



## RESEARCH ARTICLE

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# Scale-dependent changes in tree diversity over more than a century in eastern Canada: Landscape diversification and regional homogenization

Victor Danneyrolles<sup>1,2,3</sup> | Mark Vellend<sup>3,4</sup> | Sébastien Dupuis<sup>1</sup> | Yan Boucher<sup>3,5</sup> | Jason Laflamme<sup>3,6</sup> | Yves Bergeron<sup>2,3</sup> | Gabriel Fortin<sup>1</sup> | Marie Leroyer<sup>1</sup> | André de Römer<sup>1</sup> | Raphaële Terrail<sup>1</sup> | Dominique Arseneault<sup>1,3</sup>

<sup>1</sup>Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, Rimouski, QC, Canada; <sup>2</sup>Chaire Industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC, Canada; <sup>3</sup>Centre d'étude de la Forêt (CEF), Montréal, QC, Canada; <sup>4</sup>Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, Canada; <sup>5</sup>Direction de la Recherche Forestière, Ministère des Forêts, Québec, QC, Canada and <sup>6</sup>Direction des Inventaires Forestiers, Ministère des Forêts, Québec, QC, Canada

**Correspondence**

Victor Danneyrolles

Email: victor.danneylrolles@uqat.ca

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**Handling Editor:** Glenn Matlack**Abstract**

1. A better understanding of how disturbance impacts tree diversity at different scales is essential for our ability to conserve and manage forest ecosystems in the context of global changes. Here we test the impacts of land use-related disturbances on tree diversity since the 19th century across a broad region (>150,000 km<sup>2</sup>) of northern temperate forests in eastern Canada.
2. We used a large and unique dataset of early land surveys conducted during the 19th century (>130,000 species lists), along with modern forest inventories (>80,000 plots), to analyse long-term changes in taxonomic and functional tree diversity at several scales (grid cell resolutions ranging from 12.5 to 1,600 km<sup>2</sup>; we refer to one grid cell as a 'landscape').
3. Our results show that land use-related disturbances have led simultaneously to (a) increased diversity within landscapes and a (b) homogenization at the regional scale (i.e. decreased composition dissimilarity among landscapes). These trends were found for both taxonomic diversity and functional diversity, with temporal changes more pronounced for taxonomic than functional diversity. We also found an increase over time in the strength of correlations between environmental variables and diversity both within and among landscapes.
4. *Synthesis.* Our results support the idea that human-induced impacts on biodiversity are strongly scale-dependent and not necessarily associated with biodiversity loss. This highlights possible ways that human-driven changes in tree diversity might impact forest resistance and resilience to future global changes.

**KEYWORDS**

beta diversity, biotic homogenization, pre-colonial forests, pre-industrial forests, pre-settlement forests

## 1 | INTRODUCTION

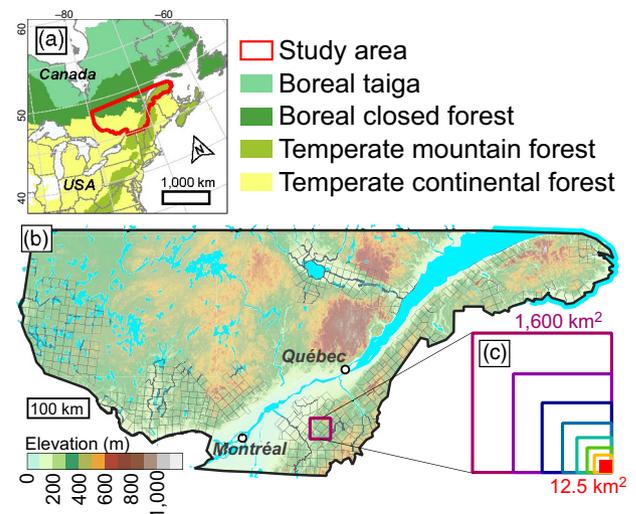
In an era of rapid global changes, increased disturbance via land use (e.g. agriculture, forestry, urbanization; Curtis, Slay, Harris, Tyukavina, & Hansen, 2018; Senf et al., 2018) as well as altered natural disturbance regimes due to climate change (e.g. drought, wildland fire, insect outbreaks; Seidl et al., 2017; Sommerfeld et al., 2018) are expected to have major impacts on biodiversity (Johnstone et al., 2016; McDowell et al., 2020; Millar & Stephenson, 2015). Disturbance can modify local community composition and diversity ( $\alpha$ -diversity) as well as compositional variation across spatial scales ( $\beta$ -diversity). Increases in taxonomic or functional similarities of communities across space (i.e. decreases in  $\beta$ -diversity), known as biotic homogenization, have been documented in many regions (Clavel, Julliard, & Devictor, 2011; McKinney & Lockwood, 1999; Olden, LeRoy Poff, Douglas, Douglas, & Fausch, 2004; Olden & Rooney, 2006). Recent reviews have argued that  $\beta$ -diversity is an important consideration in biodiversity conservation (Socolar, Gilroy, Kunin, & Edwards, 2016) with potential effects on ecosystem functions and services (Mori, Isbell, & Seidl, 2018). For example, forest tree  $\beta$ -diversity at the landscape or regional scale is generally thought to improve ecosystem multifunctionality and forest resistance and resilience to natural disturbances such as drought and insect outbreaks (Turner, Donato, & Romme, 2013; van der Plas et al., 2016). A better understanding of how anthropogenic and natural disturbance modifies forest diversity at different scales is thus key for our ability to manage ecosystems in the context of global changes.

