Landscape Ecol
DOI 10.1007/s10980-017-0591-y

RESEARCH ARTICLE

Anthropogenic disturbances strengthened tree community-environment relationships at the temperate-boreal interface

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Received: 7 March 2017 / Accepted: 4 November 2017

Abstract

Context Knowledge of how environmental gradients generate changes in community composition across forest landscapes (β-diversity) represents a critical issue in the era of global change, which exerts especially powerful impacts by shifting disturbance regimes.

Objectives We analyzed the response of tree communities to increased disturbance rates that were linked to European settlement at the temperate-boreal interface of eastern Canada. We tested whether disturbance has led to spatial homogenization or heterogenization, and to decoupling or strengthening of community-environment relationships.

Methods We used a reconstruction of pre-industrial tree communities based on historical land survey records (1854–1935), together with modern data, to assess changes in tree β-diversity patterns. Then, β-diversity was partitioned into fractions explained by spatial (dbMEM) and environmental variables (latitude, elevation, slope, drainage and surface deposits) in order to assess changes in spatial structures and community-environment relationships.

Results In pre-industrial times, environmental variables explained only a small proportion of β-diversity since dominant taxa were present across the range of environmental gradients, whereas habitat specialists were very rare. Between pre-industrial and modern times, our analysis highlights an increase in β-diversity and the proportion of β-diversity that was explained by environmental variables. Increased disturbance rates have favored early-successional habitat specialist taxa and reduced the habitat breadth of pre-industrial generalists, thereby increasing the strength of community-environment relationships.

Conclusions Our results support that disturbance can alter the strength of community-environment relationships and also suggest that functional traits of species within the regional pool could predict whether or not disturbance alters such relationships.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-017-0591-y) contains supplementary material, which is available to authorized users.

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Keywords Community assembly · Environmental niche · Environmental filtering · Land-use changes · Meta-community

Introduction

Within a regional species pool (γ-diversity), variation in community composition (β-diversity) is thought to reflect niche processes such as environmental filtering and biotic interactions, as well as neutral processes such as ecological drift and dispersal limitation (Vellend 2010, 2016; Chase and Myers 2011; Götzenberger et al. 2012). The relative importance of environmental filtering is generally dominant when the regional species pool is small, as is the case in northern temperate and boreal tree communities where γ-diversity is lower (Myers et al. 2013). Knowledge of how environmental gradients generate diversity across forest landscapes represents a critical issue in the era of global change, which exerts especially powerful impacts by shifting disturbance regimes. For example, climate change alters fire regimes (Westerling et al. 2006; Flannigan et al. 2009) and insect outbreaks (Haynes et al. 2014). Land-use alters natural disturbance regimes (Bowman et al. 2011) and adds new anthropogenic disturbances (e.g., agriculture, logging; Foley 2005).

Disturbances represent key drivers of ecological diversity (Fraterrigo and Rusak 2008) and may have various effects on β-diversity patterns. On one hand, gradients of disturbance frequency and intensity influence spatial heterogeneity in community structure and composition (e.g., Carreño-Rocabado et al. 2012; Cyr et al. 2012; Gennaretti et al. 2014a). Disturbances can also lead to divergent community structure and composition across environmental gradients (Cooper et al. 2003; Pausas and Verdú 2008; Harvey and Holzman 2014) and may even increase the strength of community-environment relationships (Hogan et al. 2016). Moreover, disturbance can increase β-diversity through an increase in the strength of ecological drift and neutral sampling, specifically when it decreases the average number of individuals in a community (i.e., community size; Myers et al. 2015; Catano et al. 2017). On the other hand, disturbances may lead to spatial homogenization and decoupling of community-environment relationships by promoting a small pool of disturbance-tolerant generalist species across entire environmental gradients (e.g., Chase 2007; Vellend et al. 2007). This last phenomenon has been widely reported in European and northeastern North American forests that were subjected to long-term intensive land-use (e.g., Schulte et al. 2007; Vellend et al. 2007; Hanberry et al. 2012a, 2012b; Thompson et al. 2013). Given these contradictory results, greater knowledge of how disturbances alter β-diversity patterns and their relationships with environmental gradients would represent an advance in community assembly theory, whilst also improving our ability to conserve and restore biodiversity in human-modified forest landscapes (Myers et al. 2015; Socolar et al. 2016; Wainwright et al. 2017).

