

RESEARCH ARTICLE

Tree biodiversity in northern forests shows temporal stability over 35 years at different scales, levels and dimensions

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Abstract

1. At global scales, species richness is declining. However, at local scales, understanding exactly how, where and why biodiversity is changing becomes challenging since researchers have assessed biodiversity trends using different indicators, data sources and methods (e.g. repeated measurements at the same site over time vs. space-for-time substitutions).
2. In this study, we present a multifaceted analysis of biodiversity change by assessing how tree diversity in Québec, Canada changed between two sampling periods (1970–1977 and 2005–2016), in regards to different: *levels* of diversity (alpha diversity, temporal turnover and spatial beta diversity), *dimensions* of diversity (taxonomic, functional and phylogenetic), *metrics* of diversity (presence–absence and abundance based), and *spatial scales* of analysis (plot, 50, 100 and 200 km). We then assess how well potential drivers of biodiversity change (climate change and land cover change) explain the observed changes in alpha diversity. Since the data came from plots that remained forested over the course of the study, we used historical land cover change data and scenario analyses to test whether results from forest plots were likely to be representative of the broader landscape.
3. Across all levels, dimensions, metrics and spatial scales of analysis, we found either increases or no net change in diversity over time, with wide distributions of values around the mean. Presence–absence metrics often indicated increases in diversity over time, while abundance-based metrics were more likely to show no net change. Potential drivers such as climate change and land cover change explained only a small fraction of the variation in alpha diversity change (i.e. why particular sites experienced positive vs. negative change) at the plot scale (adjusted $R^2 \approx 0.03$), but a greater fraction at coarser spatial scales (adjusted R^2 of ~ 0.10 to ~ 0.50). Results from these forest plots are likely representative of the diversity change within the study region, since estimates of alpha diversity change only became negative under scenarios with the most extreme disturbance impacts.
4. *Synthesis.* None of our indicators showed evidence of declines in alpha or beta diversity of trees in temperate and boreal forests in Quebec (except for simulations with extremely high forest loss), but we did find temporal turnover in

composition. Our results go beyond previous studies by analysing the many different aspects of biodiversity that might change over time, highlighting the need to shift from blanket descriptions of 'biodiversity loss' to more nuanced discussions around 'biodiversity change'.

KEYWORDS

alpha diversity, Anthropocene, beta diversity, biodiversity change, functional traits, global change ecology, phylogenetic diversity, species richness

1 | INTRODUCTION

Recent changes in biodiversity over time in different locations and at different spatial scales show complex and sometimes contradictory patterns (Hill et al., 2016; McGill et al., 2015). At global scales, species richness on Earth is declining; species in well-studied groups are going extinct over 100 times faster than background rates of extinction (Barnosky et al., 2011; Ceballos et al., 2015). At local scales, however, studies show contrasting changes in biodiversity that are difficult to parse (Cardinale et al., 2018; Primack et al., 2018; Vellend, Dornelas, et al., 2017). For example, there is often no net change on average in local scale species richness in areas that have not undergone substantial land-use change (Dornelas et al., 2014; Vellend et al., 2013). However, when natural vegetation is converted to agriculture, some areas experience declines in species richness (Newbold et al., 2015), while other places experience increases in species richness when non-native species colonizations exceed native species extinctions (Miller et al., 2021; Sax & Gaines, 2003). Disturbances such as forest loss can elevate rates of biodiversity change, but this is true for both losses and gains (Daskalova et al., 2020). The debate surrounding these results has highlighted three important research questions: (1) Do results for local scale species richness also apply to different scales or indicators of diversity? (2) Can variation in the direction and magnitude of temporal biodiversity change be explained based on potential drivers of environmental change? (3) Does specifically incorporating land cover change affect estimates of diversity change that were obtained by analysing repeated measurements of diversity at the same sites over time? Here we address all three questions using a dataset of >5000 tree inventory plots surveyed over a ~35-year period in temperate and boreal forests of Québec, Canada.

Although global and local biodiversity trends may appear to be at odds, they could plausibly follow different trajectories if the rates by which some species expand their ranges into new areas are balanced by the rates of species loss from the same areas (and if aggregated local species losses in turn lead to global extinctions) (Hill et al., 2016). This implies biotic homogenization regionally or globally, with species composition among local sites becoming more similar (Daru et al., 2021; Finderup Nielsen et al., 2019). Diversity within individual sites (alpha diversity) and among different sites (beta diversity) can be important for maintaining resilience and high levels of ecological function (Cardinale et al., 2012; Mori et al., 2018; Wang &

Loreau, 2016). To provide a more holistic assessment of biodiversity change, it is therefore important to examine biodiversity across different *levels*—alpha diversity (diversity change in a single community over time), temporal turnover (compositional change in a community over time) and spatial beta diversity (change in compositional dissimilarity among communities over time) (Figure 1; McGill et al., 2015).

Although species richness has been the most commonly studied indicator of biodiversity, different *dimensions* of diversity—taxonomic, functional and phylogenetic diversity—may follow different trends over time (Li et al., 2020; Swenson et al., 2012). Meta-analyses have reported changes in local taxonomic diversity (Dornelas et al., 2014; Murphy & Romanuk, 2014; Vellend et al., 2013), but too few local scale trends in functional and phylogenetic diversity have been published to draw general conclusions (Vellend, Baeten, et al., 2017). Yet, understanding changes in functional and phylogenetic diversity are informative, in that they take into account the functional and evolutionary similarities between species, and they can have stronger positive effects on ecological functioning than taxonomic diversity (Cadotte et al., 2012; Srivastava et al., 2012). Species richness also does not take into account species abundances, which can have equally important effects on ecological functions (Balmford et al., 2003). Abundance-based metrics are less sensitive than species richness to the presence or absence of rare species (Magurran, 2004), and so might show weaker temporal trends.

Spatial scale affects many aspects of ecological dynamics (Levin, 1992; Wiens, 1989), including biodiversity change (Chase et al., 2019). Species losses and gains have an asymmetric component, whereby all individuals of a species within a given area must be lost to result in local extirpation, but the introduction of just one individual of a new species leads to a gain in richness (Chase et al., 2019). This asymmetry suggests that losses (at least in terms of richness) might be more frequent at local scales while gains are observed more often at regional scales (Cassey et al., 2006), and thus researchers must be careful to consider the spatial scale of analysis in discussions of biodiversity change.

While meta analyses have shown considerable site-to-site variation in local biodiversity trends (Dornelas et al., 2014; Vellend et al., 2013), there is still much to learn about how different drivers affect the magnitude and direction of diversity change (Antão et al., 2020; Bernhardt-Römermann et al., 2015; Daskalova et al., 2020). Factors such as land-use change and climate change

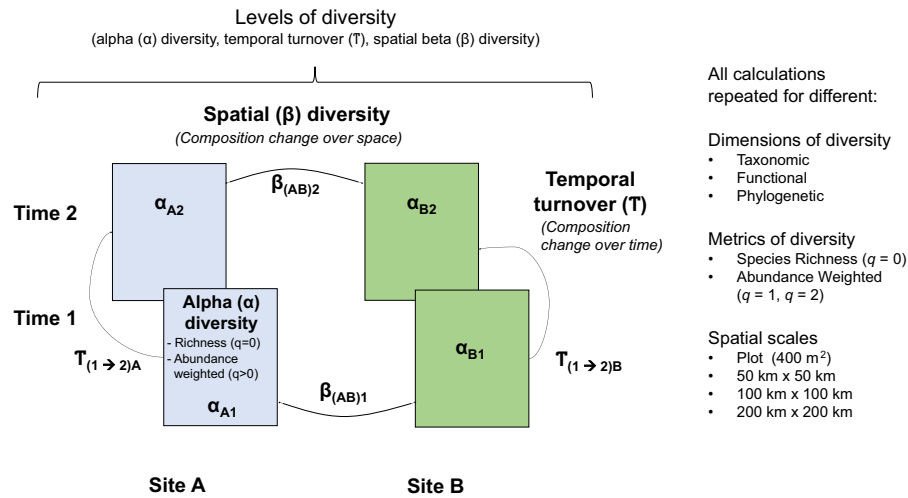


FIGURE 1 Biodiversity change can be measured across different *levels* of diversity (alpha diversity, temporal turnover and spatial beta diversity), each of which can be quantified for different *dimensions*, *metrics* and *spatial scales* of analysis.