Disturbance acts as an environmental filter that selects disturbance-adapted traits within the species pool (Vellend, 2016). On the one hand, this may lead to biotic homogenization through the selection of a relatively narrow pool of traits or species (Chase, 2007; Gámez-Virués et al., 2015; Vellend et al., 2007). However, such disturbance-driven selection may also be a source of heterogeneity, for example, by generating a mosaic of patches with different disturbance intensities and histories across the landscape (Carreño-Rocabado et al., 2012; Cyr, Gauthier, & Bergeron, 2012; Questad & Foster, 2008). As such, impacts of disturbance upon  $\beta$ -diversity may be strongly scale-dependent, with potential increases in  $\beta$ -diversity among localities (i.e. within landscapes) via increased patchiness, and decreases among landscapes within regions via increases of the same few disturbance-adapted species in different landscapes (Finderup Nielsen, Sand-Jensen, Dornelas, & Bruun, 2019). Within a landscape, increased  $\beta$ -diversity among localities should manifest as increased  $\alpha$ -diversity metrics (e.g. Gini-Simpson or Shannon index) for the entire landscape. For functional diversity, which is considered most relevant to understanding ecosystem function (Mori et al., 2018), changes might be minimal if the species pool exhibits a high degree of functional redundancy (Sonnier, Johnson, Amatangelo, Rogers, & Waller, 2014).

Disturbance may also alter relationships between community properties and other environmental variables (e.g. climatic or topographic gradients). Disturbance has been hypothesized to weaken

composition–environment relationships, for example by favouring a small pool of disturbance-tolerant generalist species across the entire environmental gradient (Thompson, Carpenter, Cogbill, & Foster, 2013; Vellend et al., 2007). However, if disturbance regimes (type or intensity) are correlated with environmental gradients, disturbance might increase the strength of composition–environment relationships (Danneyrolles, Arseneault, & Bergeron, 2018; Hogan, Zimmerman, Uriarte, Turner, & Thompson, 2016; Wearn et al., 2018).

Here we quantify changes in tree diversity since the 19th century across a large region at the temperate–boreal interface in eastern Canada (Figure 1). Over this period, these forests have undergone major shifts in tree species composition due to increased disturbance rates linked to Euro-American settlement and industrialization more so than climate change (Danneyrolles, Arseneault, & Bergeron, 2016b; Danneyrolles et al., 2019; Dupuis, Arseneault, & Sirois, 2011). In this region, pre-industrial forest landscapes experienced natural disturbance regimes of varying frequency and severity, but low severity events such as gap openings or insect outbreaks were the most frequent disturbances (Boucher, Arseneault, & Sirois, 2006; Lorimer & White, 2003). Subsequently, Euro-American settlement and industrialization has led to the superimposition of an anthropogenic disturbance regime that is locally severe but highly spatially variable (diverse types of logging treatment and to a lesser extent agricultural clearing and settlement fires; Boucher et al., 2006; Boucher, Arseneault, Sirois, & Blais, 2009; Boucher & Grondin, 2012). In general, this period has seen strong increases in fast-growing, early successional taxa such as *Populus* spp. and *Betula papyrifera*, as well as more shade-tolerant taxa that nonetheless respond positively to logging, such as *Acer* spp. and *Abies balsamea* (Danneyrolles et al., 2019). Decreases in abundance have been observed for previously dominant shade-tolerant, late-successional taxa, such as *Picea* spp., *Thuja occidentalis*, *Tsuga canadensis* and *Fagus grandifolia*. Similar shifts in



**FIGURE 1** Location of the study area (a) and townships from which historical survey data were extracted (b; grey polygons). The purple square in (b) shows a 1,600-km<sup>2</sup> area, with nested grid-cell (landscape) sizes shown enlarged in (c). Forest zones in (a) were modified from the FAO Global Ecological Zones mapping

composition have been observed further to the south and have been linked to biotic homogenization at the regional scale (Hanberry, Palik, & He, 2012; Schulte, Mladenoff, Crow, Merrick, & Cleland, 2007; Thompson et al., 2013). However, it remains unclear how these land use-driven compositional changes have modified the tree diversity patterns in smaller spatial areas (e.g. the landscape scale) where the potential link between diversity and ecosystem function is most relevant (Mori et al., 2018; Vellend et al., 2017). Moreover, it is also largely unknown whether functional diversity follows the same post-industrial trends as tree taxonomic diversity.

We used a large and unique dataset of early land surveys conducted during the 19th century, prior to major human influence, along with modern forest inventories, to conduct an in-depth analysis of long-term changes in tree diversity at multiple spatial scales. This study builds on an analysis of compositional changes using the same dataset (Danneyrolles et al., 2019). Historical and modern observations (>130,000 taxa lists made in the 19th century and >80,000 modern forest inventory plots conducted during the 1980–2010 period) were both aggregated and analysed at different spatial resolutions over a large area (>150,000 km<sup>2</sup>). We refer to the spatial grain in a given analysis (12.5 km<sup>2</sup> minimum, 1,600 km<sup>2</sup> maximum) as a 'landscape'. Under the hypothesis that patchy land use-related disturbances have caused initially uncommon, disturbance-adapted species to increase in abundance in similar ways across landscapes, we test two main predictions: (a) tree diversity has increased within landscapes via increased patchiness and (b) there has been biotic homogenization (i.e. decreased compositional dissimilarity) among landscapes across the study region. We also examine changes in community–environment relationships. For all analyses, we asked whether taxonomic and functional diversity show similar trends.