In this study, we analyze the long-term response of tree communities to increased disturbance rates that were linked to European settlement and industrialization at the temperate-boreal interface of eastern Canada. We used a reconstruction of pre-industrial communities based upon historical land survey records (1854–1935), together with modern data, to assess changes in tree β-diversity patterns and community-environment relationships. One common way to assess the relative importance of community-environment relationships is to partition the β-diversity into fractions that are explained by environmental variables (e.g., Cottenie 2005; Legendre et al. 2009; Myers et al. 2013). We used this methodological framework to test two alternative hypotheses:

1. *The homogenization-decoupling hypothesis* Pre-industrial tree communities were strongly structured by natural environment filters, which generated diversified landscapes. Increased disturbance rates following European settlement subsequently favored a small pool of more disturbance-tolerant generalist taxa across entire environmental gradients. In this case, we expect spatial homogenization (i.e., a decrease in β-diversity) and decoupling of community-environment relationships (i.e., a decrease in the proportion of β-diversity that is explained by environmental variables).

2. *The heterogenization-strengthening hypothesis* Pre-industrial dominant taxa were generalists with respect to environmental gradients, which consequently generated relatively homogeneous landscapes. Increased rates of disturbances following European settlement subsequently increased spatial

heterogeneity and habitat filtering by favoring more specialist taxa and reducing the habitat breadth of pre-industrial generalists. This alternative hypothesis predicts an increase in β-diversity and the strength of community-environment relationships.

Materials and methods

Study area and historical background

The study area covers 22,000 km^2 of eastern Canada (Fig. 1). The region is located at the transition between temperate mixedwood and boreal conifer-dominated forests (Rowe 1972). It corresponds to the maple-yellow birch and balsam-fir yellow birch bioclimatic domains according to the provincial classification scheme of Quebec (Robitaille and Saucier 1998; Fig. 1). Mean annual temperature and total precipitation (1981–2010) respectively range from 5.2 °C and 918 mm at the southern extreme of the study area (Rapide des Joachims) to 2.3 °C and 885 mm in the north (Montbeilliard). Surface deposits correspond to clays that were deposited by the pro-glacial Barlow Lake in lowland areas (Vincent and Hardy 1977) and glacial tills, together with rocky outcrops, in upland areas. In this region, several factors that influence the establishment and growth of tree species are linked to the complex topographic gradient (drainage, nutrient availability, soil depth, micro-climate; Fraser 1954; MacHattie and McCormack 1961; Brown 1981).

The time period that is covered by the historical data (1854–1935) corresponds to the end of the Little Ice Age (LIA; about 1250 AD–1850 AD; Gennaretti et al. 2014b). The drier climate of the LIA was particularly favorable to the propagation of fires in certain parts of eastern North America (Bergeron and Archambault 1993; Bergeron et al. 2006; Clifford and Booth 2015). In our study area, large crown fires were frequent in the north (Grenier et al. 2005), while their frequency decreased to the south (Drever et al. 2006). First Nations populations in the region at that time can be roughly estimated at several thousand individuals (Couture 1983; Riopel 2002), who exerted rather localized ecological effects across the landscape (Danneyrolles et al. 2016a).

European settlement and industrialization have resulted in the increase of both logging and fire. Industrial logging began at the end of the 19th C., and mainly focused on selective cutting of tall pine trees (*Pinus* spp.; Riopel 2002). At the beginning of the 20th C., Euro-American settlement and temporary favorable climatic conditions resulted in an important peak in burned areas (from about 1910–1930; Lefort et al. 2003; Grenier et al. 2005). Logging activities intensified following the construction of a paper mill in Témiscaming in 1917, which led to the rapid development of partial cutting of small-diameter spruces (*Picea* spp.) and fir (*Abies balsamea*; Lienert 1966). Clear-cutting practices emerged with the mechanization of forestry in the 1970s. Yet, large scale natural disturbance such as outbreaks of spruce budworm (*Choristoneura fumiferana*) remained frequent in the study area with at least three major outbreaks over the last centuries (1840–1865; 1910–1930; 1970–1990; Bouchard et al. 2006a, b).

Community and environmental data

In total, 5910 observations on pre-industrial forest communities were extracted from 79 logbooks reporting land surveys of township and forest concession limits, which were conducted from 1854 to 1935. These observations were precisely geo-referenced using historical and modern digital cadastral maps, and are usually spaced 200–300 m apart along transects scattered over the study area (Fig. 1). For this study, only taxa list observations were retained (e.g., "Pine, spruce, yellow birch, cedar and a few maples"). Terrail et al. (2014) have compared these types of taxa lists with early forest inventories from the preindustrial era and have statistically demonstrated that the position of taxa in the taxon list reliably reflects their relative basal area. Thus, a relative rank of abundance (r) was assigned to each taxon that was listed according to its position in the taxon list (i.e., from rank 4; dominant, to rank 0; absent). These observations are also divided into two geometric types: line description (only those with length < 300 m were retained; 29% of observations) and point observations (71% of observations). Finally, only observations that corresponded to pre-logging conditions have been selected, since surveyors clearly mentioned when they encountered logged forests along transects (e.g. "*cuts*", "*old cuts*", "*logged*").

