiversity loss impacts natural ecosystems? *Journal of Vegetation Science* 27:646-53

114. Whittaker RH. 1975. *Communities and ecosystems*. Macmillan

115. Willis K, McElwain J. 2014. *The Evolution of Plants*. OUP Oxford

116. Wilson EO, Peter FM, Sciences NA, Institution S. 1988. *Biodiversity*. National Academy Press

117. Wing SL. 2004. Mass extinctions in plant evolution. In *Extinctions in the history of life*, ed. PD Taylor:61-98. Cambridge, UK: Cambridge University Press. Number of 61-98 pp.

118. Winter M, Kühn I, La Sorte FA, Schweiger O, Nentwig W, Klotz S. 2010. The role of non-native plants and vertebrates in defining patterns of compositional dissimilarity within and across continents. *Global Ecology and Biogeography* 19:332-42

119. Winter M, Schweiger O, Klotz S, Nentwig W, Andriopoulos P, et al. 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences* 106:21721-5

120. Wolkovich EM, Cook BI, Allen JM, Crimmins TM, Betancourt JL, et al. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485:494-7

121. Wood TE, Takebayashi N, Barker MS, Mayrose I, Greenspoon PB, Rieseberg LH. 2009. The frequency of polyploid speciation in vascular plants. *Proceedings of the National Academy of Sciences* 106:13875-9

122. World Conservation Monitoring Center. 1992. *Global Biodiversity: Status of the Earth's Living Resources*. London: Chapman & Hall

123. Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology* 17:927-42

124. Zartman CE. 2003. Habitat fragmentation impacts on epiphyllous bryophyte communities in central Amazonia. *Ecology* 84:948-54

125. Zavaleta ES, Shaw MR, Chiariello NR, Thomas BD, Cleland EE, et al. 2003. Grassland responses to three years of elevated temperature, CO2, precipitation, and N deposition. *Ecological Monographs* 73:585-604

126. Zuppinger-Dingley D, Schmid B, Petermann JS, Yadav V, De Deyn GB, Flynn DF. 2014. Selection for niche differentiation in plant communities increases biodiversity effects. *Nature* 515:108-11

BIBLIOGRAPHIE

Adler, P.B., HilleRisLambers, J., and Levine, J.M. (2007). A niche for neutrality. Ecol. Lett. *10*, 95–104.

Aitken, S.N., Yeaman, S., Holliday, J. a., Wang, T., and Curtis-McLane, S. (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. *1*, 95–111.

Alatalo, J., Jägerbrand, A., and Molau, U. (2014). Seven years of experimental warming and nutrient addition causes decline of bryophytes and lichens in alpine meadow and heath communities. PeerJ 1–22.

Alonso, D., Étienne, R.S., and McKane, A.J. (2006). The merits of neutral theory. Trends Ecol. Evol. *21*, 451–457.

Archaux, F., Henry, P.Y., and Gimenez, O. (2012). When can we ignore the problem of imperfect detection in comparative studies? Methods Ecol. Evol. *3*, 188–194.

Bagella, S. (2014). Does cross-taxon analysis show similarity in diversity patterns between vascular plants and bryophytes? Some answers from a literature review. C. R. Biol. *337*, 276–282.

Barabás, G., D'Andrea, R., and Stump, S.M. (2018). Chesson's coexistence theory. Ecol. Monogr.

Barthlott, W., Mutke, J., Rafiqpoor, D., Kier, G., and Kreft, H. (2005). Global centers of vascular plant diversity. Nov. Acta Leopoldina NF *92*, 61–83.

Barthlott, W., Hostert, A., Kier, G., Küper, W., Kreft, H., Mutke, J., Rafiqpoor, M.D., and Sommer, J.H. (2007). Geographic patterns of vascular plant diversity at continental to global scales. Erdkunde *61*, 305–315.

Bates, J.W., Thompson, K., and Grime, J.P. (2005). Effects of simulated long-term climatic change on the bryophytes of a limestone grassland community. Glob. Chang. Biol. *11*, 757–769.

Bell, G. (2001). Neutral Macroecology. Science (80-.). *293*, 2413–2418.

Bergamini, A., Ungricht, S., and Hofmann, H. (2009). An elevational shift of cryophilous bryophytes in the last century - an effect of climate warming? Divers. Distrib. *15*, 871–879.

Berteaux, D. (2014). Changements climatiques et biodiversité du Québec : vers un patrimoine naturel (Presses de l'université du Québec).

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C., and Gégout, J.-C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. Nature *479*, 517–520.

Bilton, M.C., Metz, J., and Tielbörger, K. (2016). Climatic niche groups: A novel application of a common assumption predicting plant community response to climate change. Perspect. Plant Ecol. Evol. Syst. *19*, 61–69.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., et al. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol. Appl. *20*, 30–59.

Bodin, J., Badeau, V., Bruno, E., Cluzeau, C., Moisselin, J.-M., Walther, G.-R., and Dupouey, J.-L. (2013). Shifts of forest species along an elevational gradient in Southeast France: climate change or stand maturation? J. Veg. Sci. *24*, 269–283.

