



## RESEARCH PAPER

Global Ecology  
and BiogeographyA Journal of  
Macroecology

WILEY

# Changes in landscape-scale tree biodiversity in the north-eastern USA since European settlement

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**Funding information**

Support was provided by the Natural Sciences and Engineering Research Council of Canada and the U.S. National Science Foundation's Long Term Ecological Research program (DEB-1832210).

**Editor:** Allen Hurlbert

**Abstract**

**Aim:** Despite global biodiversity losses, trends at local and regional scales are context dependent. Recent studies have been criticized for lacking baselines preceding human impacts, and few such studies have addressed the landscape scale. Our aim was to quantify temporal trends in landscape-scale tree diversity during an unambiguous period of massively increased anthropogenic disturbance and to test the hypothesis that land use can increase landscape-scale diversity via increased environmental heterogeneity.

**Location:** Eastern USA.

**Time period:** 1620–2008.

**Major taxa studied:** Trees.

**Methods:** We combined data from archival land surveys and modern-day forest inventories in the north-eastern USA to quantify tree genus diversity at the scale of towns ("landscapes"). We modelled change in diversity over time as a function of the proportion of the landscape historically converted to agriculture, historical temperature increases and nitrogen deposition, and other abiotic and spatial variables. We also tested for scale-dependent changes in beta diversity.

**Results:** Overall, tree genus diversity (Shannon and Simpson indices) changed minimally over time on average, but the magnitude of change increased with the maximum historical percentage of the town in agriculture. Other predictor variables had minimal influence. Beta diversity increased over time for nearby pairs of towns and decreased over time for more distant towns.

**Main conclusions:** Forests have regrown on much former agricultural land, and our results support the hypothesis that increased landscape-scale environmental heterogeneity, attributable to land use, increased tree diversity. Where agricultural land use was uncommon, declines in diversity might be attributable to effects of logging and fire suppression. Even the strongest driver of biodiversity loss at local and global scales (human land use) can lead to increases in biodiversity at the landscape scale, in addition to scale dependence of biotic differentiation versus homogenization.

**KEYWORDS**

beta diversity, biodiversity change, forests, land use, scale dependence

## 1 | INTRODUCTION

Human activities have had a profound impact on the biota of the Earth, most notably via an elevated rate of extinction of species at the global scale (Barnosky et al., 2011). The consequent global net loss of species in recent centuries for some taxa (vertebrates especially) has inspired a massive literature on the causes and consequences of “biodiversity loss” (Cardinale et al., 2012; Perrings et al., 1997). However, at sub-global scales, immigration of new species can match or exceed local or regional extirpations, resulting in negative, flat or positive biodiversity trends, depending on the spatial scale, time window, taxon or causal influences under study (Blowes et al., 2019; Dornelas et al., 2014; Sax & Gaines, 2003; Vellend et al., 2013; Vellend, Baeten, et al., 2017; Vellend, Dornelas, et al., 2017). This realization has led to a shift in focus to “biodiversity change” (i.e., not only loss) and to studies of the circumstances under which different temporal trends might be expected (Blowes et al., 2019; Chase et al., 2019; McGill et al., 2015; Pereira et al., 2012).

Human land use (the conversion of “natural” habitats to human use) is thought to be the leading driver of recent and contemporary biodiversity change (Pereira et al., 2012). At the global scale, many extinctions have been linked to such habitat conversion, and at the local scale (e.g., a 100 m<sup>2</sup> plot or a 1 ha field) conversion of natural vegetation to intensive agriculture most often leads to biodiversity loss (Newbold et al., 2015). However, at landscape or regional spatial scales (e.g., tens to thousands of square kilometres), land use can increase the heterogeneity of environmental conditions experienced by plants and animals, thus potentially favouring an increase in diversity (Desrochers et al., 2011; McGill et al., 2015). However, there are few studies quantifying landscape-scale changes in diversity over time (Danneyrolles et al., 2021; McGill et al., 2015; Vellend, Baeten, et al., 2017).