Modern forest communities were documented with modern forest maps (photo-interpretation 2001–2011; 1:20,000 scale; Berger 2008) to assign a modern

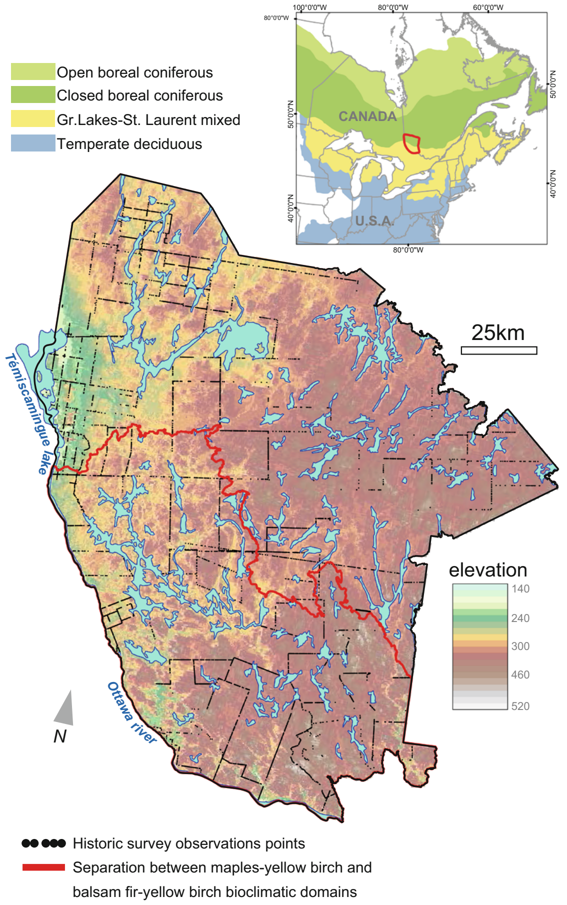

Fig. 1 Study area and location of historical observations along the western border of Quebec and Ontario, Canada

equivalent of composition to each historical observation (see Appendix S1 in the Supporting Information for detailed methods). These maps delimited stands by identifying the main taxa that were present in the canopy, thereby allowing the construction of dominance and presence maps for each taxon. A relative rank of abundance (*r*) was then assigned to taxa based upon their relative cover in the intersections between (*i*) a 100-meter buffer zone around each point or line centers of historical observations, and (*ii*) Thiessen polygons that were generated from these observations (Appendix S1). A 100-meter buffer was chosen to match the standard spacing used by preindustrial surveyors for their observation (> 80% of spacing between preindustrial observations were approximately 200 meters). Intersections with Thiessen polygons were then used to delimitate overlapping buffer polygons generated by historical observations that were spaced by less than 200-meter apart (see illustration in Appendix S1). Some species from this modern data-set were grouped at the genus level to match the taxa that were mentioned by surveyors, while rarely mentioned taxa (< 5%) within historical and modern observations were grouped as "others". Modern and historical data-sets appeared strongly comparable since they both identified the main tree taxa which were present in the canopy along transects, and that our method captured a very similar number of taxa per observation in both data-sets (α-diversity; Fig. 2).

Several environmental variables (Table 1) were used to analyze community-environment relationships. Because there are not enough weather stations in this area to assign accurate climate data to each observation, latitude was retained to represent the regional temperature gradient, with mean annual temperature ranging from 5.2 °C at the southern extreme of the study area to 2.3 °C in the north (Rapide des Joachims and Montbeillard weather stations, respectively). Eight other variables that are linked to the topographic gradient were derived from modern forest maps (Berger 2008): elevation (Fig. 1), slope, drainage and five classes of surface deposits (Table 1, see maps in Appendix S2).

Data analysis

Data analysis was conducted in four stages. First, we calculated the overall β-diversity that was represented by multivariate dispersion (Anderson et al. 2006) of all sites for each time period. Only taxa presence-absence data were retained for the β-diversity analysis because this metric is considered to be a robust measure of community composition (Anderson et al. 2011; Bastow Wilson 2012), which avoids potential bias in abundances of pre-industrial and modern data. Taxa presence-absence was used to compute dissimilarity matrices (Sørensen dissimilarity; Legendre and De Cáceres 2013). Multivariate dispersion (i.e., β-diversity), in turn, was defined as the dissimilarity of individual sites relative to the centroid of all sites. We tested for differences in β-diversity between preindustrial and modern times with a permutation-based test of multivariate homogeneity of group dispersion using the "*betadisper*" function of the R *vegan* package (999 permutations, Oksanen et al. 2015).