(temperature, precipitation and growing season length) may be important (Korell et al., 2021; Newbold et al., 2015; Sala et al., 2000). In addition, land designations (e.g. public, private, protected areas, hunting/fishing regions) may affect biodiversity change because they often have different regulations about the types of actions permitted on the land (Robinson et al., 2014). Although detailed data on local forest use seldom exist, these different land designations may serve as a broad indication of the intensity of human use. For example, many protected areas have restricted hunting, fishing and logging. In designated hunting zones, grazing pressure from large herbivores (e.g. deer, moose) could be reduced, which could in turn affect plant recruitment dynamics and diversity (Bradshaw & Waller, 2016). Here we test how well these potential drivers—climate change, land-use change and land designations—explain biodiversity change.

Studies of local biodiversity change primarily fall into two categories (Cardinale et al., 2018): those that have evaluated biodiversity trends based on repeated measurements at the same site over time (e.g. Dornelas et al., 2014; Vellend et al., 2013), and those that have used space-for-time substitution to infer biodiversity change based on a gradient of human impact (e.g. Davison et al., 2021; Gerstner et al., 2014; Newbold et al., 2015). Although repeated measurement studies provide the most direct evidence of temporal diversity change, they may not adequately capture the spatial variation of temporal change. Sites used in repeated measurement studies may well have experienced some historical disturbance (i.e. they are not all pristine sites), but are unlikely to have experienced extreme disturbance since repeated measurements are rare in sites where substantial land use change has occurred during the period of study. In contrast, space-for-time studies provide spatial replication of different land uses, but causal inference is challenged by potentially confounding variables (e.g. different land uses occur under different topographic and soil conditions) and by time-lags between land use change and its effects on biodiversity (Triantis et al., 2010). Here, we integrate aspects of both methods

to estimate and explore scenarios of diversity change over time and across space. We use long-term repeated measurement data and satellite-derived maps of land cover change to assess whether the biodiversity study sites are representative of land cover changes occurring across the broader landscape. This enables us to explore scenarios of the degree of diversity change that might be observed under different assumptions about the effects of land cover change.

In this study we examine the dynamics of forest communities in Québec, Canada to assess how tree biodiversity has changed over the past ~35 years (from the period 1970–1977 to the period 2005–2016) across different: (i) *levels* of diversity (alpha diversity, temporal turnover and spatial beta diversity), (ii) *dimensions* of diversity (taxonomic, functional and phylogenetic), (iii) *metrics* of diversity (presence–absence and abundance based) and (iv) local to regional *spatial scales* of analysis (plot, 50, 100 and 200 km) (Figure 1). For alpha diversity, we extend the analyses to assess the degree to which changes can be predicted by climate change, land cover change and land designation. Lastly, we simulate potential negative effects from land cover change that are not possible with the empirical data alone, asking whether accounting for land cover change affects the estimated changes in alpha diversity.

We test a series of predictions based on empirical results from the literature and on hypotheses about the effects of disturbance and climate change (Vellend, Baeten, et al., 2017), as follows:

- Alpha diversity will show minimal if any temporal change (Dornelas et al., 2014; Vellend et al., 2013).
- Functional and phylogenetic alpha diversity will show greater change than taxonomic diversity (Magnago et al., 2014).
- Richness-based metrics of alpha diversity will show greater temporal changes than abundance weighted metrics (Magurran, 2004).
- Alpha diversity is more likely to increase at large spatial scales than small spatial scales (Chase et al., 2019).

- Compositional shifts over time are ubiquitous across dimensions, metrics and scales of biodiversity (De Frenne et al., 2013; Dornelas et al., 2014).
- Spatial beta diversity will show decreases (i.e. there has been biotic homogenization; Magurran et al., 2015).
- Environmental variables will predict more variance in alpha diversity change at large than small spatial scales, given greater stochasticity in community assembly at small spatial scales (Vellend, 2016).
- Disturbance has a greater effect on alpha diversity change than climate in this region, with a negative effect of disturbance at the plot scale (destruction of trees) but positive effects at larger scales (increased plot-to-plot heterogeneity) (Danneyrolles et al., 2019).
- Any effect of temperature on alpha diversity will be positive given many temperature- or growing season-limited species, while we do not expect strong effects of precipitation given relatively high overall regional precipitation (Peng et al., 2011).
- Simulation of disturbance (removal of trees) has a negative effect on diversity change that is nonlinear, with greater effects at the most extreme levels of disturbance (Gotelli & Colwell, 2001).

2 | MATERIALS AND METHODS

2.1 | Study area and input data

To assess changes in forest biodiversity over the past ~35 years (from the period 1970–1977 to the period 2005–2016), we used inventory data from forest plots across temperate and boreal forests within the province of Québec, Canada (Figure 2; Données Québec, 2017; MFFP, 2016). The locations of these plots were randomly selected by the Government of Québec from all forested regions of the province, while ensuring a minimum number of plots in different bioclimatic regions (one plot per 103 km² in *Betula alleghaniensis/papyrifera* regions, one per 26 km² in other deciduous regions and one per 259 km² in the *Picea* spp. region; MFFP, 2014). The five most dominant species across our study region are: *Picea mariana*, *Abies balsamea*, *Betula papyrifera*, *Acer saccharum* and *Acer rubrum*. This forest inventory program was designed to track the progression of natural forests over time (MFFP, 2016). These forest plots are not all located in pristine areas, as land cover change datasets (described in Section 2.4) show that some plots experienced disturbances during the study period (see also Brice et al., 2020). Within each 400 m² forest plot, government technicians recorded the species name and diameter at breast height (DBH) for each tree with a DBH of at least 9.1 cm. In our analyses we included only the 5619 plots which were sampled between 1970 and 1977 (which we call ~1975), and again between 2005 and 2016 (~2010). In all analyses subsequently discussed in this paper, ‘abundance’ is simply a count of the number of trees; preliminary analyses indicated similar results using summed basal area.

2.1.1 | Phylogenetic data

As input data to calculate phylogenetic diversity (indices described below) we extracted phylogenetic relationships between all tree species found in Québec from a previously published mega-phylogeny of plants (Li et al., 2019; Qian & Jin, 2016). Two species (*Alnus incana* and *Ulmus rubra*) were present in the forest plots, but not listed in the phylogenetic data. For these species, we merged their abundances with their closest relative in the same genus in the phylogeny (*Alnus viridis* and *Ulmus thomasii*).