Few explicit biodiversity monitoring studies allow quantification of changes over time periods of decades or centuries. As such, recent meta-analyses of local-scale biodiversity change have relied either on space-for-time substitutions, in which one must assume that a difference in land use between two sites is not confounded by other environmental differences (e.g., Newbold et al., 2015), or on many relatively short time series (e.g., 5–30 years long; Dornelas et al., 2014; Vellend et al., 2013), which have been criticized for possibly missing important anthropogenic influences (Cardinale et al., 2018; Gonzalez et al., 2016). To overcome these limitations, at least in part, Funderup Nielsen et al. (2019) recently compiled plant inventories for 14 Danish regions covering a 140-year period during which agriculture was intensified; they found substantial within-region increases in species richness, in addition to homogenization of species composition (decreased beta diversity) across regions. However, even in that study the “baseline” (the mid to late 1800s) involved landscapes already converted largely to agriculture. Using data from early French surveyors and modern forest inventories in Québec, Canada, Danneyrolles et al. (2021) showed increased local diversity and decreased beta diversity, although they did not examine the distance dependence of changes in beta diversity.

In what is now the eastern USA, starting in the 1600s, early European surveyors recorded the identity of one or more “witness” trees at points used to demark property boundaries. Dozens of such points were spread across a landscape, and researchers have used these data to reconstruct pre-settlement forest composition (e.g., Thompson et al., 2013). Modern data on forest trees from the U.S. forest inventory and analysis (FIA) program (Burrill et al., 2018) are collected in plots (each plot covers c. 675 m<sup>2</sup>), such that sampled trees are concentrated within (multiple) small areas rather than being more evenly spread across the landscape. Collectively, datasets of this nature permit robust comparisons of composition and diversity across time at the scale of towns (e.g., Thompson et al., 2013), but comparing the number of taxa observed (richness) is problematic given the sensitivity of richness to the observation of rarities.

Before the arrival of Europeans, native peoples certainly had an ecological impact via some land clearing, settlements and prescribed fire. The time of the early land surveys nonetheless demarcates an unambiguous transition from localized, low-intensity land use to widespread, high-intensity land use (Munoz et al., 2014; Southgate, 2019). In the north-eastern USA, agriculture reached its peak land coverage (> 50%) in the mid-19th century, after which farm abandonment led to widespread forest regrowth, such that > 80% of the landscape is now forested (Thompson et al., 2013). Fire suppression and insect pests have also contributed to forest compositional change in some parts of this region (Lovett et al., 2006; Nowacki & Abrams, 2008, 2015). A comparison of historical and contemporary forest surveys at the scale of towns across the entire north-east (from Pennsylvania to Maine) revealed increases in the relative representation of some taxa (e.g., maples), decreases in others (e.g., beech, oaks and chestnut), and an overall homogenization of species composition at the regional scale (Thompson et al., 2013). Land-use history (specifically, the maximum historical proportion of a township in agriculture) was the best predictor of compositional changes.

As with most other studies using pre-settlement survey data, the synthesis by Thompson et al. (2013) focused on changes in composition (i.e., the abundances of particular taxa in different places and at different times). Thus, despite intense interest in biodiversity per se as a potentially important determinant of ecosystem functioning (Cardinale et al., 2012), we do not know how indices of biodiversity (i.e., regardless of which particular taxa are present in a given place) have changed during this time frame. That said, combining these historical data with recent survey data comes with two limitations with respect to comparisons of biodiversity. First, taxonomic resolution in the historical data is at the genus level rather than the species level. Second, as mentioned already, although aggregations of point or plot observations at the scale of towns permit robust temporal comparisons for relatively common taxa, it is impossible to ensure equivalent sampling effort for capturing rare taxa, thus complicating the interpretation of any comparison of taxon richness across time. However, data across time periods can be made closely comparable taxonomically by aggregating data to the genus level, and resampling procedures (e.g., that fix richness values across time; see Materials and

Methods) can allow for robust comparisons to be made for abundance-based diversity indices, such as Shannon's or Simpson's (Magurran, 2013).