## 2 | MATERIALS AND METHODS

### 2.1 | Tree community composition data

Pre-industrial tree communities were characterized using early land survey data extracted from logbooks reporting the original surveys by European settlers of >500 townships between 1,790 and 1,900 (Supporting Information 1). Surveys were conducted along the boundaries of a township (typically 16 km × 16 km; Supporting Information 1); range lines were subdivided within townships into roughly 1.6 km portions (Supporting Information 1), within which surveyors reported forest composition in the form of lists of taxa (e.g. 'hemlock, beech and maples'). Each list was one of two geometric types: point observations (69% of the total number of observations, usually spaced 100–200 m apart) or line descriptions (31%; usually pertaining to a ~260 m length of a lot boundary). In total, we used 136,013 lists of taxa from 1,790 to 1,900 that were precisely georeferenced using historical and modern digital cadastral maps (Figure S1). These lists mentioned a minimum of one taxon, but more typically two to four taxa (first and third quartiles, respectively, of the distribution of taxon number across lists) with a median of three taxa

per observation (Supporting Information 1). In order to aggregate both line and point observations into calculations of landscape-scale species frequencies (described below), a weight was first calculated for each observation as the length of a line observation or the mean distance from a point observation to the two adjacent observations (i.e. the mean distance to the previous and next observations along the survey line; Dupuis et al., 2011). This effectively gives less weight to short line segments or to points very close to other points. Linear observations of >1,600 m were removed prior to analysis and final weights used in analyses were truncated to a minimum of 100 m and a maximum of 1,600 m in order to limit excessive differences between observations weights.

Modern tree communities were characterized using Quebec government forest inventories, which have been conducted since the 1980s. Inventories are conducted in 400-m<sup>2</sup> circular plots distributed across different types of productive forest through stratified random sampling. Only plots that were located within a maximum distance of 3 km from historical observations were retained (Supporting Information 1), resulting in a total of 86,562 plots. Within these plots, all stems with a DBH >9 cm were measured and then used to compute basal area per species per plot. Several species were grouped at the genus level to match the taxonomic resolution of historical surveys (*Picea* spp., *Pinus* spp., *Acer* spp., *Populus* spp.). Because 19th-century surveyors only specified the most abundant taxa in their observations, we restricted the number of taxa per modern plot in order to obtain more comparable datasets. Taxa that represented <5% of the total basal area of a modern plot were removed; this threshold was chosen to obtain roughly the same number of taxa per observation in both historical and modern raw datasets (Supporting Information 1).

### 2.2 | Grid aggregation

We aggregated both pre-industrial and modern observations at eight different grid resolutions (i.e. landscape sizes) in order to test the robustness of results across spatial scales. The finest grain was a square cell of approximately 3.5 × 3.5 km, with the other seven grids constructed by subsequent doubling the area of one grid cell (12.5, 25, 50, 100, 200, 400, 800 and 1,600 km<sup>2</sup>; Figure 1). For each spatial grain, we only retained cells that had a minimum density of 0.5 observations/km<sup>2</sup> in both the historical and modern datasets (i.e. >7 observations for 12.5 km<sup>2</sup> cells and >800 observations for 1,600 km<sup>2</sup> cells). The 12.5 km<sup>2</sup> minimum represents the smallest grain possible in order to have a reasonable number of observations per landscape in both historical and modern observations.

For each of the 17 main taxa present in our study area (Supporting Information 2), absolute frequency was calculated as the number of observations where the taxon was present divided by the number of observations in the grid cell. Historical observations were weighted as described above (according to line length or distance among points), and taxon absolute frequency was estimated as the cumulative weight of observations in which the taxon

was mentioned divided by the total weight of observations. Relative taxon frequency (henceforth just 'taxon frequency') was then calculated by dividing the absolute frequency of a given taxon by the sum across taxa within a grid cell. A previous study validated the high accuracy of this method for estimating 19th-century forest composition by comparison with the results obtained using detailed early forest inventories available for a restricted portion of our study area (Terrail, Arseneault, Fortin, Dupuis, & Boucher, 2014).

Given different numbers of observations across time periods for each grid cell, we used random resampling to overcome the consequent potential bias in estimating diversity. For each cell separately, we first identified the time period with fewer observations ( $n_{\min}$ ), and then randomly resampled  $n_{\min}$  observations from the other time period 999 times, retaining the mean taxon frequencies across the 999 samples for subsequent analyses.

## 2.3 | Trait data and functional diversity

To analyse changes in tree functional diversity, we selected 10 functional traits that reflect key aspects of tree biology (Bruelheide et al., 2018; Díaz et al., 2016; Weiher et al., 1999): longevity, height at maturity, growth rate, wood density, evergreenness, deciduousness, SLA, leaf nitrogen content, seed dry mass and seed abundance (see all values and sources in Supporting Information 2). Many traits can be of functional significance in multiple ways, but generally we used traits linked to species' successional status or adaptation to disturbance (e.g. longevity; Weiher et al., 1999), the ability to compete for light (e.g. growth rate, height at maturity and leaf area), dispersal ability (i.e. seed mass and abundance; Bruelheide et al., 2018), as well as water use efficiency and drought tolerance (e.g. wood density, leaf area and nitrogen content; Bruelheide et al., 2018; Weiher et al., 1999).

Longevity and height at maturity were taken from the PLANTS database (USDA & NRCS, 2017). For growth rates, wood density, evergreenness/deciduousness, SLA, seed mass and seed abundance, we averaged the values from the TRY database (Kattge et al., 2011). For species grouped at the genus level (*Picea* spp., *Pinus* spp., *Acer* spp. and *Populus* spp), all trait values were averaged across the main species present in study area (Supporting Information 2). We then calculated community-weighted means (CWMs; each taxon weighted by its frequency) of these 10 functional traits for all grid cells in each time period separately. Trait values across taxa were all standardized to vary from 0 to 1 prior to the calculation of CWMs in order to give them an equal weight in subsequent analysis.