2.1.2 | Functional trait data

To calculate indices of functional diversity that are directly comparable to those for phylogenetic diversity, we first constructed a functional dendrogram (a bifurcating tree with species at the tips, as in a phylogeny). As input, we used data collated for 17 different functional traits: average maximum height, growth rate, leaf size, wood density, wood decay resistance, vegetative reproduction, seed mass, abiotic pollination, biotic pollination, shade tolerance, drought tolerance, waterlogging tolerance, endomycorrhiza, ectomycorrhiza, leaf longevity, leaf mass per area and nitrogen content per leaf mass unit (Paquette & Messier, 2011). Five of these traits (vegetative reproduction, abiotic pollination, biotic pollination, endomycorrhiza and ectomycorrhiza) had binary values (possible/not possible), while the other traits values were numeric. In the rare cases where trait data were missing for a species (4/53 species; see traits file in data repository), we applied the trait values from that species' closest relative(s). Since the trait data for seed mass and wood density were not normally distributed, we applied a square root and log transformation, respectively, to these trait values. We then scaled data for each numeric trait from 0 to 1 to ensure that each trait received equal weight in subsequent analyses. Following recommendations from Swenson (2014), to reduce collinearity among traits, we conducted a principal components analysis (PCA) on all traits and then selected the first 16 principal component axes, which explained 94% of the variation. We used these PCA axes to create a Euclidean distance matrix quantifying the dissimilarities between species. We created a functional trait dendrogram using the unweighted pair-group method with arithmetic mean to cluster the species. We then forced the dendrogram to be ultrametric to maximize comparability with the phylogenetic diversity analyses.

2.2 | Measuring different levels, dimensions and scales of diversity

2.2.1 | Alpha diversity

We calculated alpha diversity at each forest plot and for each time period (~1975 and ~2010) using Hill numbers, which are diversity estimates indicating the effective number of species within

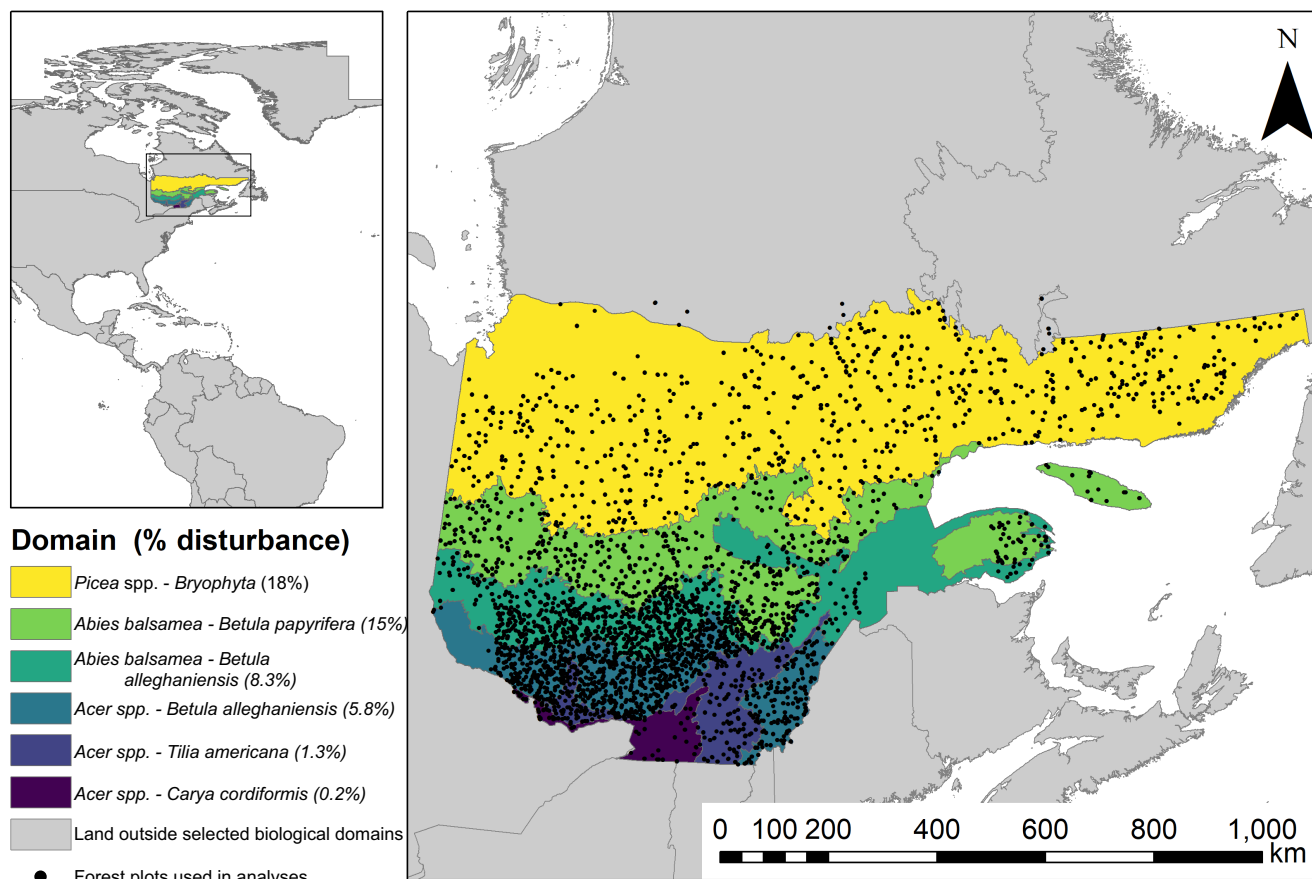


FIGURE 2 The forest plots used in this study ($n = 5619$) span the temperate and boreal forests of Quebec, Canada. Cumulative forest disturbance from 1975 to 2010 varies considerably between bioclimate domains. Northern regions tend to have much greater amounts of forest disturbance than southern regions. The percentages listed in the legend indicate the total per cent of forest disturbance within each of the bioclimatic domains in the study region.

a community (Chao et al., 2010, 2014; Jost, 2006). Diversity estimates using Hill numbers allow different weightings for rare versus common species within a community by changing the parameter 'q' (Jost, 2006). Hill numbers of taxonomic diversity for order $q = 0$ are equivalent to calculations of species richness, which can be strongly influenced by the presence or absence of rare species in a community. As the value of q increases, diversity estimates place less emphasis on rare species. For functional and phylogenetic diversity, since not all species are equally distinct, Hill numbers account for the relatedness among species as well as species' abundances (Chao et al., 2010; Chao et al., 2014). We calculated Hill numbers of order $q = 0$, $q = 1$ and $q = 2$ for taxonomic diversity using the `VEGAN` R package (Oksanen et al., 2019), and Hill numbers for functional and phylogenetic diversity using the `ENTROPART` R package (Marcon & Hérault, 2015). We conducted paired t -tests to determine if there was significant change in each alpha diversity index between the two time periods. We assessed the sensitivity of our results by repeating these analyses using a one-sample t -test on log ratios of change (i.e. $\ln[\text{Diversity}_{\text{Time 2}}/\text{Diversity}_{\text{Time 1}}]$), and found that our results were qualitatively similar (Figure S3). Since we observed changes in alpha diversity that were statistically significant but that could be considered ecologically minor,

we conducted post-hoc tests to determine the power of our t -tests to detect changes in alpha diversity.