Here, we address two key gaps in current studies of biodiversity change during the Anthropocene: a paucity of landscape-scale analyses, and an unambiguous baseline preceding a major increase in land-use intensity. Using the data from Thompson et al. (2013), we report changes in tree genus diversity within and among 701 landscapes (towns) during the 300+ years since European settlement in north-eastern North America. Based on the hypothesis that land use increases environmental heterogeneity (Desrochers et al., 2011; McGill et al., 2015), we predicted overall increases in diversity, and a positive effect of the historical proportion of a landscape in agriculture on diversity change. We tested simultaneously for possible effects of climate warming and nitrogen (N) deposition, which, along with land use, are the clearest potential drivers of biodiversity to have changed directionally over this time period. With respect to land use, the hypothesis is that localized disturbances increase landscape-scale heterogeneity, such that different species thrive in different places. Consequent small-scale increases in beta diversity (compositional dissimilarity among localities with a landscape) should manifest as increased "alpha" diversity at the scale of the whole landscape. Thompson et al. (2013) already reported a region-wide decrease in beta diversity, which, combined with the land-use heterogeneity hypothesis, implies a possible threshold locality-to-locality distance below which beta diversity might have increased rather than decreased over time. Thus, we also characterize the relationship between geographical distance and compositional dissimilarity, testing for a possible switch from increased to decreased dissimilarity over time with increasing geographical distance.

## 2 | MATERIALS AND METHODS

### 2.1 | Tree survey data

Thompson et al. (2013) compiled witness-tree data (historical) and forest inventory and analysis (FIA) data from 2003–2008 (contemporary; Burrill et al., 2018) for 1,280 towns (average 179 km<sup>2</sup> per town) in the north-eastern USA, from Pennsylvania and New Jersey in the south to Maine in the north. Only trees > 12.5 cm diameter at breast height were retained in the FIA data, in order to minimize the effect of a historical bias towards larger trees. In order to select towns for quantitative comparisons across time, Thompson et al. (2013) used rarefaction-type analyses to determine the minimum sample of trees or plots required in order to capture taxonomic composition at the level of the town. This threshold was attained for both the historical and the contemporary data in 701 towns; here, we use the same subset of towns in our analyses. For each genus *k* (there were 25 genera) in each time period *i* and town *j*, relative abundance ( $p_{ijk}$ ) was calculated as a proportion of the total number of trees. For our analyses, we used the exact same dataset, which is available in the Harvard Forest Data Archive (dataset HF210).

To quantify tree diversity within each town and time period, we calculated Shannon diversity and Simpson diversity, which increase as a function of both richness and evenness across taxa. To facilitate interpretation of differences, we converted these to Hill numbers (Chao et al., 2014): for Shannon diversity,  $D_{ij} = \exp[-\sum(p_{ijk} \times \ln(p_{ijk}))]$ , and for Simpson diversity,  $S_{ij} = 1/\sum(p_{ijk}^2)$ , in which the sums are across taxa with non-zero abundance. Compositional dissimilarity between all pairs of towns was quantified using the Bray–Curtis dissimilarity index as calculated using the *vegdist* function in the *vegan* package for R (Oksanen et al., 2019).

In addition to calculating the Shannon and Simpson diversity indices using the raw data, we also recalculated these indices using two methods to account for differences in sampling intensity across time (for sampling differences, see Supporting Information Figure S1.1). First, we held taxon richness constant across time within towns, effectively isolating differences in evenness only. For a given town, the time period with the smaller number of species ( $S_{\min}$ ) was determined, and data were kept unchanged for this time period. In the other time period, the same number of species was selected by choosing the  $S_{\min}$  most abundant species, and diversity indices were calculated for this subset of species.