## 2.4 | Changes in diversity

We first analysed changes in landscape-scale diversity by calculating within-grid cell  $\alpha$ -diversity. We used the Gini-Simpson index and Rao's quadratic entropy, since these abundance-based diversity indices, which are insensitive to missing rarest taxa, are more robust for comparing results from different data sources than

occurrence-based diversity indices (e.g. species or taxon richness; Magurran, 2013). The Gini-Simpson index for taxonomic diversity accounts for both richness and evenness; the more taxa present and the more equal their abundances, the higher the index will be (Jost, 2006). Rao's quadratic entropy is a measure of functional  $\alpha$ -diversity that similarly accounts for richness and evenness, in addition to the functional dissimilarity among taxa (Botta-Dukát, 2005; Rao, 1982). Here the matrix of functional dissimilarities among taxa was based on the Gower index of dissimilarity (ranging from 0 to 1) using the 10 traits described above. The Gini-Simpson and Rao indices are directly comparable, in that Gini-Simpson is equivalent to the Rao index in which functional dissimilarities between all pairs of species are equal to one (Ricotta & Szeidl, 2009). Both indices were converted to Hill numbers to facilitate interpretation of differences in diversity across time (Chao et al., 2014). We tested for increases over time using Bonferroni-adjusted pairwise *t* tests.

We evaluated changes in regional  $\beta$ -diversity by first quantifying taxonomic and functional dissimilarities among landscapes. First, taxonomic dissimilarities between pairs of landscapes were calculated using the abundance-based Bray-Curtis dissimilarity index (Legendre & De Cáceres, 2013). Functional dissimilarities were calculated as the Euclidean distance in 10-dimensional space defined by the CWM values of functional traits (Sonnier et al., 2014). Then, we tested for changes in  $\beta$ -diversity across time using a multivariate dispersion analysis (Anderson, Ellingsen, & McArdle, 2006) with the *betadisper* function in the VEGAN R package (Oksanen et al., 2017). This function uses a principal coordinate analysis (either with Bray-Curtis taxonomic dissimilarities or functional Euclidean distances) to compute the distance from each landscape to the centroid of its group (i.e. time period). Our hypothesis predicts a decrease over time in taxonomic and functional dissimilarities.

We estimated the contributions of each taxon and trait to changes in within- and among-cell taxonomic and functional diversity. For each taxon or trait, individual contributions were estimated by computing changes after removing the taxa or traits considered, which were subsequently subtracted from the changes in diversity with all taxa or traits included (i.e. the main results). We only present the estimated contributions obtained with the  $5 \times 5$  km ( $25 \text{ km}^2$ ) grid-cell size, but very similar results were found with other grid-cell sizes (i.e. smaller or larger landscapes).

## 2.5 | Diversity-environment relationships

We tested for changes in the strength of relationships between within- and among-cell diversity indices and environmental variables. The environment was characterized using topographical variables (11) derived from a digital elevation model and modern forestry map (MFFP, 2018) along with bioclimatic variables (19) that are frequently used in species distribution modelling (1970–2000 normal; Fick & Hijmans, 2017). We used a digital elevation model with 10-m pixels (Supporting Information 4) to compute slope, aspect, a topographic position index (the difference in elevation between a

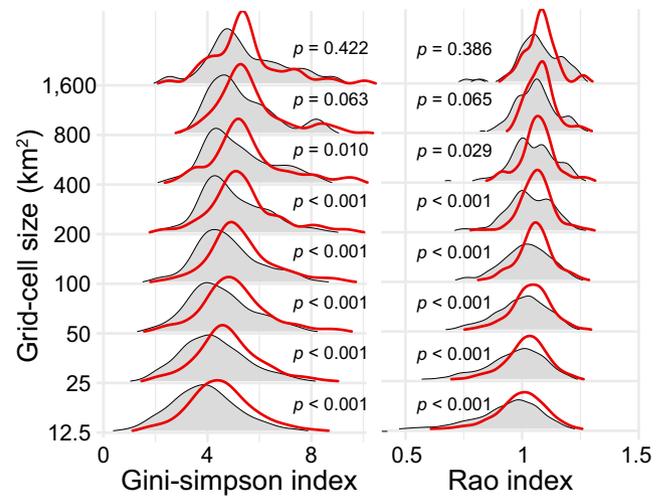
central pixel and the mean of its surrounding pixels in a 100 m radius; Guisan, Weiss, & Weiss, 1999) and a terrain ruggedness index (the mean elevation difference between a central pixel and its surrounding pixels in a 100-m radius; Riley, DeGloria, & Elliot, 1999). From surficial geology data (MFFP, 2018), we extracted a drainage index and surficial deposit types (glacial, fluvioglacial, lacustrine, marine, organic, alteration or rocky outcrop). Because no climate or topographic data were available for the historical period considered in this study, we assumed that the relative spatial variation in these variables remained approximately constant through time. All maps of environmental variables are shown in Supporting Information 4.

We first tested for changes in the relationship between within-cell diversity indices and within-cell environmental variability. Environmental variability was defined as the variance for each of the topographical variables within each grid cell. We did not retain climatic variables for this analysis because within landscapes of the size we analysed, climatic variability is almost entirely related to topography (e.g. elevation). We then used multiple linear regression to quantify the proportion of variation in the Gini-Simpson and Rao indices explained by within-cell topographical variance (all topographical variances were centred and scaled to have zero mean and unit standard deviation prior to analysis), using the adjusted  $R^2$  (hereafter  $R^2$ ) as a measure of goodness-of-fit. To avoid collinearity in the explanatory dataset, we first performed a forward selection of topographical variables based on their contribution to increasing in  $R^2$  at each step (999 permutations, 1% significance level; Blanchet, Legendre, & Borcard, 2008); final models included only these selected variables. We computed bootstrapped confidence intervals on adjusted  $R^2$  values using 999 random samples with replacement in the original dataset.