Second, we partitioned β-diversity (Legendre et al. 2005, 2009; Peres-Neto et al. 2006) into components that were explained by environmental and spatial variables through redundancy analysis (RDA; Legendre and Legendre 2012) for each time period. Taxa presence-absence was again selected to represent community composition. The nine environmental variables (Table 1) were used to construct third-degree polynomial Equations (27 monomials). Monomials with exponents allow for the modeling of non-linear relationships between environmental and responses variables (Legendre et al. 2009). Community spatial structure was analyzed with distance-based Moran's eigenvector maps (dbMEM; Dray et al. 2012; Legendre and Legendre 2012). In brief, dbMEM analysis produces a set of orthogonal spatial variables that are based upon the XY coordinates of sites and which are then used as explanatory variables. These spatial eigenfunctions (dbMEMs) represent a spectral decomposition of the spatial relationships among the study sites. An autocorrelation coefficient (Moran's I) was computed for each dbMEM and only dbMEMs that model positive autocorrelation were retained, resulting in a total of 1217 dbMEMs for our 5910 sites. Consequently, β-diversity was first partitioned between (i) environmental variables (i.e. pure environmental fraction) (ii) spatial variables (pure spatial fraction) and (iii) shared space-environment fraction. The same process was used to partition the β-diversity that was explained by different environmental variables, represented by 4 sets of monomials: latitude; elevation, slope and drainage, surface deposit and shared fractions between these four sets of variables. Forward selection with permutation tests on the increase in R2 at each step (999 permutations, 5% significance level) was then used to select the environmental and dbMEM variables that best explained variation in communities (Blanchet et al. 2008), and which were retained in the final models. Finally, we tested for differences in the fractions of variance explained by spatial and environmental variables (after forward selections) between the two time periods using the bootstrap procedure proposed by Peres-Neto et al. (2006), based on 999 iterations. All analyses were performed using R: dbMEMs were performed with the "PCNM" function of the PCNM package (Legendre et al. 2013), variation partitioning and forward selection were performed respectively with the "varpart" and "ordistep" functions within the vegan package (Oksanen et al. 2015).

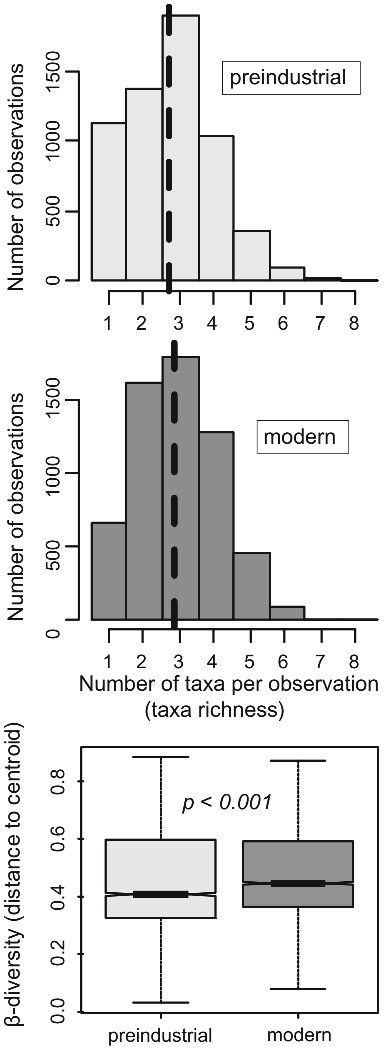

Fig. 2 Histograms of taxa richness (dashed lines represent mean number of taxa per observation) and box-and-whisker plot of β-diversity (i.e., multivariate dispersion) for each time period

To visually represent the compositional changes across environmental gradients, a principal component analysis (PCA) was performed with environmental variables (Table 1) of all sites. Among surface deposits, only tills and clays were retained since they covered more than 80% of the study area (Appendix S2). All environmental variables were standardized prior to analysis. Taxa centroids within site scores of the PCA were calculated, for each time period, and were plotted on the first two principal components.