Second, we held the number of individuals sampled constant across time within towns. On average, there were more individual trees per town in the historical data (mean = 252, range 37–4,477) than in the contemporary data (mean = 157, range 41–661; mean number of FIA plots = 4.7, range 2–20). For a given town, the period with the smaller number of trees sampled was determined ( $N_{\min}$ ), and data were kept unchanged for this time period. In the other time period, we resampled (with replacement) the same number of trees from the relative abundance distribution. This was repeated 1,000 times, and the average values of diversity indices were retained for analysis. In this latter analysis controlling the number of individuals sampled, we also calculated taxon richness, although we interpret the results cautiously, for reasons described already.

### 2.2 | Predictors of diversity change

We modelled the difference in Hill-number diversity indices between the two time periods (calculated all three ways) using several predictor variables. (Henceforth, we will refer to the diversity indices without the "Hill-number" qualifier.) Our main hypothesis focused on the consequences of land-use history, which is best captured by the maximum historical proportion of a given town under agriculture (Thompson et al., 2013). With the dual aims of assessing the influence of variables that (a) might be confounded with maximum historical agriculture, or (b) might explain substantial variation in diversity change, we also included several potentially important covariates (described in section 2.3), in addition to variables representing two other potentially important drivers of biotic change in the region: climate warming and N deposition. Given the dominant signal of land-use effects on changes in tree composition in this and nearby regions (Danneyrolles et al., 2019; Thompson et al., 2013) and the fact that

most regional warming has occurred in recent decades (NOAA, 2016) (a short period relative to the life spans of trees), we did not expect detectable effects of these two variables. However, they could not be excluded a priori. Any effect of warming was predicted to be positive, given clear positive spatial relationships between temperature-related variables and tree diversity (Currie, 1991); any effect of N deposition is more likely to be negative (Bobbink et al., 2010; Simkin et al., 2016). For warming, we used estimates of the magnitude of temperature change from 1901–2015 at the scale of climate divisions in the USA (NOAA, 2016). For N deposition, we used estimates of cumulative N deposition for the period 1850–1984 on a 1.9° latitude × 2.5° longitude grid [data from Lamarque et al. (2013), processed into a shapefile by Simkin et al. (2016) and provided to us by Samuel Simkin, personal communication].

### 2.3 | Analyses

For changes in alpha diversity, we first conducted Student's paired *t* tests for the two diversity indices. We then ran linear mixed models with either the difference in Shannon diversity or the difference in Simpson diversity as response variables. As predictor variables, we included the maximum historical proportion of the landscape in agriculture, and the climate-warming and N-deposition variables (with climate and N values for a given town estimated from interpolated maps; see Supporting Information Appendix S1). We also included three important covariables: the cumulative yearly growing degree days, the area of a given township (range 47–990 km<sup>2</sup>), and the first axis of a principal components analysis of five abiotic environment variables [proportions of clay and sand in the soil, soil pH, elevation and landscape ruggedness; see Thompson et al. (2013) and Supporting Information Appendix S1]. Finally, we included ecoregion as a random factor, and spatial autocorrelation within ecoregions was taken into account using the *nlme* package and its *corExp* function by incorporating an exponential spatial correlation structure, which accounts for the dependency between nearby observations, thus avoiding spatial pseudoreplication (Pinheiro et al., 2016). These analyses were conducted for each of the three methods used to compute the diversity indices: using the raw data, holding taxon richness constant, and the holding the number of individuals constant. The choice of covariates was guided by knowledge of common predictors of biodiversity (e.g., area, climate) and by the best predictors of compositional changes reported by Thompson et al. (2013) (e.g., maximum historical agriculture rather than the year of maximum historical agriculture).