Bouwman, A.F., Van Vuuren, D.P., Derwent, R.G., and Posch, M. (2002). A global analysis of acidification and eutrophication of terrestrial ecosystems. Water. Air. Soil Pollut. *141*, 349–382.

Braun-Blanquet, J., Roussine, N., and Nègre, R. (1952). Les Groupements Végétaux de la France Méditerranéenne (Toulouse).

Bray, J.R., and Curtis, J.T. (1957). An Ordination of the Upland Forest Communities of Southern Wisconsin. Ecol. Monogr. *27*, 325–349.

Brown, C.D., and Vellend, M. (2014). Non-climatic constraints on upper elevational plant range expansion under climate change. Proc. R. Soc. B Biol. Sci. *281*, 20141779–20141779.

Brown, J.H.J.H., and Kodric-Brown, A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. Ecology *58*, 445–449.

Bruun, H.H., Moen, J., Virtanen, R., Grytnes, J., Oksanen, L., and Angerbjörn, A. (2006). Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. J. Veg. Sci. *17*, 37–46.

Cannone, N., and Pignatti, S. (2014). Ecological responses of plant species and communities to climate warming: upward shift or range filling processes? Clim. Change *123*, 201–214.

Chase, J.M., and Leibold, M.A. (2003). Ecological niches: linking classical and contemporary approaches (University of Chicago Press).

Chase, M.W., and Reveal, J.L. (2009). A phylogenetic classification of the land plants to accompany APG III. Bot. J. Linn. Soc. *161*, 122–127.

Chave, J. (2004). Neutral theory and community ecology. Ecol. Lett. *7*, 241–253.

Chen, I., Hill, J.K., Ohlemuller, R., Roy, D.B., and Thomas, C.D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science (80-.). *333*, 1024–1026.

Cherrett, J.M., Bradshaw, A.D., Goldsmith, F.B., Grubb, P.J., and Krebs, J.R. (1989). Ecological concepts: the contribution of ecology to an understanding of the natural world. Ecol. Concepts Contrib. Ecol. to an Underst. Nat. World.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. *31*, 343–366.

Chytrý, M., Tichý, L., Hennekens, S.M., and Schaminée, J.H.J. (2014). Assessing vegetation change using vegetation-plot databases: a risky business. Appl. Veg. Sci. *17*, 32–41.

Clavel, J., Julliard, R., and Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. *9*, 222–228.

Clements, F.E. (1916). Preface to plant succession: an analysis of the development of vegetation. Plant Succession An Anal. Dev. Veg. *242*, 36–41.

Colwell, R.K., Brehm, G., Cardelus, C.L., Gilman, A.C., and Longino, J.T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science (80-.). *322*, 258–261.

Corlett, R.T., and Westcott, D.A. (2013). Will plant movements keep up with climate change? Trends Ecol. Evol. *28*, 482–488.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A., and During, H.J. (2007). Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. Ann. Bot. *99*, 987–1001.

Coumou, D., and Rahmstorf, S. (2012). A decade of weather extremes. Nat. Clim. Chang. *2*, 491–496.

Cronberg, N. (2004). Genetic differentiation between populations of the moss Hylocomium splendens (Hedw.) Schimp. from low versus high elevation in the Scandinavian mountain range. Lindbergia *29*, 64–72.

Damschen, E.I., Harrison, S., and Grace, J.B. (2010). Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). Ecology *91*, 3609–3619.

Delcourt, P.A., and Delcourt, H.R. (1983). Late-Quaternary vegetational dynamics and community stability reconsidered. Quat. Res. *19*, 265–271.

Delcourt, H.R., Delcourt, P.A., and Webb, T. (1982). Dynamic plant ecology: the spectrum of vegetational change in space and time. Quat. Sci. Rev. *1*, 153–175.

Delgado, V., and Ederra, A. (2013). Long-term changes (1982–2010) in the bryodiversity of Spanish beech forests assessed by means of Ellenberg indicator values of temperature, nitrogen, light and pH. Biol. Conserv. *157*, 99–107.

Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., De Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Lopez-Gonzalez, G., Finckh, M., et al. (2011). The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. J. Veg. Sci. *22*, 582–597.

Désamoré, A., Laenen, B., Stech, M., Papp, B., Hedenäs, L., Mateo, R.G., and Vanderpoorten,

A. (2012). How do temperate bryophytes face the challenge of a changing environment? Lessons from the past and predictions for the future. Glob. Chang. Biol. *18*, 2915–2924.

Diekmann, M., and Dupré, C. (1997). Acidification and eutrophication of deciduous forests in northwestern Germany demonstrated by indicator species analysis. J. Veg. Sci. *1*, 855–864.

Dise, N.B., and Wright, R.F. (1995). Nitrogen leaching from European forests in relation to nitrogen deposition. For. Ecol. Manage. *71*, 153–161.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., and Magurran, A.E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. Science (80-.). *344*, 296–299.