Table 1 Description of environmental variables (see maps in Appendix S2)

Variables	Description
Latitude	Latitude at the center of observations
Elevation	Elevation from an 1:50,000 elevation model at the center of observations
Slope	Five class from low slopes (1) to high slopes (5) that are derived from modern forest maps (Berger 2008) at the center of observations
Drainage	Seven class from poorly drained (1) to very well drained (7) that are derived from modern forest maps (Berger 2008) at the center of observations.
Surface deposits (5 variables)	Five variables representing relative cover area [within 100 m buffer-Thiessen intersection polygons] of till, clay, sand, rocky and organic deposits that are derived from modern forest maps (Berger 2008)

Finally, indices of dominance and prevalence (Scull and Richardson 2007; Terrail et al. 2014) were calculated for both periods to describe the compositional changes. A weight was assigned to each observation based on their mean spacing (Dupuis et al. 2011). Dominance and prevalence indices were then calculated according to the formula:

$$F_{ir} = N_{ir}/M_r$$

where N_{ir} is the total weight of taxon i at rank r in taxa lists, and M_r is the total weight of observations. The dominance index represents the F_{ir} of taxa at the dominant rank (i.e., $r = 4$), while the prevalence index represents the F_{ir} of taxa regardless their ranks on the lists (i.e., $r > 0$). The frequency index gives a more comprehensive description but may underestimate some taxa, while dominance is a more robust metric to describe the abundance when dealing with the most abundant taxa (Terrail et al. 2014). Note that these indices were only used to analyze changes in taxa composition, while β-diversity analyses were based on presence-absence data. Monte-Carlo paired tests (modern rank of taxa i vs. pre-industrial rank of taxa i, 10,000 permutations) were used to determine the significance of these changes. To map pre-industrial and modern communities, the prevalence index was calculated for 73 ecological districts (homogeneous physiographic zones, ranging from about 50–500 km^2 in area; Robitaille and Saucier 1998) comprising more than 15 observations for each period.

Results

Our results show that observed β-diversity was slightly but significantly ($p < 0.001$) higher in modern compared to pre-industrial communities (Fig. 2), despite the fact that our data were constrained to a similar distribution of α-diversities within sites. During pre-industrial times, one-fifth of the β-diversity was spatially structured (20%; Fig. 3). Less than half of this spatial structure can be related to environmental variables (8%) and environmental variables alone explained only a very small proportion of the β-diversity (3%; Fig. 3), which was mostly accounted for by latitude (Table 2). The total proportion of β-diversity that was explained by environmental variables (spatially-structured + non-spatially structured environmental variables) almost doubled from pre-industrial to present times (from 11–21%, and more than two-thirds of this variation is now spatially structured (15%). Bootstrap tests revealed significant differences between preindustrial and modern times for all spatial (both shared and pure fractions; $p < 0.001$) and environmental fractions (both shared and pure fractions; $p < 0.001$). The environmentally explained modern β-diversity is essentially linked to the combination of gradients in elevation, latitude and surface deposits (Table 2).

Compositional changes depicted in Table 3 and Fig. 4 give a good insight on how the increased disturbance rates have led to a strengthening of community-environment relationships. In preindustrial times, balsam fir (*Abies balsamea*), spruces (*Picea* spp.) and Pines (*Pinus* spp.) were the most prevalent (59.4, 57.2 and 45.9%, respectively; Table 3) and dominant taxa (18.2, 27.9 and 18.6%, respectively; Table 3). These mid- to late-successional conifers were very ubiquitous across environmental gradients, with only spruces and pines that were slightly separated across the latitudinal and slope-drainage gradients (Figs. 4 and 5). Among deciduous taxa, birches (*Betula papyrifera* and *B. alleghaniensis*) were the most dominant and prevalent (Table 3) and were also slightly separated across the latitudinal, elevation and deposit gradients (Fig. 4). Conversely, specialist taxa were very rare during preindustrial times. For example, poplars (*Populus* spp.), that were specialized to northern clay lowland (Figs. 4 and 5), recorded 13.9% in prevalence for the whole study area (Table 3). Maples (*Acer* spp.) recorded a prevalence of only 4.7% (Table 3) and were conversely specialized to southern till uplands (Figs. 4 and 5).

Increased disturbance rates between preindustrial and modern times have first led to an increase in early-successional deciduous specialist taxa. Dominance and prevalence of poplars have significantly increased (+ 14.1% and + 23.8%, respectively; Table 3) mainly on northern clay lowland (Figs. 4 and 5). Dominance and prevalence of maples increased (+ 8.9 and + 30.1%; respectively; Table 3) mainly on southern till uplands (Figs. 4 and 5). Secondly, while preindustrial generalists decreased in abundance, the breadth of their habitats has also been reduced. Spruces experienced a sharp decrease in dominance and prevalence (− 11.5 and − 20.5%, respectively, Table 3.) away from well-drained slope (Fig. 4). Pines also experienced a sharp decrease in dominance and prevalence (− 9.3 and − 19.5%, respectively; Table 3) but conversely away from well drained steep slopes (Fig. 4). Moreover, yellow birch (*Betula alleghaniensis*) and eastern white cedar (*Thuja occidentalis*) tended to specialize toward southern till upland (Fig. 4), even though they did not experience significant change in abundance (Table 3).