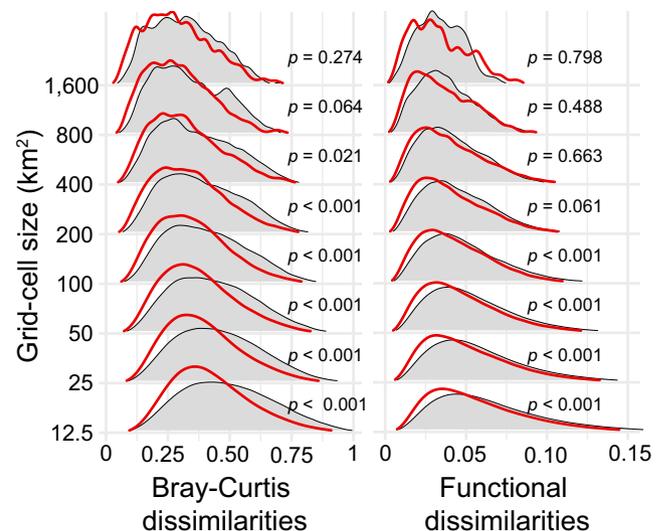
In order to partition  $\beta$ -diversity (in each time period) into fractions explained by regional-scale topographic and climatic gradients and their shared fractions, we ran distance-based redundancy analyses (dbRDA; Legendre et al., 2009; Peres-Neto, Legendre, Dray, & Borcard, 2006). Each landscape was assigned the mean value of each of the topographical and bioclimatic variables as predictors and all variables were centred and scaled prior to analysis. We used forward selection (permutation tests on the increase in adjusted  $R^2$  at each step, 999 permutations, 1% significance level; Blanchet et al., 2008) to select variables that best explained variation in taxonomic and functional composition (i.e. Bray-Curtis dissimilarities and multivariate Euclidean distances based on CWMs respectively). Forward selection procedures were implemented separately for both topographic and climatic variables, and taxonomic and functional composition, and only selected variables were retained in the final models. We computed bootstrapped confidence intervals for adjusted  $R^2$  values as described above.

### 3 | RESULTS

Overall, our results show a significant increase in within-grid cell  $\alpha$ -diversity (Figure 2) and a significant decrease in among-grid cell  $\beta$ -diversity (Figure 3) for all but the largest grid-cell sizes. These same general trends were found for both taxonomic and functional