Dubey, B., Yadav, R.R., Singh, J., and Chaturvedi, R. (2003). Upward shift of Himalayan pine in Western Himalaya, India. Curr. Sci. *85*, 1135–1136.

Dunson, W. a., and Travis, J. (1991). The Role of Abiotic Factors in Community Organization. Am. Nat. *138*, 1067–1091.

Dyke, A.S. (2005). Late quaternary vegetation history of northern north america based on pollen, macrofossil, and faunal remains. Géographie Phys. Quat. *59*, 211–262.

Elith, J., and Leathwick, J.R. (2009). Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. *40*, 677–697.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., and Paulißen, D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. Scr. Geobot. IX *18*, 1–248.

Elton, C. (1927). Animal Ecology. Anim. Ecol. 207.

Eriksson, O. (2000). Seed dispersal and colonization ability of plants - Assessment and implications for conservation. Folia Geobot. *35*, 115–123.

Erisman, J.W., and de Vries, W. (2000). Nitrogen deposition and effects on European forests. Environ. Rev. *8*, 65–93.

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. Annu. Rev. Ecol. Evol. Syst. *34*, 487–515.

Feeley, K.J., Silman, M.R., Bush, M.B., Farfan, W., Cabrera, K.G., Malhi, Y., Meir, P., Revilla, N.S., Quisiyupanqui, M.N.R., and Saatchi, S. (2011). Upslope migration of Andean trees. J. Biogeogr. *38*, 783–791.

Fenton, N.J., and Bergeron, Y. (2013). Stochastic processes dominate during boreal bryophyte community assembly. Ecology *94*, 1993–2006.

Field, C.D., Dise, N.B., Payne, R.J., Britton, A.J., Emmett, B. a., Helliwell, R.C., Hughes, S., Jones, L., Lees, S., Leake, J.R., et al. (2014). The role of nitrogen deposition in widespread plant community change across semi-natural habitats. Ecosystems *17*, 864–877.

Fox, J.W. (2013). The intermediate disturbance hypothesis revisited. Trends Ecol. Evol. *28*, 86–92.

Frahm, J.P. (2008). Diversity, dispersal and biogeography of bryophytes (mosses). Biodivers. Conserv. *17*, 277–284.

Frahm, J.P., and Klaus, D. (2001). Bryophytes as indicators of recent climate fluctuations in Central Europe. Lindbergia *26*, 97–104.

Frego, K.A. (2007). Bryophytes as potential indicators of forest integrity. For. Ecol. Manage. *242*, 65–75.

De Frenne, P., Rodriguez-Sanchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Romermann, M., Brown, C.D., Brunet, J., Cornelis, J., et al. (2013). Microclimate moderates plant responses to macroclimate warming. Proc. Natl. Acad. Sci. *110*, 18561–18565.

De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D. a., Hermy, M., Vangansbeke, P., and Verheyen, K. (2015). Light accelerates plant responses to warming. Nat. Plants *1*, 15110.

Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L. a, Seitzinger, S.P., and Sutton, M. a (2008). Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science (80-.). *320*, 889–892.

Gauch, H.G. (1982). Multivariate analysis in community ecology (Cambridge University

Press.).

Gause, G.F. (1936). The Struggle for Existence. Soil Sci. *41*, 159.

Geffert, J.L., Frahm, J.-P., Barthlott, W., and Mutke, J. (2013). Global moss diversity: spatial and taxonomic patterns of species richness. J. Bryol. *35*, 1–11.

Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A., and Merilä, J. (2008). Climate change and evolution: disentangling environmental and genetic responses. Mol. Ecol. *17*, 167–178.

Gignac, L.D. (2001). Bryophytes as indicators of climate change. Bryologist *104*, 410–420.

Gilbert, B., and Lechowicz, M.J. (2004). Neutrality, niches, and dispersal in a temperate forest understory. Proc. Natl. Acad. Sci. U. S. A. *101*, 7651–7656.

Gleason, H.A. (1926). The Individualistic Concept of the Plant Association. Bull. Torrey Bot. Club *53*, 7.

Glime, J.M. (2007). Bryophyte Ecology. Volume 1. Physiological Ecology (Ebook sponsored by Michigan Technological University and the International Association of Bryologists.).

Goffinet, B., and Shaw, A.J. (2008). Bryophyte biology, second edition.

Gornish, E.S., and Tylianakis, J.M. (2013). Community shifts under climate change: Mechanisms at multiple scales. Am. J. Bot. *100*, 1422–1434.

Gotelli, N.J., Shimadzu, H., Dornelas, M., McGill, B., Moyes, F., and Magurran, A.E. (2017). Community-level regulation of temporal trends in biodiversity. Sci. Adv. *3*, e1700315.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J.L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M.R., et al. (2012). Spplementary, Continent-wide response of mountain vegetation to climate change. Nat. Clim. Chang. *2*, 111–115.