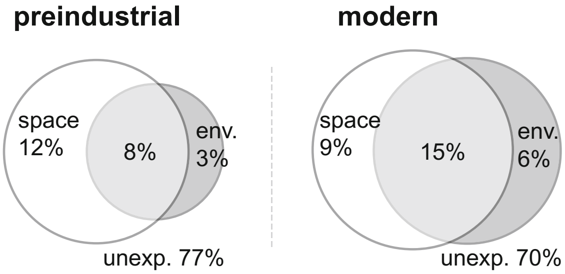

Fig. 3 Venn diagrams of variation partitioning for environmental and spatial (dbMEM) data-sets. Values indicate percent of variance explained by individual and intersection fractions, while unexplained variation is shown under diagrams. %). Bootstrap tests revealed significant differences between preindustrial and modern times for all spatial (both shared and pure fractions; $p < 0.001$) and environmental fractions (both shared and pure fractions; $p < 0.001$)

Discussion

Our results largely reject the homogenization-decoupling hypothesis, while tending to confirm the heterogenization-strengthening hypothesis. Modern overall β-diversity was significantly but only slightly higher than pre-industrial β-diversity (Fig. 2). Thus, our data did not record strong heterogenization of tree communities. Yet, our results clearly showed a significant increase in the strength of community-environment relationships, which was mostly associated with the shared environment space fraction (Fig. 3). This contrasts with several previous studies that demonstrated the homogenization-decoupling trend as a consequence of European settlement of northeastern North America (e.g., Schulte et al. 2007; Hanberry et al. 2012a, b; Thompson et al. 2013).

Environmental ubiquity of pre-industrial dominant taxa

An important aspect of our findings is that environmental variables only explained a small proportion of preindustrial β-diversity. This response likely reflects unmeasured environmental factors (e.g., micro-site conditions, biotic interactions), beyond the strong environmental ubiquity of the most abundant preindustrial taxa. Spruces, pines and balsam fir tended to be present across the whole range of environmental

Table 2 Comparison of variation partitioning results between pre-industrial and modern time periods for environmental data-sets

	Pre-industrial		Modern	
	[all. %]	[ind. %]	[all. %]	[ind. %]
Latitude	7	4	11	4
Elevation	4	1	12	4
Slope-drainage	3	1	5	1
Surface deposit	3	1	10	2

Values indicate percent of variation explained by each environmental data-set and including shared fractions with other datasets ([all.]) and percent of variation explained by each environmental data-set and not explained by other data-sets ([ind.])

Table 3 Pre-industrial and modern dominance and prevalence indices (%) for the entire study area

TAXA	Preindustrial		Modern		Δ
	dom.	prev.	dom.	prev.	
Spruces	27.9	57.2	16.3	36.7	−**
Balsam fir	18.2	59.4	7.4	41.9	−**
Pines	18.6	45.9	9.3	26.5	−**
White cedar	4.7	17.2	3.9	18.1	NS
Larch	2.9	10.9	0.7	2.6	−**
Poplars	5.5	13.9	19.6	37.7	+**
Paper birch	11.0	35.0	20.6	59.4	+**
Yellow birch	9.1	29.4	11.1	32.0	NS
Maples	1.2	4.7	10.1	34.8	+**
Others	0.8	3.5	1.0	4.1	+**

Δ indicates the results of Monte-Carlo paired tests (±: alternative hypothesis; * $p < 0.01$; ** $p < 0.001$; *NS* Non-significant)

gradients, whereas environmental specialists (e.g., poplars, maples) were very rare. Nevertheless, pre-industrial β-diversity was only slightly lower than modern β-diversity and was spatially structured (rather toward large landscape units at the regional scale than finer-scaled patches at the local scale; Supplementary materials S3). We speculate that legacies of the significant fire activity during the Little Ice Age (LIA; Grenier et al. 2005; Drever et al. 2006) likely explain this regional broad-scaled spatial structure of pre-industrial communities. Fire-sensitive taxa (balsam fir, yellow birch, white cedar) tended to be more frequent in areas that had not been subjected to high fire frequency during the LIA (Cyr et al. 2012; Danneyrolles et al. 2017), whereas fire-prone taxa (spruces, pines, paper birch) dominated the rest of the study area. Spatial patterns of natural disturbance had likely been the key mechanism that structured pre-industrial β-diversity at the landscape scale, while habitat selection was less important.