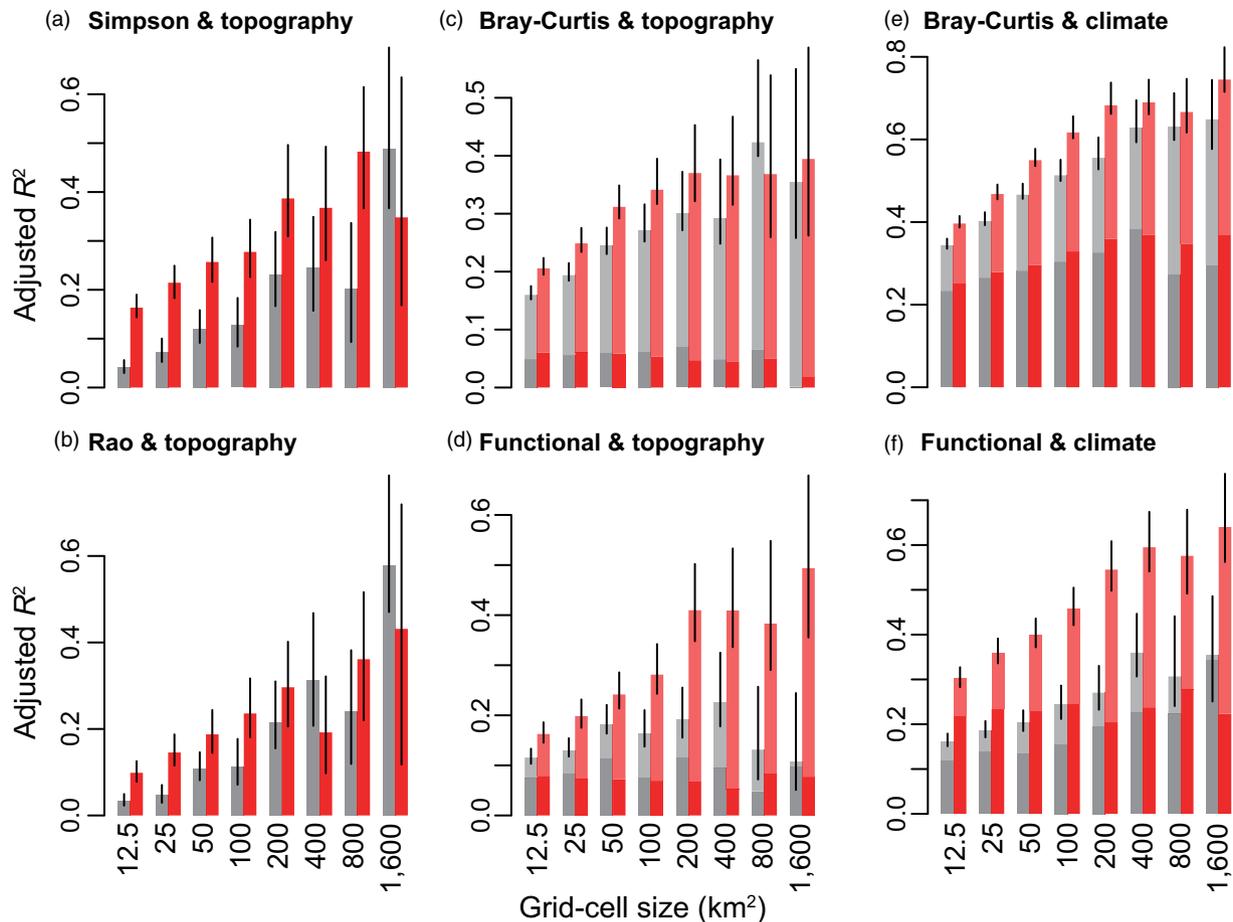


**FIGURE 2** Changes over time for the Gini-Simpson and Rao diversity indices (within landscapes) for the eight grid-cell (landscape) sizes. These indices account for both richness and evenness of taxa (Gini-Simpson) or traits (Rao); higher values indicate more taxa or trait values present and more equal abundances. Historical pre-industrial smoothed distributions are shown in grey while modern distributions are shown in red;  $p$  values are from Bonferroni-corrected pairwise  $t$  tests



**FIGURE 3** Changes in beta diversity over time, as quantified by Bray-Curtis dissimilarities and Euclidean functional distances for the eight grid-cell (landscape) sizes analysed. Historical pre-industrial distributions are shown in grey while modern distributions are shown in red;  $p$  values are from multivariate dispersion tests

diversity but were more pronounced for taxonomic than functional diversity. Also, we found an increase over time in the strength of relationships between environmental variables and both  $\alpha$ -diversity and  $\beta$ -diversity (Figure 4). For all these analyses, temporal changes showed reduced statistical significance at or above grid-cell sizes of ~200–400 km<sup>2</sup>.



**FIGURE 4** Changes in the strength of relationship between community characteristics and environmental variables for the eight grid-cell sizes analysed. Histograms show the adjusted  $R^2$  values obtained when using within-cell variance in topographic variables to predict the Gini-Simpson index (a) or the Rao functional index (b), and when using topographical and climatic variables to predict Bray-Curtis dissimilarities (c and e respectively) or functional distances (d and f respectively). Grey and red bars correspond to the pre-industrial and modern time periods respectively. For histograms (c–f), darker colours show the proportion of variance explained by only topographic or climatic variables, while lighter colours show the proportion of variance shared between topographic and climatic variable. Error bars show the bootstrapped 95% confidence intervals

Increases in within-grid cell  $\alpha$ -diversity were revealed by mean changes in the Gini-Simpson index ranging from maximum of +0.66 at the finest grid-cell size (12.5 km<sup>2</sup>) to +0.06 with the largest grid-cell size (1,600 km<sup>2</sup>; Figure 2). Similarly, changes in Rao index ranged from +0.07 at the smallest grid-cell size (12.5 km<sup>2</sup>) to +0.01 at the largest (1,600 km<sup>2</sup>; Figure 2). Decreases in among-grid cell  $\beta$ -diversity were exhibited by mean changes over time for Bray-Curtis dissimilarities which ranged from -0.07 with the smallest grid-cell size (12.5 km<sup>2</sup>) to -0.03 with the largest (1,600 km<sup>2</sup>; Figure 3). Mean decreases in functional Euclidean distances were less pronounced with the strongest increase of -0.01 for the smallest grid-cell size (12.5 km<sup>2</sup>). Changes in taxonomic diversity were mostly the consequence of a few taxa showing either strong increases (*Populus* spp., *B. papyrifera*, *Acer* spp. and *A. balsamea*; Figure 5; Supporting Information 3) or strong decreases (*Picea* spp., *Betula alghaniensis*, *T. occidentalis*; Figure 5; Supporting Information 3) in frequency. Similarly, changes in functional diversity were mostly related to five key traits (wood density, seed mass, seed abundance, longevity and maximum height; Figure 5; Supporting Information 3).

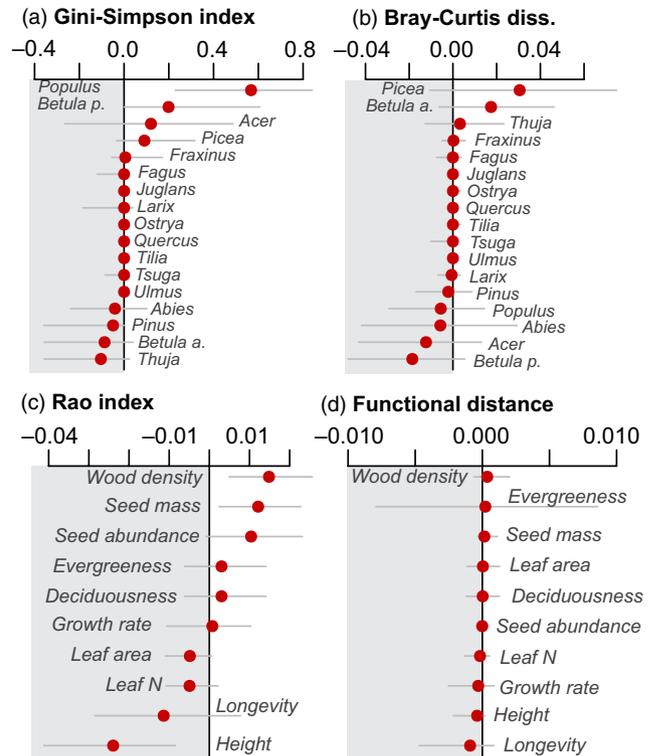
The strength of relationships between environmental variables and both  $\alpha$ -diversity and  $\beta$ -diversity increased between the two time periods (Figure 4). The strengthening of relationships between the Simpson index and within-cell environmental variance increased with an increase in grid-cell size, with increases in adjusted  $R^2$  ranging from +0.12 to +0.28 for the 200 km<sup>2</sup> and the 800 km<sup>2</sup> grid-cell sizes respectively (Figure 4a). Similarly, increases in adjusted  $R^2$  values for models predicting the Rao index generally increased with grid-cell size, for example, from +0.06 to +0.12 for the 12.5 km<sup>2</sup> and the 1,600 km<sup>2</sup> grid-cell sizes respectively (Figure 4b). Bootstrapped confidence intervals were substantially larger at the large grid-cell sizes (Figure 4a,b). At the regional scale, the proportion of variation in taxonomic composition explained by topographic variables (dbRDA adjusted  $R^2$ ) increased slightly over time by approximately 0.06 for most grid-cell sizes (Figure 4b); for functional composition differences ranged between +0.05 and +0.38 (Figure 4d). Similarly, the proportion of variation in composition explained by climatic variables increased over time by 0.04–0.13 for the taxonomic