Grabherr, G., Pauli, H., and Gottfried, M. (2010). A worldwide observation of effects of climate change on mountain ecosystems. Challenges Mt. Reg. - Track. Complex. 50–57.

Gravel, D., Canham, C.D., Beaudet, M., and Messier, C. (2006). Reconciling niche and neutrality: the continuum hypothesis. Ecol. Lett. *9*, 399–409.

Gravel, D., Bell, T., Barbera, C., Bouvier, T., Pommier, T., Venail, P., and Mouquet, N. (2011). Experimental niche evolution alters the strength of the diversity–productivity relationship. Nature *469*, 89–92.

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ccological and evolutionary theory. Am. Nat. *111*, 1169–1194.

Grinnell, J. (1917). The Niche-Relationships of the California Thrasher. Auk *34*, 427–433.

Grytnes, J.A., Heegaard, E., and Ihlen, P.G. (2006). Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. Acta Oecologica *29*, 241–246.

Hairston, N.G., Smith, F.E., and Slobodkin, L.B. (1960). Community structure, population control, and competition. Am. Nat. *94*, 421–425.

Hanski, I. (2001). Spatially realistic theory of metapopulation ecology. Naturwissenschaften *88*, 372–381.

Hanski, I., and Ovaskainen, O. (2003). Metapopulation theory for fragmented landscapes. Theor. Popul. Biol. *64*, 119–127.

Harrison, S.P., and Sanchez Goñi, M.F. (2010). Global patterns of vegetation response to millennial-scale variability and rapid climate change during the last glacial period. Quat. Sci. Rev. *29*, 2957–2980.

Harrison, S., Damschen, E.I., Grace, J.B., Ricklefs, R.E., and Damschenb, E.I. (2010). Ecological warming in the effects of climatic contingency on forest herb communities. Proc. Natl. Acad. Sci. *107*, 19362–19367.

He, X., He, K.S., and Hyvönen, J. (2016). Will bryophytes survive in a warming world? Perspect. Plant Ecol. Evol. Syst. *19*, 49–60.

Hedderson, T.A., and Longton, R.E. (1996). Life History Variation in Mosses: Water Relations, Size and Phylogeny. Oikos *77*, 31.

Hédl, R., Bernhardt-Römermann, M., Grytnes, J.-A., Jurasinski, G., and Ewald, J. (2017).

Resurvey of historical vegetation plots: a tool for understanding long-term dynamics of plant communities. Appl. Veg. Sci. *20*, 161–163.

Heinrichs, S., and Schmidt, W. (2016). Biotic homogenization of herb layer composition between two contrasting beech forest communities on limestone over 50 years. Appl. Veg. Sci. *20*, 271–281.

Hermy, M., and Verheyen, K. (2007). Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecol. Res. *22*, 361–371.

Higgins, S.I., Lavorel, S., and Revilla, E. (2003). Estimating plant migration rates under habitat loss and fragmentation. Oikos *101*, 354–366.

Hill, M.O., Preston, C.D., and Roy, D.B. (2004). Plantatt atributes of British and Irish plants: status, size, life history, geography and habitats. NERC, Cent. Ecol. Hydrol. 80.

Hill, M.O., Preston, C.D., Bosanquet, S.D.S., and Roy, D.B. (2007). Bryoatt - attributes of British and Irish mosses, liverworts and hornworts. NERC, Cent. Ecol. Hydrol. 1–88.

Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., Filstrup, C.T., Harpole, W.S., Hodapp, D., Larsen, S., et al. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. J. Appl. Ecol. *55*, 169–184.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., and Mayfield, M.M. (2012). Rethinking community assembly through the lens of coexistence theory. Annu. Rev. Ecol. Evol. Syst. *43*, 227–248.

Hoeinghaus, D.J., Winemiller, K.O., and Birnbaum, J.S. (2007). Local and regional determinants of stream fish assemblage structure: Inferences based on taxonomic vs. functional groups. J. Biogeogr. *34*, 324–338.

Hubbell, S.P. (2001). The Unified Neutral Theory of Biodiversity and Biogeography (Princeton University Press).

Huber, M., and Knutti, R. (2012). Anthropogenic and natural warming inferred from changes in Earth's energy balance. Nat. Geosci. *5*, 31–36.

Hudson, J.M.G., and Henry, G.H.R. (2010). High Arctic plant community resists 15 years of experimental warming. J. Ecol. *98*, 1035–1041.

Hutchinson, G.E. (1957). Concluding Remarks. Cold Spring Harb. Symp. Quant. Biol. *22*, 415–427.

Ibáñez, I., Katz, D.S.W., Peltier, D., Wolf, S.M., and Connor Barrie, B.T. (2014). Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. J. Ecol. *102*, 882–895.

Isselin-Nondedeu, F. (2014). Plant community ecology: current issues and multiple approaches. Acta Bot. Gall. *161*, 223–232.

Jump, A.S., Huang, T.-J., and Chou, C.-H. (2012). Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. Ecography (Cop.). *35*, 204–210.