Increased β-diversity and strengthening of community-environment relationships

Increased disturbance rates following European settlement have favored more specialized taxa across environmental gradients. Poplars have mostly increased in northern lowlands that are dominated by clay deposits, which allow their vigorous proliferation by roots suckering following disturbances (Bergeron and Charron 1994; Bergeron 2000). Conversely, maples abundance increased on well-drained and warmer upper slopes of southern higher elevations, where they were more competitive (Barras and Kellman 1998; Danneyrolles et al. 2016b). Simultaneously, preindustrial generalists

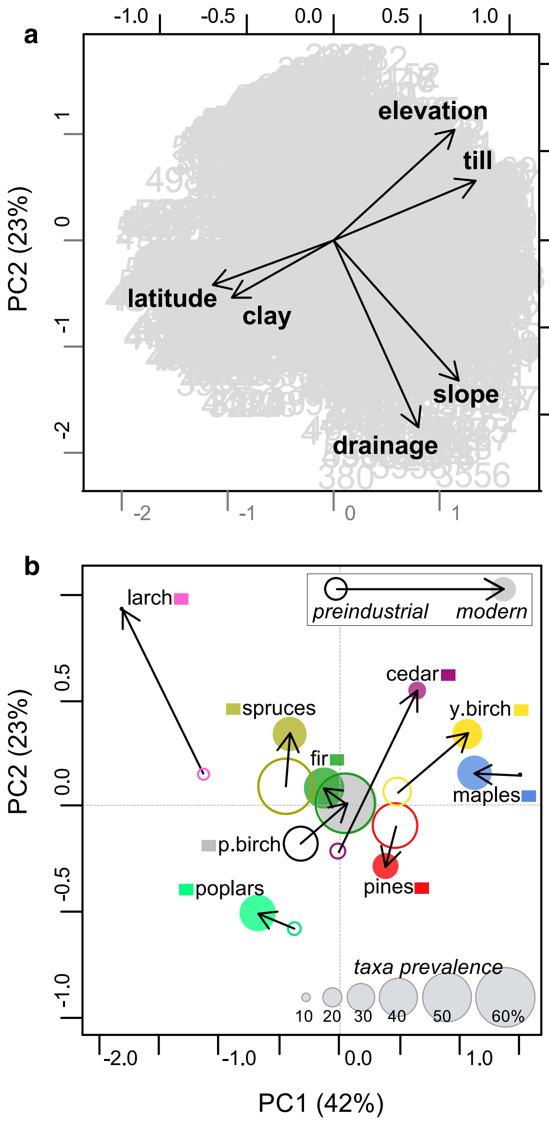

Fig. 4 Principal component analysis (PCA), axis 1 explains 42% and axis 2 explains 23% of environmental variability, respectively. Biplot (**a**) shows the positions of sites (grey numbers) and correlations of environmental variables with axes 1 and 2. Plot (**b**) shows the centroids of taxa presence within the site scores, during both pre-industrial (empty circles) and modern (full discs) periods, circles diameter is proportional to taxa prevalence

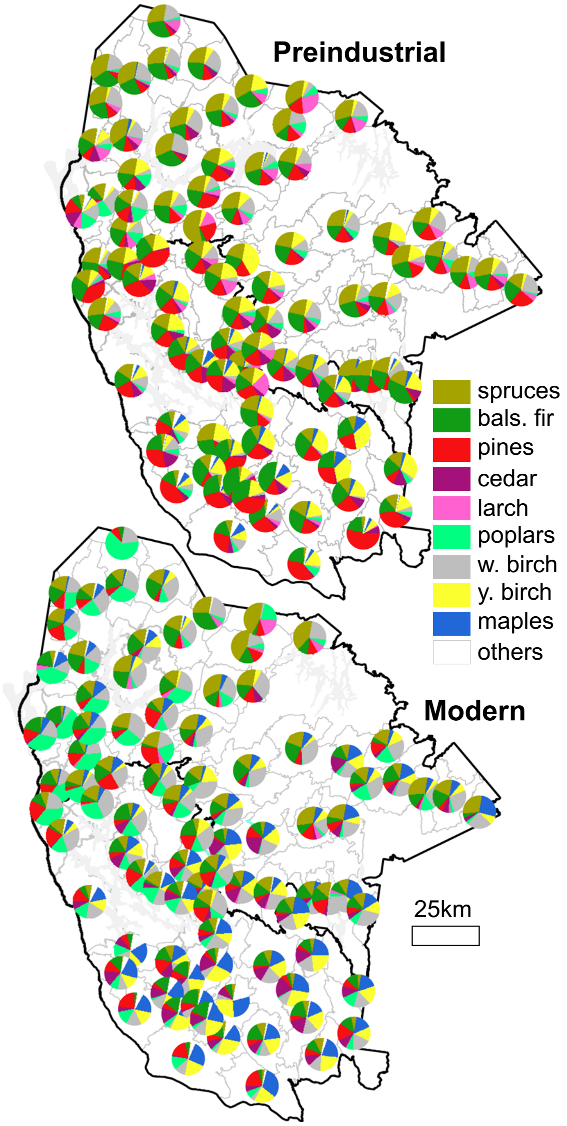

Fig. 5 Relative prevalence of each taxon within each ecological district that includes more than 15 observations