2.2.2 | Temporal turnover and spatial Beta diversity

There are numerous metrics to calculate temporal turnover and spatial beta diversity for all dimensions of diversity (taxonomic, functional and phylogenetic). While some pairs of metrics reflect different features of the underlying data, many are highly correlated with one another (Anderson et al., 2011; Koleff et al., 2003; Swenson, 2011; Tucker et al., 2017). We selected metrics that incorporate presence-absence information as well as relative abundance to determine if the results were qualitatively similar. Using the same dissimilarity metrics to calculate temporal turnover and spatial beta diversity, for taxonomic diversity we calculated the Sorensen and Bray-Curtis metrics, using the `VEGAN` R package (Oksanen et al., 2019). For functional and phylogenetic diversity, we calculated both tree-based and distance-based metrics of dissimilarity, including UniFrac (using R package `GUNIFRAC`; Chen, 2018), and mean pairwise distance (using R functions outlined in Swenson, 2014). Since the mean pairwise distance requires at least two species, we omitted sites that

only contained one species for analyses with this metric. We tested for systematic temporal turnover (overall directional shifts in composition, indicated by a shift in the centroid of multivariate space) between the two time periods using permutational analysis of variance (PERMANOVA; Anderson, 2001). We assessed whether there were changes in spatial beta diversity using a permutational analysis of multivariate dispersions (PERMDISP; Anderson, 2006; Anderson et al., 2006) to assess whether the average distance to the centroid changed between the two time periods. At the plot scale, these PERMANOVA and PERMDISP analyses were conducted using all 5619 forest plots across the study region.

2.2.3 | Spatial scales

We assessed whether diversity changes were consistent across four hierarchical spatial scales: plot, 50 km × 50 km, 100 km × 100 km and 200 km × 200 km. Due to diversity–area relationships, the number of forest plots included within an area can impact the observed diversity. Therefore, to keep the number of forest plots consistent between different grid cells at a given spatial scale, we randomly subsampled 7, 15 and 50 forest plots within each of the 50, 100 and 200 km grid cells respectively. Any grid cell that did not have at least that many plots was excluded from a given analysis. These sample sizes were chosen as a compromise between maximizing the number of plots per grid cell and minimizing the number of cells we needed to exclude (Figure S1). We repeated this randomized subsampling procedure 1000 times, and each time we calculated the total abundance of each species across all selected plots as input to calculate the diversity metrics. In other words, each grid cell became our new unit of analysis for biodiversity measurements, and spatial beta diversity calculations assessed the dissimilarity between each pair of grid cells. For alpha diversity, we calculated the mean diversity in ~1975 and ~2010 across the 1000 replicates for subsequent analysis. For temporal turnover and spatial beta diversity, we calculated the mean dissimilarity value for each pair of grid cells across the 1000 replicates. Using these mean values, our subsequent statistical analyses were identical to those previously described.

We also assessed the sensitivity of the number of plots per grid cell by repeating the process with fewer and greater numbers of forest plots at each spatial scale (at 50 km, 4 plots and 10 plots; at 100 km, 10 and 20; and at 200 km, 25 and 110). At the plot scale, no sensitivity analysis was conducted since all 5619 plots were used in the analyses.

2.3 | Explaining diversity change

We tested whether some of the most common drivers of biodiversity change (i.e. climate change, land cover change and land designation; Maxwell et al., 2016; Pereira et al., 2010; Sala et al., 2000) could explain the direction and magnitude of alpha diversity change observed in our sites. We assessed average changes in climate

conditions (growing season days, mean growing season temperature, total growing season precipitation, average annual maximum temperature, average annual minimum temperature and total annual precipitation) between the two time periods (i.e. average climate from 1970 to 1977 vs. average from 2005 to 2016). We found qualitatively similar results when we repeated the analysis with climate time-lags of 10 and 20 years. These climate data were obtained from the government of Canada (MacDonald et al., 2020) with raster pixels of 10 km × 10 km (McKenney et al., 2006, 2011; Pedlar et al., 2015). We generated climate changes values for the 50, 100 and 200 km grid cells by averaging climate values across the forest plots within each cell. During the first time period of our study (1970–1977), the average maximum daily temperature ranged from 0.4 to 11.6°C across our study region, the annual precipitation ranged from 540 to 1320 mm, and the number of growing season days (i.e. consecutive days warmer than 0°C) ranged from 56 to 171. Over the duration of our study, different regions of our study area were affected by climate change to varying degrees. Across the forest plots, the maximum daily temperature increased between 0.7 and 2.3°C, annual precipitation changed between –16 mm and +10 mm and the number of growing season days changed between –2 and +28.

We assessed land cover change from forest disturbance maps showing whether each 30 m pixel was disturbed (via logging and/or fire) during the interval 1985–2010 (see Section 2.4 for details on the disturbance data). At the coarser spatial scales, we calculated the proportion of pixels within each grid cell that experienced forest disturbance. At the plot scale this variable had two possibilities, undisturbed or disturbed.

We assessed the proportion of area under each major land designation (i.e. private land, protected area, hunting–fishing regions and general public land) for each plot and for all grid cells (Données Québec, 2019). Each plot was characterized by one of these designations, while larger grid cells might have non-zero proportions of multiple designations. We grouped all types of parks and conservation areas (e.g. national park, ecological reserve, wildlife refuge) into one variable called ‘protected area’. After categorizing the proportion of each land designation, we excluded ‘general public land’ as a variable in our statistical model so that these land designation variables were not completely collinear. We applied a logit transformation to all the proportion variables (land designations, harvesting and wildfire) to approximate normal distributions.

We scaled the climate variables to a mean of zero and unit variance so that the variables could be compared on a common scale, and then conducted two principal component analyses (PCAs) to reduce the number of climate variables. We conducted a PCA on temperature variables (maximum temperature, minimum temperature and number of growing season days), and then extracted the first two PCA axes, which explained about 93% of the variation. Similarly, we extracted the first axis from a PCA on precipitation variables (growing season precipitation and annual precipitation).

We then used an AIC model selection approach to evaluate the associations between our explanatory variables and alpha diversity change. We ran multiple regressions with all possible combinations

of explanatory variables, and then extracted model-averaged coefficients and R^2 values from models within two AIC units of the most parsimonious model, using the 'MuMIn' package in R (Barton, 2020). We checked the model residuals for evidence of spatial autocorrelation using a Moran's I .

2.4 | Accounting for land cover change

Since the forest inventory surveys involve repeated measurements of the same forest plots over time, results might over or underestimate biodiversity change if, on average, the plots that were measured experienced a different amount of disturbance than the overall landscape. We focus this analysis on addressing critiques of underestimated biodiversity loss (Gonzalez et al., 2016), recognizing that over intermediate times-scales disturbance can increase tree density and diversity (Harper et al., 2002). We conducted a simulation analysis to estimate possible diversity changes across a range of disturbance scenarios. We focused on the plot scale because at the coarser spatial scales there are often too few forest plots within each grid cell to reliably simulate disturbance. These simulations required two key assumptions: what proportion of plots should have experienced disturbance if the plots were representative of changes across the landscape, and how much impact on diversity these disturbances would likely cause.

To estimate the proportion of plots that should have experienced disturbance, first we calculated the observed amount of disturbance across the landscape using a Canada-wide forest disturbance dataset from 1985 to 2010 at a 30m pixel resolution (White et al., 2017). These data show that the greatest amount of disturbance is due to forest harvesting (~64%), followed by forest fires (~36%). Land conversion to roads or other human-created permanent structures is extremely low in Québec. Since some regions of Québec have undergone greater forest change than others, we calculated the proportion of pixels that experienced forest disturbance separately for each bioclimatic domain (an area of characteristic climate and vegetation; Saucier et al., 1998). Although the spatially explicit satellite data do not span our entire study duration, there is no directional trend (i.e. an increase or decrease) in forest disturbance over the period of data (Figure S2). Therefore, to account for the fact that our forest disturbance data span 26 years but our study duration spans ~35 years, we multiplied the proportion of pixels disturbed in each biological domain by 35/26 to estimate the total proportion over the entire study period (Figure 2). We excluded the northern spruce-lichen bioclimatic domain from this analysis because there were only 18 forest plots within this region. Although this disturbance dataset indicates that some of our plots experienced disturbance (i.e. the forest plot data do not just come from pristine locations), we nonetheless added the observed amounts of disturbance to our virtual landscapes on top of any existing disturbance already captured in our forest plots. Although adding this additional disturbance may result in overestimates of the real impacts of disturbance, our aim was to assess whether

these extreme scenarios could cause alpha diversity change to become negative.