Kapfer, J., Virtanen, R., and Grytnes, J.A. (2012). Changes in arctic vegetation on Jan Mayen Island over 19 and 80 years. J. Veg. Sci. *23*, 771–781.

Kelly, A.E., and Goulden, M.L. (2008). Rapid shifts in plant distribution with recent climate change. Proc. Natl. Acad. Sci. *105*, 11823–11826.

Kelly, C.K., Bowler, M.G., Pybus, O., and Harvey, P.H. (2008). Phylogeny, niches, and relative abundance in natural communities. Ecology *89*, 962–970.

Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H., and Barthlott, W. (2005). Global patterns of plant diversity and floristic knowledge. J. Biogeogr. *32*, 1107–1116.

Kimura, M. (1985). The Neutral Theory of Molecular Evolution. Am. Anthropol. *87*, 440–441.

Klanderud, K., and Birks, H.J.B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. The Holocene *13*, 1–6.

Klasner, F.L., and Fagre, D.B. (2002). A half century of change in Alpine treeline patterns at

Glacier National Park, Montana, U.S.A. Arctic, Antarct. Alp. Res. *34*, 49–56.

Koide, D., Yoshida, K., Daehler, C.C., and Mueller-Dombois, D. (2017). An upward elevation shift of native and non-native vascular plants over 40 years on the island of Hawai'i. J. Veg. Sci. *28*, 939–950.

von Konrat, M., Hagborg, A., Söderström, L., Mutke, J., Renner, M., Gradstein, S.R., Engel, J., Zhu, R.-L., and Pickering, J. (2008). Early land plants today: global patterns of liverwort diversity, distribution, and floristic knowlege. In Bryology in the New Millennium, H. Mohamed, B. Baki, A. Nasrulhaq-Boyce, and L. Pky, eds. (Kuala Lumpur: University of Malaya), pp. 425–438.

Kreft, H., and Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. Proc. Natl. Acad. Sci. *104*, 5925–5930.

Lalanne, A., Bardat, J., Lalanne-Amara, F., Gautrot, T., and Ponge, J.-F. (2008). Opposite responses of vascular plant and moss communities to changes in humus form, as expressed by the Humus Index. J. Veg. Sci. *19*, 645–652.

Lalanne, A., Bardat, J., Lalanne-Amara, F., and Ponge, J.F. (2010). Local and regional trends in the ground vegetation of beech forests. Flora Morphol. Distrib. Funct. Ecol. Plants *205*, 484–498.

Lamarque, P., Lavorel, S., Mouchet, M., and Quetier, F. (2014). Plant trait-based models identify direct and indirect effects of climate change on bundles of grassland ecosystem services. Proc. Natl. Acad. Sci. *111*, 13751–13756.

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Bruce Williamson, G., Benítez-Malvido, J., and Vasconcelos, H.L. (2011). The fate of Amazonian forest fragments: A 32-year investigation. Biol. Conserv. *144*, 56–67.

Lavergne, S., Mouquet, N., Thuiller, W., and Ronce, O. (2010). Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. Annu. Rev. Ecol. Evol. Syst. *41*, 321–350.

Lee, T.D., and La Roi, G.H. (1979). Bryophyte and understory vascular plant beta diversity in relation to moisture and elevation gradients. Vegetatio *40*, 29–38.

Leibold, M. a (2008). Ecology: Return of the niche. Nature *454*, 39–41.

Leibold, M. a., and McPeek, M. a. (2006). Coexistence of the niche and neutral perspectives in community ecology. Ecology *87*, 1399–1410.

Leibold, M. a., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., et al. (2004). The metacommunity concept: A framework for multi-scale community ecology. Ecol. Lett. *7*, 601–613.

Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P., and Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. Science (80-.). *320*, 1768–1771.

Lesica, P., and McCune, B. (2004). Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. J. Veg. Sci. *15*, 679–690.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Am. *15*, 237–240.

Ligrone, R., Duckett, J.G., and Renzaglia, K.S. (2000). Conducting tissues and phyletic relationships of bryophytes. Philos. Trans. R. Soc. B Biol. Sci. *355*, 795–813.

Lindo, Z., and Gonzalez, A. (2010). The bryosphere: An integral and influential component of the Earth's biosphere. Ecosystems *13*, 612–627.

Longton, R.E. (1988). Adaptations and strategies of polar bryophytes. Bot. J. Linn. Soc. *98*, 253–268.

Lotka, A.J. (1926). Elements of Physical Biology. Sci. Prog. Twent. Century *21*, 341–343.

Lyons, K.S., Amatangelo, K.L., Behrensmeyer, A.K., Bercovici, A., Blois, J.L., Davis, M., DiMichele, W.A., Du, A., Eronen, J.T., Tyler Faith, J., et al. (2016). Holocene shifts in the assembly of plant and animal communities implicate human impacts. Nature *529*, 80–83.

Van Der Maarel, E., and Franklin, J. (2013). Vegetation Ecology: Historical Notes and Outline. Veg. Ecol. Second Ed. 1–27.