have tended to specialize on more narrow habitats at the extremes of the topographic gradient. Boreal conifers (spruces, balsam fir) were restricted to poorly drained lower slopes, where colder and wetter conditions allowed them to maintain a substantial competitive advantage (Barras and Kellman 1998; Danneyrolles et al. 2016b). Conversely, pines were restricted to low productive, xeric steep slopes, where they maintained a strong competitive advantage (Abrams 2001).

The interaction between dispersal limitation of species and environmental selection (Vellend 2010, 2016) may also have played an important role in the strengthening of community-environment relationships. While poplars and maples were very rare and restricted to spatially confined specific environmental conditions in preindustrial times, dispersal limitations (e.g., vegetative dispersion of poplars) could have restricted their expansion to environmentally similar adjacent areas. This may explain why the most important increase in strength of community-environment relationships was associated with the shared environment-space fraction. This interpretation is well supported by recent findings in herbaceous plant communities, where disturbance tends to increase β-diversity when dispersal is limited, while homogenizing communities with increased dispersal (Catano et al. 2017).

Broader practical and theoretical significance

Anthropogenic disturbance has caused β-diversity to increase, decrease or remain unchanged, depending upon the processes that are involved and the scale of observation (Socolar et al. 2016). In our study area, increased disturbance rates that were linked to European settlement has both slightly increased β-diversity and strengthened community-environment relationships at the landscape scale. This may reflect the fact that in our study area, the effects exerted by anthropogenic disturbance (i.e., industrial logging) have been analogous to those of natural disturbance (i.e., fire, insect outbreaks). Conversely, more intense disturbance lies outside the range of natural variability (e.g., land cultivation and subsequent abandonment), and may result in decreasing β-diversity and decoupling of community-environment relationships (Vellend et al. 2007). Such past agricultural land-use is common in other regions of northeastern North America, which likely explains why our results contrast with those of other historical studies that have reported the homogenization trend as a result of European settlement (e.g., Schulte et al. 2007; Hanberry et al. 2012b; Thompson et al. 2013).

From a more theoretical perspective, recent studies have emphasized that disturbance may mainly alter β-diversity through stochastic processes by modifying the average number of individuals and species in communities (neutral sampling effect), rather than through changes in deterministic processes (Myers et al. 2015; Catano et al. 2017). Our study supports that disturbance can also alter the strength of deterministic niche processes of community assembly (Vellend et al. 2007; Hogan et al. 2016). Dispersal can strongly interact with both deterministic and stochastic processes (Vellend 2010), with for example low dispersal tending to increase β-diversity through neutral sampling effects following disturbance (Catano et al. 2017). Our results suggest that low dispersal may likewise increase the strength of community-environment relationships following disturbance (Vellend et al. 2014). More broadly, our findings suggest that functional traits of species within the regional pool could predict whether or not disturbance alters the strength of community-environment relationships (Questad and Foster 2008). Three key categories of traits appear central: disturbance tolerance (e.g., early- vs. late-successional), habitat specialization (e.g., specialist vs. generalist) and dispersal capacities. The various combinations of these traits in different regional species pools should be considered when aiming to generalize the effects of disturbance upon β-diversity and community-environment relationships across ecosystems.

Acknowledgements We thank Sébastien Dupuis for his help in constructing the geo-referenced database from the survey records. We also thank Iván Jiménez for having very kindly shared some of his R codes, Lili Perreault and William F.J. Parsons for carefully editing the manuscript. We acknowledge Mark Vellend, the associate editor and two anonymous reviewers for their constructive feedback on early versions of the manuscript. This project was financially supported by the Natural Science and Engineering Research Council of Canada (NSERC), the Fonds de Recherche du Québec Nature et Technologies (FRQNT), the forest product company TEMBEC (Témiscaming, QC), the Conference Régionale des Élus de l'Abitibi-Témiscamingue (CREAT) and the Ministère des Forêts, Faune et Parcs du Québec (MFFP).

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