index (Figure 4e) and 0.14–0.29 for the functional index (Figure 4f). However, these temporal increases were mostly associated with the shared topographic-climatic fraction (Figure 4), with the overall proportion of variation in community composition explained by all environmental gradients increasing by only 0.02–0.10 for taxonomic composition and 0.14–0.30 for functional composition.

## 4 | DISCUSSION

### 4.1 | Land use-driven landscape diversification and regional homogenization

Our results largely support the hypothesis of scale-dependent temporal changes in diversity, with simultaneous increases in tree diversity within landscapes and decreases in  $\beta$ -diversity (homogenization) among landscapes across the region. It appears very likely that the increase in landscape-scale diversity is a direct consequence of compositional changes engendered by Euro-American settlement and industrialization (Danneyrolles et al., 2019; Dupuis et al., 2011; Friedman & Reich, 2005; Thompson et al., 2013). In an earlier paper using similar inventory data, we found much stronger changes in community-level indices related to disturbance adaptations of taxa than to their climatic affinities (Danneyrolles et al., 2019). While pre-industrial landscapes in the northeastern USA and southeastern Canada experienced natural disturbances of varying frequency and severity (Lorimer & White, 2003), low severity events such as gap openings or insect outbreaks were the most frequent disturbances; severe stand-replacing events such as wind-throw or fire were relatively rare (Boucher et al., 2006, 2009; Lorimer & White, 2003). The subsequent superimposition of an anthropogenic disturbance regime that is locally severe but highly spatially variable (diverse types of logging treatment and to a lesser extent agricultural clearing and settlement fires) has created a heterogeneous mosaic of secondary forests at various stages of regeneration or maturity (Boucher et al., 2006, 2009; Boucher & Grondin, 2012). Disturbance-adapted taxa and their associated traits have increased in many parts of the landscape, which has increased heterogeneity compared to the pre-industrial less-disturbed mosaic (Danneyrolles et al., 2018; Wang, 2007). This interpretation is supported by the result that early successional *Populus* spp. and *B. papyrifera*, along with the more shade-tolerant but logging-favoured *Acer* spp., and some associated functional traits (e.g. lower seed mass and higher seed abundance) are the largest contributors to the increase in landscape-scale diversity (Figure 5). However, this increase in landscape-scale diversity has been accompanied by decreases in some pre-industrial late-successional or long-lived taxa (*T. occidentalis*, *B. alleghaniensis* and *Pinus* spp.; Figure 5) and associated traits (longevity and maximum height; Figure 5). It is also important to underline that the increase in landscape-scale diversity is observed as an average trend, but some areas also experienced losses, for example in areas strongly disturbed where the whole landscape may have been converted to young regenerating forests.



**FIGURE 5** Estimated contributions of each taxon and trait to changes in within- and among-cell taxonomic (a,b) and functional (c,d) diversity for the 25 km<sup>2</sup> grid-cell size. Red dots represent median values while grey error bars represent the first and third quartiles of each distribution

At the regional scale (i.e. the full extent of the study area), widespread increases of disturbance-adapted taxa appear to have led to homogenization, which has been found in many other studies of northeastern North America (Hanberry et al., 2012; Schulte et al., 2007; Terrail, Dupuis, et al., 2019; Thompson et al., 2013) and elsewhere (Clavel et al., 2011; McKinney & Lockwood, 1999). In pre-industrial times, some of the dominant taxa and their associated functional traits showed marked spatial aggregation (clumping) at the regional scale (e.g. *T. occidentalis*, *T. canadensis*, *Pinus* spp., *F. grandifolia*; Supporting Information 3). While these taxa have decreased since pre-industrial times, the three main disturbance-favoured taxa (i.e. *Populus* spp., *B. papyrifera*, *Acer* spp.) tended to increase in most landscapes, thus leading to an overall increased similarity among landscapes across the entire region (Figure 5; Supporting Information 3). The scale dependence of biodiversity changes (landscape diversification and regional homogenization) is also well-supported by our analysis at different grid resolutions: within-landscape diversity changes (i.e. changes in Gini-Simpson and Rao index) were weaker at coarse grid-cell sizes (>200 km<sup>2</sup>), suggesting that at this scale diversification starts to reverse into homogenization.

Finally, both landscape- and regional-scale changes in tree diversity were stronger when considering taxonomic composition compared to functional composition. This reflects the high functional redundancy in these tree communities, in which major changes in

taxonomic diversity are not necessarily linked to equivalent changes in functional diversity (Sonnier et al., 2014).