MacArthur, R.H., and Wilson, E.O. (1963). An Equilibrium Theory of Insular Zoogeography. Evolution (N. Y). *17*, 373.

MacArthur, R.H., and Wilson, E.O. (1967). The theory of island biogeography (Princeton Landmarks in Biology).

Magnago, L.F.S., Edwards, D.P., Edwards, F.A., Magrach, A., Martins, S. V., and Laurance, W.F. (2014). Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J. Ecol. *102*, 475–485.

Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.M., Elston, D. a, Scott, E.M., Smith, R.I., Somerfield, P.J., and Watt, A.D. (2010). Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends Ecol. Evol. *25*, 574–582.

Magurran, A.E., Deacon, A.E., Moyes, F., Shimadzu, H., Dornelas, M., Phillip, D.A.T., and Ramnarine, I.W. (2018). Divergent biodiversity change within ecosystems. Proc. Natl. Acad. Sci. *115*, 1843–1847.

St. Martin, P., and Azim, M.U. (2017). The status of non-vascular plants in trait-based ecosystem function studies. Perspect. Plant Ecol. Evol. Syst.

Mateo, R.G., Broennimann, O., Normand, S., Petitpierre, B., Araújo, M.B., Svenning, J.-C., Baselga, A., Fernández-González, F., Gómez-Rubio, V., Muñoz, J., et al. (2016). The mossy north: an inverse latitudinal diversity gradient in European bryophytes. Sci. Rep. *6*, 25546.

McGill, B. (2015). Land use matters. Nature *520*, 38–39.

McGill, B., and Collins, C. (2003). A unified theory for macroecology based on spatial patterns of abundance. Evol. Ecol. Res. *5*, 469–492.

McGill, B.J., Dornelas, M., Gotelli, N.J., and Magurran, A.E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. Trends Ecol. Evol. *30*, 104–113.

McKenney, D.W., Hutchiinson, M.F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., Milewska, E., Hopkinson, R.F., Price, D., and Owen, T. (2011). Customized spatial climate models for North America. Bull. Am. Meteorol. Soc. *92*, 1611–1622.

Merow, C., Wilson, A.M., and Jetz, W. (2017). Integrating occurrence data and expert maps for improved species range predictions. Glob. Ecol. Biogeogr. *26*, 243–258.

Molau, U., and Alatalo, J.M. (1998). Responses of subarctic-alpine plants communities to simulated environmental change, biodiversity of bryophytes , lichens and vascular plants. Ambio *27*, 322–329.

Mouquet, N., and Loreau, M. (2003). Community patterns in source-sink metacommunities. Am. Nat. *162*, 544–557.

Nascimbene, J., and Spitale, D. (2017). Patterns of beta-diversity along elevational gradients inform epiphyte conservation in alpine forests under a climate change scenario. Biol. Conserv. *216*, 26–32.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., et al. (2015). Global effects of land use on local terrestrial biodiversity. Nature *520*, 45–50.

Økland, T., Bakkestuen, V., Økland, R.H., and Eilertsen, O. (2004). Changes in forest understorey vegetation in Norway related to long-term soil acidification and climatic change. J. Veg. Sci. *15*, 437–448.

Olden, J.D., and Rooney, T.P. (2006). On defining and quantifying biotic homogenization. Glob. Ecol. Biogeogr. *15*, 113–120.

Pannek, A., Duprè, C., Gowing, D.J.G., Stevens, C.J., and Diekmann, M. (2015). Spatial gradient in nitrogen deposition affects plant species frequency in acidic grasslands. Oecologia *177*, 39–51.

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. Annu. Rev. Ecol. Evol. Syst. *37*, 637–666.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., et al. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature *399*, 579–583.

Parmesan, C., Root, T.L., and Willig, M.R. (2000). Impacts of Etreme Weather and Climate on Terrestrial Biota. Bull. Am. Meteorol. Soc. *81*, 443–450.

Parolo, G., and Rossi, G. (2008). Upward migration of vascular plants following a climate warming trend in the Alps. Basic Appl. Ecol. *9*, 100–107.

Pauli, H., Gottfried, M., and Grabherr, G. (1996). Effects of climate change on mountain ecosystems - upward shifting of alpine plants. World Resour. Rev. *8*, 382–390.

Pauli, H., Gottfreid, M., Reiter, K., Klettner, C., and Grabherr, G. (2007). Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA master site Schrankogel, Tyrol, Austria. Glob. Chang. Biol. *13*, 147–156.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J.L.B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R.F., et al. (2012). Recent Plant Diversity Changes on Europe’s Mountain Summits. Science (80-.). *336*, 353–355.

Pearson, R.G., and Dawson, T.P. (2005). Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. Biol. Conserv. *123*, 389–401.

Phoenix, G.K., Emmett, B.A., Britton, A.J., Caporn, S.J.M., Dise, N.B., Helliwell, R., Jones, L., Leake, J.R., Leith, I.D., Sheppard, L.J., et al. (2012). Impacts of atmospheric nitrogen deposition: Responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. Glob. Chang. Biol. *18*, 1197–1215.