Harvesting and fire can result in highly variable changes in the number and identity of tree species over a multi-decadal time period (Bergeron, 2000; Bergeron & Dansereau, 1993), along with variable rates of recovery depending on the degree of disturbance, climate conditions and soil properties (Harper et al., 2002). However, a substantial proportion of trees will often regrow within 10 years (White et al., 2017), indicating that at least partial recovery of diversity happens reasonably quickly. Since there are no data available on the impacts of disturbance in this particular set of plots or their recovery dynamics over time, we opted to use six impact scenarios in which we simulated the removal (without subsequent replacement) of 25%, 50%, 75%, 90%, 95% or 100% of the individual trees within a plot. The trees remaining form virtual plot-level communities from which we can calculate indices of alpha diversity as described above.

In the simulation analysis, we randomly selected forest plots within each biological domain to experience disturbance (where the proportion of disturbed plots followed the percentage values outlined in Figure 2). We then randomly selected individual trees within these plots to be destroyed by the disturbance (at each of the six scenario levels). We repeated these simulations 100 times, and then calculated the mean alpha diversity at the second time period (~2010) across all replicates. Using the full set of plots (disturbed and undisturbed) we then assessed whether there was significant change in alpha diversity between ~1975 and ~2010 using a paired t-test.

3 | RESULTS

3.1 | Measuring different levels, dimensions and scales of diversity

3.1.1 | Alpha diversity showed positive or no-net change across all indicators

The average change in alpha diversity was positive from ~1975 to ~2010 for all dimensions of diversity (taxonomic, functional and phylogenetic) at the plot scale (Figure 3). However, the average increase in diversity was very small in comparison to the substantial variation among plots—some plots experienced large losses in diversity while other plots experienced large gains in diversity. Plots with substantial losses or gains in diversity were distributed throughout the study region (Figure S6). These trends were qualitatively similar across different metrics of diversity at the plot scale (i.e. 400m²), although, as predicted, the average magnitude of change was greater when higher weights were applied to rare species (i.e. changes in alpha diversity were greater for Hill numbers of order $q = 0$ than for $q = 1$ or $q = 2$; Figure 4). The magnitude of positive diversity changes tended to be greater for taxonomic diversity than for functional diversity, which in turn tended to be greater than for phylogenetic diversity (Figure 4, Figure S4). At the plot scale, the average species richness was 3.7; for functional and phylogenetic diversity, the

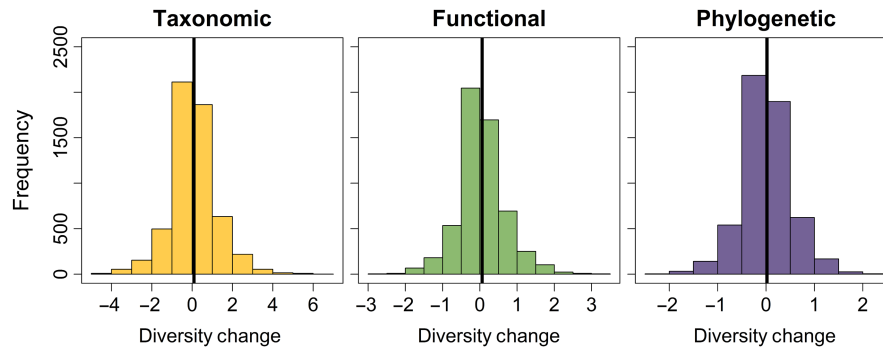


FIGURE 3 The mean change in diversity (black vertical line) over the past ~35 years was slightly positive for all dimensions of diversity (taxonomic (0.088), functional (0.018) and phylogenetic (0.059); $p < 0.001$), but there was considerable site level variation around the mean (standard errors: 0.015, 0.007 and 0.008). Figures show Hill numbers of order $q = 1$. Change is expressed as the raw difference over time (e.g. $TD_{2010} - TD_{1975}$ for the left panel).

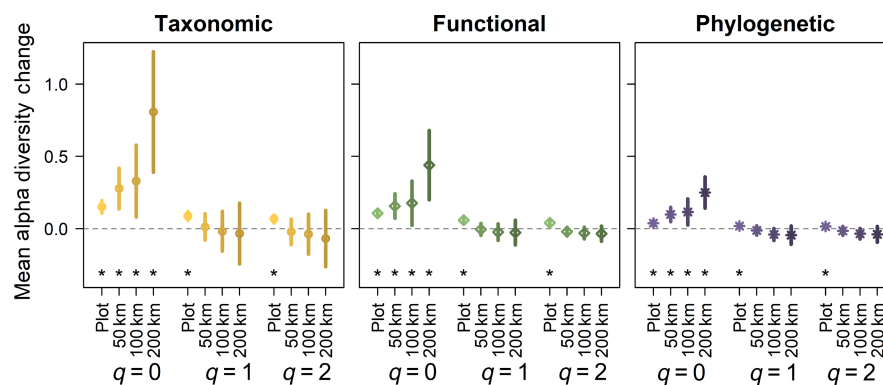


FIGURE 4 All dimensions of diversity (taxonomic, functional and phylogenetic) showed qualitatively similar patterns of mean change in alpha diversity (raw difference over time for a given metric) across spatial scales (plot, 50, 100 and 200 km). For presence–absence diversity metrics ($q = 0$), the mean change in diversity increased at coarser spatial scales. However, for abundance-based metrics of $q = 1$ and $q = 2$, the mean change in diversity was generally not different from zero at the 50, 100 and 200 km scales. Bars indicate 95% confidence intervals. Asterisks indicate that the mean change was different from zero ($p < 0.05$).

average effective numbers of species (i.e. with $q = 0$) were 2.8 and 2.4 respectively.

Different diversity metrics showed contrasting results at different spatial scales. In line with our predictions, the mean change for the presence–absence metric (i.e. $q = 0$) was more strongly positive at coarser spatial scales (Figure 4). However, for abundance-based metrics ($q = 1$ and $q = 2$) the mean biodiversity change at scales larger than the plot was generally not significantly different from zero.

3.1.2 | Temporal turnover occurred across all biodiversity indicators

At the plot scale, we found systematic compositional turnover over time for all dimensions and metrics, except for the abundance-based metric for phylogenetic dissimilarity (i.e. based on the mean pairwise distance, D_{pw}) (Table 1). In regards to spatial scale, there was significant taxonomic turnover at all spatial scales and for all metrics. While there was significant functional and phylogenetic turnover

at all scales for the presence–absence metric (UniFrac), turnover was not significant for the abundance-based metric (mean pairwise distance) at the largest spatial scale. For taxonomic turnover at the plot scale, the median value of Sorensen's dissimilarity was 0.20, although values varied from no temporal turnover to complete turnover. For functional and phylogenetic turnover (UniFrac dissimilarity), the median values were 0.30 and 0.21. At coarser spatial scales, median turnover values were slightly lower than at the plot scale; at the 200 km scale median dissimilarities were 0.11, 0.15 and 0.09 for taxonomic, functional and phylogenetic diversity.