For beta diversity, we plotted Bray–Curtis dissimilarity versus the geographical distance between pairs of towns and explored the shape of these relationships for the two time periods using locally weighted regression and smoothing (function *loess* in the *stats* package in R). We obtained confidence intervals for each curve using nonparametric bootstrapping. Each dataset was resampled 500 times, each time using 50,000 of the possible 245,350 dissimilarity values (subsampling was used to reduce computation time). Using

the same bootstrap samples, we calculated the difference between the curves to obtain a bootstrapped confidence interval on the difference between the two time periods (Crainiceanu et al., 2012). This analysis was conducted using only the raw data and the data corrected for taxon richness, but not using the resampling procedure corrected for the number of trees. When resampling individuals, one expects systematically lower diversity than in the full sample (see Results), but the average species abundance vectors (which could be used to calculate dissimilarity) will converge on the originals and thus do not form a valid basis for subsequent analysis. The computation time for recalculating 245,350 dissimilarity values 1,000 times, each involving a subsequent bootstrapping of 500 samples to generate confidence intervals, was deemed excessive.

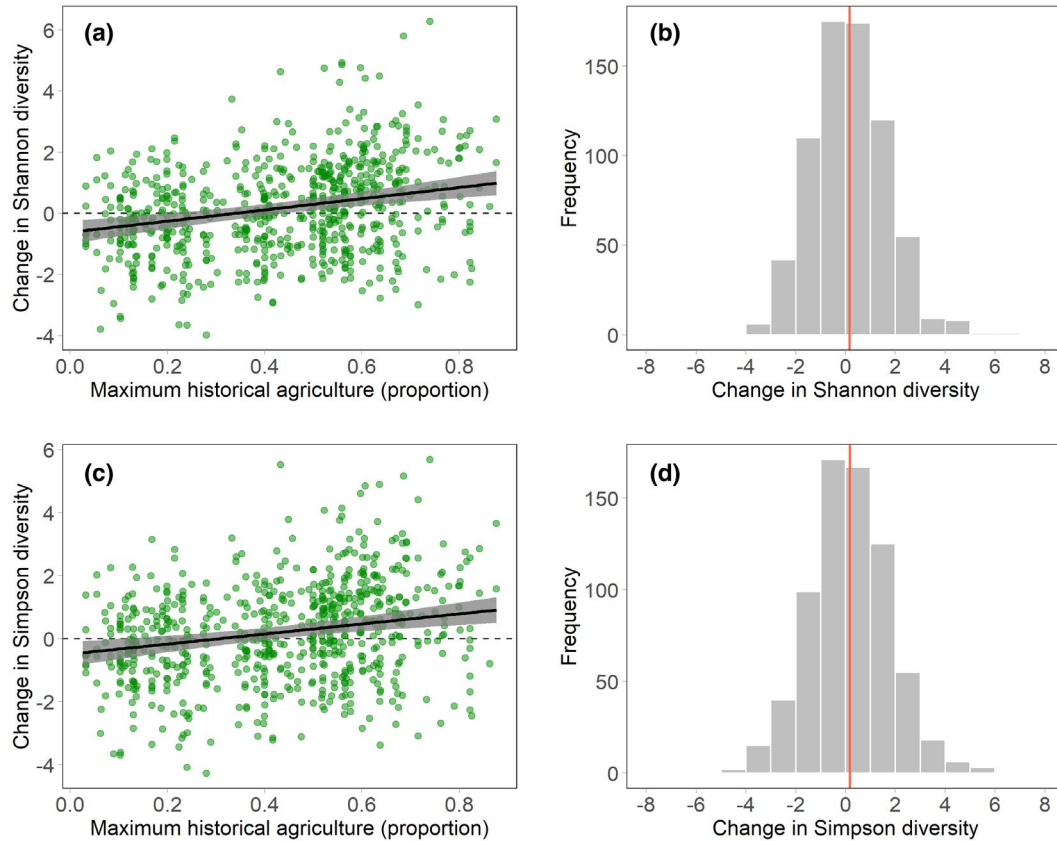
## 3 | RESULTS

Average changes in diversity over time were not consistent across methods of calculating diversity indices (see next paragraph), but all three methods yielded essentially identical results with respect to the relationships between diversity change and the maximum historical proportion of the landscape in agriculture, and between dissimilarity and geographical distance. In the main text, we present graphs based on diversity indices calculated while holding richness constant across time, with other results reported in the Supporting Information Appendices S1 and S2.