## 4.2 | Strengthened community–environment relationships

Our results also show a strengthening of tree community–environment relationships at landscape and regional scales, which could be explained by two non-exclusive mechanisms. First, this might be explained by a correlation between land-use intensity and environmental variables. In many landscapes, anthropogenic disturbance regimes have been strongly aligned with the topographical gradient. Land-use legacies are more pronounced on rich lowland soils (e.g. crop and pasture abandonment), while mid- and high elevations have been used mostly for logging (and to a lesser extent for pastures; Domon & Bouchard, 2007; Ruiz & Domon, 2009). Undisturbed areas have been confined to less productive, rough terrain, such as steep slopes, rocky outcrops or poorly drained organic deposits. Thus, the modern mosaic of young and mature forests magnifies spatial structure created by these variables, an interpretation supported by the high correlations of modern Gini-Simpson and Rao indices with those variables (i.e. higher correlation of Gini-Simpson and Rao index with within-cell variance in elevation and surface deposits; Supporting Information 4). Similarly, at the regional scale, it is also clear that the land uses that had the greatest impact (e.g. crop agriculture, pasture, settlement fires) were concentrated in areas at lower elevations with the warmest climate and best soils, while areas further to the north and at higher elevations have been almost exclusively used for logging since the pre-industrial era. These areas have likely followed divergent compositional trajectories, and although overall dissimilarities have decreased, compositional dissimilarities are now more correlated with gradients of temperature, elevation and surface deposits than during pre-settlement time (Supporting Information 4).

At the same time, the strengthening of community–environment relationships may also be linked to disturbance-favoured taxa having narrower niche breadths than common pre-industrial taxa along topographical and climatic gradients. At the landscape scale, *Populus* spp. have experienced their greatest increases on rich lowland soils with high clay content, which allows vigorous proliferation through root suckering following disturbance (Danneyrolles et al., 2016b; Terrail, Morin-Rivat, de Lafontaine, Fortin, & Arseneault, 2019). Conversely, *Acer* spp. and *B. papyrifera* tended to increase more in mid- and upper slopes where soils show coarser textures and more favourable micro-climatic conditions (Boucher et al., 2006; Danneyrolles, Arseneault, & Bergeron, 2016a; Danneyrolles et al., 2018). Meanwhile, dominant generalist taxa in pre-industrial times may have experienced reductions in their realized niche breadths. For example, *Picea* spp., *T. occidentalis*, *Pinus* spp. and *T. canadensis* that were common in all topographic positions in pre-industrial landscapes have been restricted to either poorly drained lower slopes or to steep slopes with abundant rocky outcrops, where they maintained a strong competitive

advantage (Danneyrolles et al., 2017; Dupuis et al., 2011; Laflamme, Munson, Grondin, & Arseneault, 2016).

## 5 | CONCLUSIONS

Our results highlight that changes since Euro-American settlement and industrialization of the last century in eastern Canada have resulted in tree communities that have simultaneously increased in diversity at the landscape scale while showing homogenization at the regional scale. Similar long-term trends were also reported for north-eastern US tree communities (Thompson et al., 2013) as well as in Northern European floras (Finderup Nielsen et al., 2019). This trend largely supports the idea that human-induced changes in biodiversity are not necessarily associated only with diversity loss, and that diversity change is strongly scale-dependent (Blowes et al., 2019; Chase et al., 2019; McGill, Dornelas, Gotelli, & Magurran, 2015; Vellend et al., 2013, 2017).

Changes in diversity have implications for ecosystem conservation and management (Mori et al., 2018; Socolar et al., 2016). Forest tree diversity is generally thought to improve ecosystem resistance and resilience to rapid environmental changes (Guo, Fei, Potter, Liebhold, & Wen, 2019; Turner et al., 2013; van der Plas et al., 2016), which are expected in the coming decades (e.g. increased temperature, drought, native or invasive insect and pathogens outbreaks; Seidl et al., 2017). From this perspective, our results have two main implications. First, despite some substantial changes in taxonomic diversity, due to strong functional redundancy within this northern tree species pool, changes in functional diversity have been less marked. Because functional diversity is thought to be more directly linked to ecosystem functioning (Mori et al., 2018), this suggests that resistance and resilience mechanisms associated with diverse tree communities may have been partially preserved. Second, our results also suggest that such resistance and resilience mechanisms may have shifted to finer spatial scales. Because landscapes are currently more diverse and heterogeneous than they were in the past, they might be more resilient to catastrophic events but at the same time, forests may be more vulnerable at larger scales due to biotic homogenization. A very concrete example could be the case of defoliator insects whose favoured hosts have strongly increased across the whole region (e.g. *Malacosoma disstria* that affects *Populus* spp. and *Acer* spp.; Cooke & Lorenzetti, 2006, or *Choristoneura fumiferana* that affects *A. balsamea* and *Picea* spp.; Boulanger & Arseneault, 2004; Navarro, Morin, Bergeron, & Girona, 2018). These host species (*Populus* spp., *Acer* spp. and *A. balsamea*) are currently distributed much more homogeneously across the region than they were in the past, which may have increased vulnerability to large outbreaks, particularly if insect activity increases with climate change (Seidl et al., 2017). How these scale-dependent changes in biodiversity combine to influence future ecosystem functioning remains an important topic for future research.

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## AUTHORS' CONTRIBUTIONS

V.D., M.V. and D.A. designed the study and methodology with substantial inputs from Y. Boucher and J.L.; S.D., G.F., M.L., A.d.R., R.T. and V.D. extracted and compiled the historical data; V.D. analysed the data and wrote the first draft with substantial inputs from M.V., D.A., Y. Boucher, J.L. and Y. Bergeron.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13474>.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study (aggregated tree composition and environmental variables at different spatial resolutions) are available at <https://doi.org/10.6084/m9.figshare.12625283.v1> (Danneyrolles et al., 2020).

## ORCID

Victor Danneyrolles  <https://orcid.org/0000-0002-4839-8164>

Dominique Arseneault  <https://orcid.org/0000-0002-3419-2480>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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