3.2 | Spatial Beta diversity seldom showed evidence of change over time

Contrary to our prediction of declines in spatial beta diversity (i.e. homogenization), at the plot scale beta diversity increased for all dimensions for the presence–absence metrics of dissimilarity (Table 1b). However, there was no significant change in beta diversity for abundance-based metrics. At the 50, 100 and 200 km scales,

TABLE 1 Table (a) shows the p values for tests of systematic compositional change over time (i.e. temporal turnover; PERMANOVA analyses). Table (b) shows the change in spatial beta diversity (PERMDISP analyses); positive values indicate an increase in beta diversity over time, while negative values indicate a decrease. The mean beta diversity values (i.e. mean distance to centroid) for the first time period (1970–1977) are indicated in brackets. Statistically significant changes ($p < 0.05$) are indicated in bold and with an asterisk. For taxonomic diversity, the presence–absence and abundance weighted metrics underlying both analyses are the Sorensen and Bray–Curtis indices respectively. For both functional and phylogenetic diversity, the corresponding metrics are the UniFrac and mean pairwise distance indices.

	Presence–Absence				Abundance weighted			
	Plot	50 km	100 km	200 km	Plot	50 km	100 km	200 km
(a) Temporal turnover								
Taxonomic	0.001*	0.001*	0.001*	0.029*	0.001*	0.001*	0.002*	0.048*
Functional	0.001*	0.001*	0.002*	0.017*	0.001*	0.001*	0.004*	0.115
Phylogenetic	0.001*	0.001*	0.001*	0.002*	0.999	0.028*	0.017*	0.338
(b) Spatial beta diversity								
Taxonomic	+0.006*	0.010	0.004	–0.021	–0.001	–0.005	–0.003	–0.003
	(0.487)	(0.335)	(0.310)	(0.301)	(–0.584)	(0.426)	(0.373)	(0.341)
Functional	+0.004*	0.009	0.003	–0.024	0.002	–0.021	–0.021	–0.018
	(0.483)	(0.396)	(0.377)	(0.364)	(1.103)	(0.913)	(0.848)	(0.839)
Phylogenetic	+0.005*	0.011	0.007	–0.020	–0.408	–5.110	–6.716	–5.336
	(0.407)	(0.293)	(0.268)	(0.259)	(345.3)	(308.8)	(290.6)	(286.4)

changes in beta diversity were not significantly different than zero for any dimension of diversity.

3.3 | Explaining diversity change

The degree to which climate change, disturbance and land designation explained changes in alpha diversity varied considerably across spatial scales of analysis (Figure 5). At the plot scale, these variables explained little of the variation in the change in alpha diversity (typically adjusted $R^2 < 0.05$). These variables explained a greater fraction of the variation as the spatial scale (i.e. grid cell size) became larger (e.g. adjusted $R^2 \approx 0.1$ – 0.50 for the 200 km scale). The explanatory ability (adjusted R^2 value) tended to be slightly higher for presence–absence ($q = 0$) than for abundance-based ($q = 1$ and $q = 2$) metrics of diversity at the plot and 50 km scales (e.g. for plot-scale PD, 0.05 for $q = 0$ vs. 0.02 for $q = 2$), but higher for $q = 1$ than $q = 0$ at the 100 and 200 km scales (e.g. for 200 km-scale PD, 0.46 for $q = 1$ vs. 0.34 for $q = 0$). The explanatory ability was similar across the different dimensions of diversity (taxonomic, functional and phylogenetic), although it tended to be slightly higher for phylogenetic diversity.

Across the different spatial scales, and dimensions and metrics of diversity, model selection via AIC indicated that disturbances from harvesting and wildfire were the potential drivers that were associated with alpha diversity change (Figure S5). In Figure S5 and description below, we discuss ‘the change in alpha diversity change’ rather than alpha diversity, meaning that strong associations indicate more ‘change in alpha diversity’ rather than more ‘alpha diversity’. In line with our predictions, the amount of disturbance showed different relationships across spatial scales; diversity change at the plot scale was negatively associated with wildfire, but was positively associated with wildfire at

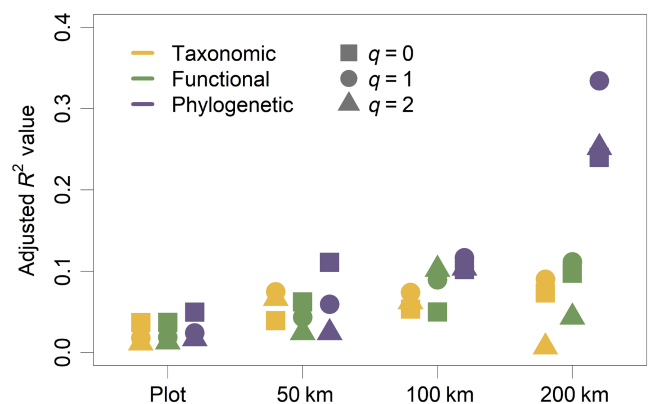


FIGURE 5 Climate change, land cover change and land designation collectively explain more variation in changes in alpha diversity (i.e. higher adjusted R^2 value) at coarser spatial scales of analysis. Different colours indicate the different dimensions of diversity (taxonomic, functional and phylogenetic) and different shapes indicate the presence–absence ($q = 0$) and abundance-based ($q = 1$, $q = 2$) metrics of diversity.

coarser spatial scales (i.e. 50, 100 and 200 km scales). Although we predicted that increasing temperatures would be associated with positive changes in alpha diversity, different indicators of temperature showed contrasting results; at the plot scale diversity change was positively associated with change the temperature PCA axis 2 (which was influenced substantially by the minimum annual temperature and with change in the growing season temperature), but negatively associated with temperature PCA axis 1 (which was influenced substantially by change in the maximum annual temperature). Changes in precipitation did not show any substantial or consistent relationships with changes in alpha diversity. In general, associations between land designation

(public, private and hunting–fishing zones) and alpha diversity change were weak. Across spatial scales and dimensions and metrics of diversity, confidence intervals for each land designation spanned zero, except for a few instances (i.e. a negative association with alpha diversity change on private land for species richness at the plot scale; positive associations in hunting–fishing areas for functional diversity ($q = 0$) at the plot, 50 and 100 km scales, and also for taxonomic diversity at the 100 km scale).

3.4 | Accounting for land cover change

When simulating disturbance impacts, we found that plot-level declines in diversity only occurred in scenarios with severe disturbances (i.e. substantial tree removal; Figure 6). For all dimensions of diversity, diversity only showed declines in scenarios in which the vast majority of the individuals ($\geq 90\%$ for taxonomic and functional diversity; $\geq 80\%$ for phylogenetic diversity) in the selected forest plots were destroyed and no forest recovery was permitted. Even with complete removal of all trees, the absolute magnitude of decline was no greater than the small magnitude of increase in the original analysis (≤ 0.2). Qualitatively similar patterns were observed for all metrics ($q = 0$, $q = 1$ and $q = 2$) (Figure S7).