Proctor, M.C.F. (1990). The physiological basis of bryophyte production. Bot. J. Linn. Soc. *104*, 61–77.

Pulliam, H.R. (2000). On the relationship between niche and distribution. Ecol. Lett. *3*, 349–361.

Raabe, S., Müller, J., Manthey, M., Dürhammer, O., Teuber, U., Göttlein, A., Förster, B., Brandl, R., and Bässler, C. (2010). Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. For. Ecol. Manage. *260*, 1956–1964.

Rafferty, N.E., and Nabity, P.D. (2017). A global test for phylogenetic signal in shifts in flowering time under climate change. J. Ecol. *105*, 627–633.

Rice, S.K., Aclander, L., and Hanson, D.T. (2008). Do bryophyte shoot systems function like vascular plant leaves or canopies? Functional trait relationships in Sphagnum mosses (Sphagnaceae). Am. J. Bot. *95*, 1366–1374.

Richard, P.J.H. (1995). Le couvert végétal du Québec-Labrador il y a 6000 ans BP : essai. Géographie Phys. Quat. *49*, 117.

Richard, P.J.H., and Grondin, P. (2009). Histoire postglaciaire de la vegetation. Man. For. 170–176.

Root, T., Price, J., Hall, K., and Schneider, S. (2003). Fingerprints of global warming on wild animals and plants. Nature *421*, 57–60.

Rydin, H. (2008). Population and community ecology of bryophytes. In Bryophyte Biology, (Cambridge University Press), pp. 393–444.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., et al. (2000). Global biodiversity scenarios for the year 2100. Science (80-.). *287*, 1770–1774.

Savage, J., and Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. Ecography (Cop.). *38*, 546–555.

Schaminée, J.H.J., Hennekens, M.S., Milan, C., and Rodwell, J.S. (2009). Vegetation-plot data and databases in Europe : an overview. Preslia *81*, 173–185.

de Schrijver, A., de Frenne, P., Ampoorter, E., van Nevel, L., Demey, A., Wuyts, K., and Verheyen, K. (2011). Cumulative nitrogen input drives species loss in terrestrial ecosystems. Glob. Ecol. Biogeogr. *20*, 803–816.

Seppelt, R.D., Green, T.G. a., Schwarz, A.-M.J., and Frost, A. (1992). Extreme southern locations for moss sporophytes in Antarctica. Antarct. Sci. *4*, 37–39.

Shaw, J. (2001). Biogeographic patterns and cryptic speciation in bryophytes. J. Biogeogr. *28*, 253–261.

Shaw, J., and Renzaglia, K. (2004). Phylogeny and diversification of bryophytes. Am. J. Bot.

91, 1557–1581.

Shmida, A., and Wilson, M. V (1985). Biological Determinants of Species Diversity. J. Biogeogr. *12*, 1–20.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Baraloto, C., Carlucci, M.B., Cianciaruso, M. V., et al. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol. Lett. *18*, 1406–1419.

Simkin, S.M., Allen, E.B., Bowman, W.D., Clark, C.M., Belnap, J., Brooks, M.L., Cade, B.S., Collins, S.L., Geiser, L.H., Gilliam, F.S., et al. (2016). Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. Proc. Natl. Acad. Sci. *113*, 4086–4091.

Smith, T.M., and Reynolds, R.W. (2005). A global merged land-air-sea surface temperature reconstruction based on historical observations (1880-1997). J. Clim. *18*, 2021–2036.

Smith, M.D., Knaap, A.K., and Collins, S.L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. Ecology *90*, 3279–3289.

Soons, M.B., Hefting, M.M., Dorland, E., Lamers, L.P.M., Versteeg, C., and Bobbink, R. (2017). Nitrogen effects on plant species richness in herbaceous communities are more widespread and stronger than those of phosphorus. Biol. Conserv. *212*, 390–397.

Spaak, J.W., Baert, J.M., Baird, D.J., Eisenhauer, N., Maltby, L., Pomati, F., Radchuk, V., Rohr, J.R., Van den Brink, P.J., and De Laender, F. (2017). Shifts of community composition and population density substantially affect ecosystem function despite invariant richness. Ecol. Lett. *20*, 1315–1324.

Sporn, S.G., Bos, M.M., Hoffstätter-Müncheberg, M., Kessler, M., and Gradstein, S.R. (2009). Microclimate determines community composition but not richness of epiphytic understory bryophytes of rainforest and cacao agroforests in Indonesia. Funct. Plant Biol. *36*, 171.

Stevens, C.J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D.J.G., Bleeker, A., Diekmann, M., Alard, D., Bobbink, R., Fowler, D., et al. (2010). Nitrogen deposition threatens species richness of grasslands across Europe. Environ. Pollut. *158*, 2940–2945.

Stockli, V., Wipf, S., Nilsson, C., and Rixen, C. (2012). Using historical plant surveys to track biodiversity on mountain summits. Plant Ecol. Divers. *4*, 415–425.

Tansley, A.G. (1935). The use and abuse of vegetational concepts and terms. Ecology *16*, 284–307.

Thimonier, A., Dupouey, J.L., Bost, F., and Becker, M. (1994). Simultaneous eutrophication and acidification of a forest ecosystem in North-East France. New Phytol. *126*, 533–539.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, a D., Davies, Z.G., Musche, M., and Conradt, L. (2001). Ecological and evolutionary processes at expanding range margins. Nature *411*, 577–581.

Thomas, C.D., Thomas, C.D., Cameron, A., Cameron, A., Green, R.E., Green, R.E., Bakkenes, M., Bakkenes, M., Beaumont, L.J., Beaumont, L.J., et al. (2004). Extinction risk from climate change. Nature *427*, 145–148.

Tilman, D. (1982). Resource competition and community structure (Princeton University Press).

Tingley, M.W., and Beissinger, S.R. (2009). Detecting range shifts from historical species occurrences: new perspectives on old data. Trends Ecol. Evol. *24*, 625–633.

Tuba, Z., Slack, N.G., and Stark, L.R. (2011). Bryophyte ecology and climate change (Cambridge: Cambridge University Press.).

Turetsky, M.R. (2003). The role of Bryophytes in carbon and nitrogen cycling. Bryologist *106*, 395–409.

Urban, M.C. (2015). Accelerating extinction risk from climate change. Science (80-.). *348*, 571–573.

Vanderpoorten, A., and Goffinet, B. (2009). Introduction to Bryophytes (Cambridge, UK: Cambridge University Press).

Vanhellemont, M., Baeten, L., and Verheyen, K. (2014). Relating changes in understorey diversity to environmental drivers in an ancient forest in northern Belgium. Plant Ecol. Evol. *147*, 22–32.

Vanneste, T., Michelsen, O., Graae, B.J., Kyrkjeeide, M.O., Hassel, K., Lindmo, S., and Frenne, P. De (2017). Impact of climate change on alpine vegetation of mountain summits in Norway. Ecol. Res. *32*, 579–593.

Vellend, M. (2010). Conceptual synthesis in community ecology. Q. Rev. Biol. *85*, 183–206.

Vellend, M. (2016). The Theory of Ecological Communities. Monogr. Popul. Biol. *57*, 229.

Vellend, M., and Orrock, J.L. (2009). Ecological and genetic models of diversity : Lessons across disciplines. Theory Isl. Biogeogr. Rev. 439–461.

Vellend, M., Brown, C.D., Kharouba, H.M., McCune, J.L., and Myers-Smith, I.H. (2013). Historical ecology: Using unconventional data sources to test for effects of global environmental change. Am. J. Bot. *100*, 1294–1305.

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J.L., Messier, J., Myers-Smith, I.H., and Sax, D.F. (2017). Plant biodiversity change across scales during the anthropocene. Annu. Rev. Plant Biol. *68*, 563–586.

Vittoz, P., Camenisch, M., Mayor, R., Miserere, L., Vust, M., and Theurillat, J.-P. (2010). Subalpine-nival gradient of species richness for vascular plants, bryophytes and lichens in the Swiss Inner Alps. Bot. Helv. *120*, 139–149.

Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. Nature *118*, 558–560.

Walther, G.R. (2010). Community and ecosystem responses to recent climate change. Philos. Trans. R. Soc. B Biol. Sci. *365*, 2019–2024.

Walther, G.-R., Beißner, S., and Burga, C. a. (2005). Trends in the upward shift of alpine plants. J. Veg. Sci. *16*, 541–548.

Wentz, F.J., Ricciardulli, L., Hilburn, K., and Mears, C. (2007). How Much More Rain Will

Global Warming Bring? Science (80-.). *317*, 233–235.

Whittaker, R.H. (1975). Communities and ecosystems - Second edition (London: Macmillan).

William, M. (2006). Deforesting the Earth: from prehistory to global crisis, an abridgement (The University of Chicago Press, Chicago).

Yagouti, A., Boulet, G., Vincent, L., Vescovi, L., and Mekis, É. (2008). Observed changes in daily temperature and precipitation indices for southern Québec, 1960–2005. Atmosphere-Ocean *46*, 243–256.

Yu, D., Terborgh, J., and Potts, M.D. (1998). Can high tree species richness be explained by Hubbell's null model? Ecol. Lett. *1*, 193–199.

Zechmeister, H.G., Tribsch, A., Moser, D., Peterseil, J., and Wrbka, T. (2003). Biodiversity "hot spots" for bryophytes in landscapes dominated by agriculture in Austria. Agric. Ecosyst. Environ. *94*, 159–167.

Zwiener, V.P., Lira-Noriega, A., Grady, C.J., Padial, A.A., and Vitule, J.R.S. (2018). Climate change as a driver of biotic homogenization of woody plants in the Atlantic Forest. Glob. Ecol. Biogeogr. *27*, 298–309.