4 | DISCUSSION

Our assessments of biodiversity change over ~35 years in Québec forests showed clear temporal turnover in composition, with alpha

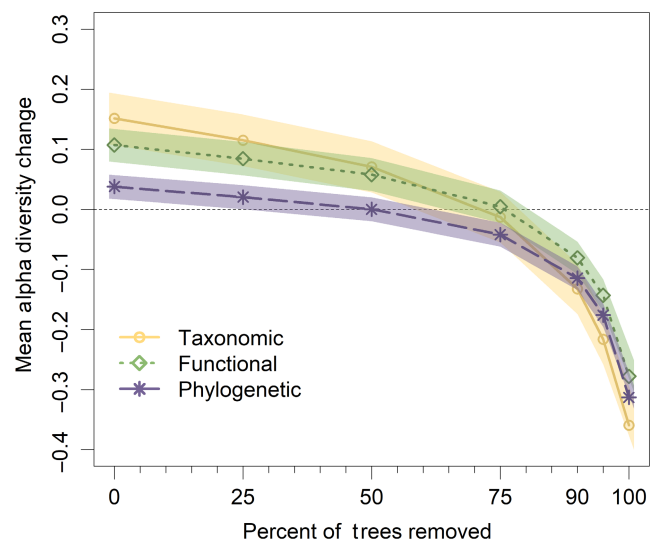


FIGURE 6 The estimated mean change in alpha diversity (raw difference in a given metric) decreases nonlinearly with the magnitude of simulated disturbance impacts. Alpha diversity change only indicates a decline in diversity once the simulated disturbance removed ~90% (taxonomic and functional diversity) or ~80% (phylogenetic diversity) of individual trees within the community. Shaded areas indicate 95% confidence intervals. This figure shows results from the presence–absence metrics of $q = 0$.

diversity changes showing high variability (spanning both positive and negative change) and minor mean differences from zero. These trends for turnover and alpha diversity were consistent for all dimensions and metrics of diversity across all spatial scales. Statistical models that include many of the main potential drivers of change only explained a relatively small part of the variation of changes in alpha diversity (i.e. why some sites experienced biodiversity gains while other sites experienced biodiversity losses) at the plot scale (i.e. 400 m²), but explained a greater fraction of the variation at the 50, 100 and 200 km scales. Our scenario analyses indicate that results obtained from the repeated-measurements approach of assessing biodiversity change remained robust after incorporating the direct impacts of land cover change. Overall, these results across levels, dimensions and metrics of diversity and spatial scales of analyses highlight the need for a shift from blanket discussions of ‘biodiversity loss’ to ‘biodiversity change’ in order to articulate the nuances across different indicators of diversity.

4.1 | Measuring different levels, dimensions and scales of diversity

Our results show temporal turnover in composition across all levels and dimensions of measurement (Table 1), but minimal net directional change in alpha diversity relative to broad distributions of values. This dynamic appears to apply quite generally, as it has been found in other case studies (e.g. MacLean et al., 2018) and in meta-analyses (e.g. Dornelas et al., 2014). Small deviations from zero for alpha diversity change (such as the positive changes found in this study) are also not inconsistent with the literature, since subsets of data in meta-analyses can deviate from zero (e.g. for different taxonomic groups Pilotto et al., 2020), as do some entire meta-analyses themselves (e.g. Elahi et al., 2015). In Québec, biodiversity is projected to increase in the future due to climate change, as species from the south—where there is greater biodiversity—move northward (Berteaux et al., 2018). The range limits of several dominant tree species in Québec, such as *Acer saccharum* (sugar maple) and *Acer rubrum* (red maple), are already moving northward with these changing climate regimes (Boisvert-Marsh et al., 2014; Sittaro et al., 2017), possibly contributing to the community-level changes observed in this study. The small, net positive changes in alpha diversity found in our study might thus be, at least in part, early indications of changes due to a warming climate. However, given the small magnitude of this positive change and the fact that our study had the statistical power to detect very small changes in alpha diversity at the plot scale (± 0.02 to 0.06), we suggest that this minor positive trend in alpha diversity currently may not differ from results of no-net change in an ecologically meaningful way. The standard deviations of the distributions of temporal change were much greater than the mean deviation from zero (Figure 3). These results imply that many individual plots have experienced meaningful changes in diversity—either positive or negative—despite an average trend close to zero.

Changes in alpha diversity were similar across different dimensions (taxonomic, functional and phylogenetic). Since previous meta-analyses have focused largely on species richness, an important caveat has been that changes in species richness may not be indicative of changes in functional and phylogenetic diversity (Primack et al., 2018). Here we found no tendency for changes in functional and phylogenetic diversity to deviate strongly from changes in taxonomic diversity. Assessments of functional and phylogenetic diversity are increasingly prevalent in ecological studies (McGill et al., 2006; Winter et al., 2013), because these dimensions of diversity are more directly linked to ecosystem functioning than taxonomic diversity (Cadotte et al., 2012; Srivastava et al., 2012) and more informative for assessing whether ecological changes are stochastic or deterministic (Swenson et al., 2012). Although there may be functional traits that influence responses to environmental change or effects on ecosystem function that we did not include in this study (Aubin et al., 2016), the list of 17 functional traits covers the major axes known to characterize tree function and has shown differences from taxonomic diversity in other studies in terms of associations with ecosystem functions (Paquette & Messier, 2011). The congruence of taxonomic, functional and phylogenetic diversity depend on the metrics used and on the structures of the functional dendrogram or phylogenetic tree (Tucker & Cadotte, 2013). Our results suggest that at least in some cases when using Hill numbers as metrics of diversity, estimates of taxonomic diversity may provide a useful approximation of functional and phylogenetic diversity in regions where functional trait data have not been collected or phylogenetic relationships have not been characterized.

Changes in spatial beta diversity may help explain the observed differences in alpha diversity change between the plot scale and landscape scales (i.e. 50–200 km). Researchers have predicted and have often found decreases in landscape-scale beta diversity (e.g. Baiser et al., 2012; McGill et al., 2015), which we might have expected to cancel out the plot scale increases in alpha diversity when moving to coarser spatial scales. The increases that we observed in beta diversity among plots ($q = 0$) run counter to our hypothesis of biotic homogenization. We can only speculate as to the underlying causes of increased beta diversity among plots, but spatially variable disturbance may have contributed. The magnitude of forest exploitation in Québec increased substantially during the second half of the 20th century, with the intensity and frequency of disturbance showing high spatial variability (Coulombe et al., 2004). Different disturbances (or lack thereof) can cause divergence in species composition among plots (Newbold et al., 2015), such that logging or fire in 5%–10% of a landscape (see Figure 2) might increase overall beta diversity among plots within a landscape, thereby contributing to increases in landscape scale alpha diversity (also see Danneyrolles et al., 2020; Vellend et al., 2021). This would be consistent with notions that habitat fragmentation (independent of habitat loss) can in fact increase diversity (Fahrig, 2017), and is consistent with our result that diversity change was positively associated with disturbance at coarser spatial scales.

At coarser spatial scales, our contrasting results of increases in diversity for richness metrics ($q = 0$) and no-net change for abundance metrics ($q = 1$ and $q = 2$) indicate that changes in both alpha and spatial beta diversity were largely driven by changes in the presence–absence of rare species, functional trait values and phylogenetic lineages, rather than by substantial change in dominance structure. These differences could arise due to the relatively short duration of the study in comparison to the life spans of trees; the ~35-year period might be long enough to detect colonizations or local extinctions (effectively small changes in abundance to or from zero) but not long enough for substantial shifts in abundance to occur. However, despite the short study duration, our results showed temporal turnover in composition across all dimensions of diversity for both presence–absence and abundance metrics. Since PERMANOVAs test for a directional shift in the centroid of a multivariate ‘species space’ across all communities, stochastic changes in composition within each community would not give a significant result; our results therefore indicate that communities are showing subtle systematic shifts in community composition, despite a lack of consistent changes in diversity across metrics.

Although we detected systematic species turnover across the entire dataset, the underlying causes are likely numerous and variable across space, as documented in previous studies (e.g. Chase et al., 2019; Elahi et al., 2015). The largest overall increase in abundance was observed for *Fagus grandifolia* (+31%), which is consistent with other studies reporting increased beech abundance in Québec, although the many hypothesized causes (e.g. reduced competition from *Acer saccharum* due to base cation depletion or herbivory) remain largely a matter of speculation (Gauthier et al., 2015; Gravel et al., 2011). Here we found that the overall abundance of *Acer saccharum* was largely unchanged (–2%). Using an overlapping dataset, Brice et al. (2020) quantified transitions among forest types (boreal, mixed, temperate and pioneer), with the most common transitions over the past ~40 years (mixed-to-temperate and pioneer-to-boreal) having opposing effects on conifers such as fir (*Abies balsamea*) and spruce (*Picea* spp.). Indeed, we found only modest changes for these taxa (+7% and +6% respectively), suggesting also that they have recovered from declines due to spruce budworm outbreaks that were detected for parts of Québec in data from ~20 years ago (Duchesne & Ouimet, 2008). A substantial increase in red maple (*Acer rubrum*, +30%) might be related to disturbance-induced transitions from mixed to temperate forests (Brice et al., 2020) or to a positive response to climate warming (Sittaro et al., 2017). While we detected significant changes in composition, and some significant changes in biodiversity, they are likely underlain by multiple causes and species-specific responses.

4.2 | Explaining diversity

We found a striking tendency for lower explanatory power of models predicting alpha diversity based on potential drivers at the plot scale than at coarser scales. This trend is consistent with studies

predicting spatial variation in species diversity that found stronger diversity–environment relationships at larger versus smaller scales (e.g. Field et al., 2009). Lower explanatory power at the plot scale may have occurred because stochastic community processes are expected to be most important in small areas (Vellend, 2016), or because important drivers (e.g. edaphic factors) were not included in the model. Unfortunately, we could not include edaphic variables as these data were not available for all forest plots. Higher explanatory power at coarser spatial scales may have occurred if some stochastic plot-to-plot variation in diversity change, or uncertainty in the estimation of environmental conditions, averaged out at the coarser scales.

Although we predicted that increases in temperature would lead to increased alpha diversity; different indicators of temperature did not all show the same results (Figure S5). Increases in the average daily minimum temperature and growing season temperature may have provided opportunities for some species to extend their ranges further north (Boisvert-Marsh et al., 2014; Sittaro et al., 2017), although microclimate conditions may also influence recruitment and community dynamics (Zellweger et al., 2020). Since tree diversity exhibits a strong latitudinal gradient (Brown & Lomolino, 1998) diversity in these northern forests is likely to increase with species migrations towards the poles (Berteaux et al., 2010). On the other hand, increases in the average daily maximum temperature led to declines in diversity. Increasing the maximum temperature may have induced water stress, leading to declines in some species (Peng et al., 2011). In line with this perspective, diversity change at the 100 and 200 km scales was more often positively associated than negatively associated with increases in the precipitation.

Our results indicate that disturbance was associated with declines in alpha diversity at the plot scale, but with increases in alpha diversity at broader spatial scales, possibly due to increases in landscape heterogeneity (as described above). At the plot scale, results were consistent with our hypothesis that the effects of disturbance would be greater than the impacts of climate change (Figure S5). Taken together, these results imply that the substantial impacts from harvesting, and especially from wildfire, are mediated by spatial scale.

4.3 | Accounting for land cover change

Our results about alpha diversity change appear robust after accounting for the potential impacts on biodiversity from land cover change. A pertinent critique of previous meta analyses using repeated measures (Dornelas et al., 2014; Vellend et al., 2013) was that the study sites may be biased towards places that have not experienced land cover change (Gonzalez et al., 2016). Our modelled scenarios of impact showed that the scenarios in which the mean alpha diversity change was negative (i.e. when >80%–90% of the individual trees were destroyed) are extremely unlikely in Québec, because 98% of disturbances in Québec forests in recent decades have been temporary land cover changes due to forest fires or forest harvesting

(White et al., 2017). Forests can often recover from harvesting that affects 80% of the area over a period of 10 years, and from complete harvesting over 25–30 years (Reich et al., 2001; White et al., 2017). Since disturbances occurred continuously over the ~35 year study duration, we would expect disturbed forest plots to be in a range of recovery stages during the second sampling period, suggesting that simulations destroying >80% or >90% of individuals are likely to be unrealistic. Overall, estimates of diversity change from our scenario analyses indicate that our qualitative conclusions appear robust.

Our approach, which combines plot measurements with satellite-based land cover data, might be useful for future biodiversity change studies since it bridges the gap between the repeated measurements approach—which adequately characterizes changes in time, but deals imperfectly with space (e.g. Dornelas et al., 2014; Vellend et al., 2013) and the space-for-time substitution approach—which adequately characterizes changes across space, but deals imperfectly with time (e.g. Newbold et al., 2015). In our study system, the estimated changes in alpha diversity showed a strong nonlinear response with the percentage of trees removed (i.e. declined sharply once >90% destroyed; Figure 6), likely due to the spatial patterns of disturbance and to the distribution of species abundances within the forest plots. In our study region, most disturbances occurred in the northern regions of the province (Figure 2), which are regions that generally have relatively low species richness and are dominated by a few species (e.g. black spruce and balsam fir). Therefore, although the simulated disturbances in these low-diversity regions often caused substantial tree mortality, these disturbances did not result in overall declines in diversity unless almost all individual trees were removed. In regions of the world where there are high rates of permanent land use change (i.e. from forest to non-forest) and where there is greater evenness among species abundances, incorporating the direct effects of land use change into estimates of local diversity change is likely to show more substantial impacts on diversity (e.g. Newbold et al., 2020).

4.4 | Implications

Although global scale species richness is clearly declining (Ceballos et al., 2015; Dirzo et al., 2014), we found either no significant net change or a positive change in tree diversity in Québec forests across all levels, dimensions and metrics of diversity at all spatial scales using a repeated-measures approach. Even after accounting for the impacts of land cover change, a decline in alpha diversity is extremely unlikely. The subtle differences between different measurements of diversity, and the fact that different researchers are using different measurements all under the umbrella of 'biodiversity', make it challenging to characterize and communicate the multi-level, multi-dimensional and multi-scale nature of biodiversity change in the Anthropocene. Our results support recent calls for a communication shift from a blanket description of global 'biodiversity loss' to more nuanced discussions around 'biodiversity change' (Blowes et al., 2019; Dornelas et al., 2014). In many regions of the

world and especially in northern forests, this shift to 'biodiversity change' is critical since our results did not show declines in biodiversity, but did show variations in the magnitude and direction of change across different measurements of diversity. Measuring diversity across multiple levels, dimensions, metrics and spatial scales is integral to provide a more holistic understanding of the status of biodiversity in our rapidly changing world.

AUTHORS' CONTRIBUTIONS

E.T.H.C., M.V. and E.M.B. developed the research idea and designed the study methodology; E.T.H.C. analysed the data and led the writing of the manuscript. All authors critically reviewed the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

This project used publicly available data to run the analyses. Data for the forest inventory plots and land designations can be obtained from: <https://www.donneesquebec.ca/recherche/fr/dataset/places-echantillons-temporaires-4e-inventaire-2004-a-aujourd-hui> and: <https://www.donneesquebec.ca/recherche/dataset/couch-e-des-territoires-recreatifs-du-quebec-a-l-echelle-de-1-100-000>. Climate data can be obtained from: https://doi.org/10.26050/WDCC/CCH_3876085. R code to run the analyses can be found on the Zenodo repository <https://doi.org/10.5281/zenodo.6636582> (Crockett, 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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