Differences in diversity across time were correlated strongly between the two indices ( $r > .95$  for all three methods). Although results of Student's paired *t* tests were not consistent across methods of calculating diversity indices, in all cases average differences were small in magnitude relative to standard deviations. After correcting for richness, there was a significant increase over time for both Shannon diversity (historical, 5.23; contemporary, 5.38;  $t = -2.74$ ,  $p = .006$ ; Figure 1b) and Simpson diversity (historical, 4.11; contemporary, 4.29;  $t = -3.04$ ,  $p = .002$ ; Figure 1d). In contrast, the raw data showed a significant decline in Shannon diversity over time (historical, 5.82; contemporary, 5.50;  $t = 4.03$ ,  $p < .001$ ) and no significant change in Simpson diversity (historical, 4.38; contemporary, 4.35;  $t = 0.48$ ,  $p = .63$ ; Supporting Information Figure S2.1). After controlling for the number of individuals, Shannon diversity showed a significant decline over time (historical, 5.63; contemporary, 5.38;  $t = 3.32$ ,  $p < .001$ ); there was no difference for Simpson diversity (historical, 4.32; contemporary, 4.28;  $t = 0.47$ ,  $p = .64$ ), and taxon richness showed a significant decline (historical, 9.83; contemporary, 8.61;  $t = 12.9$ ,  $p < .001$ ; Supporting Information Figure S2.2).

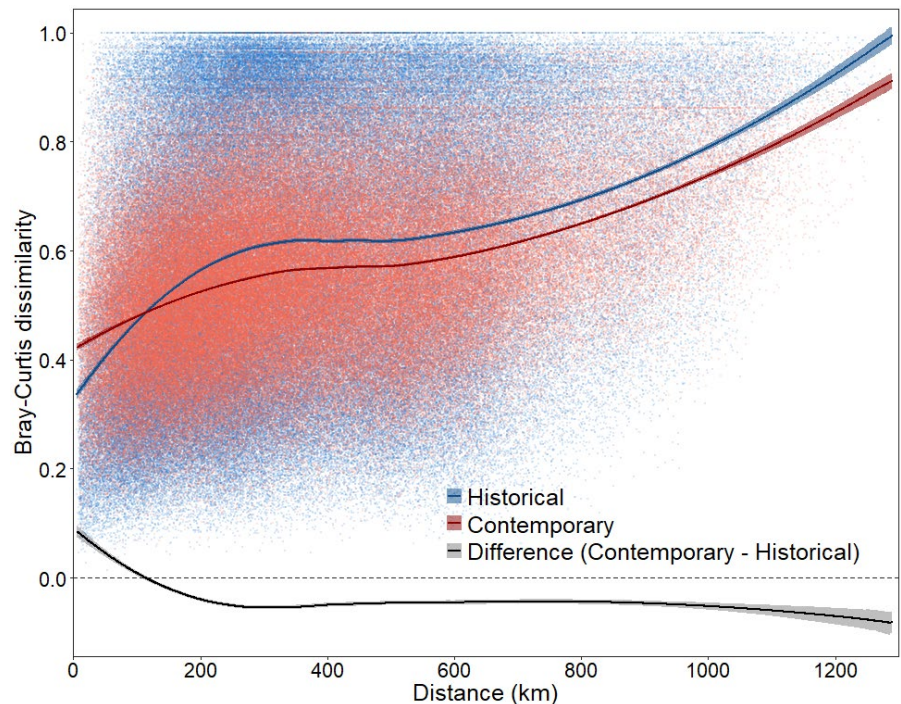
For both diversity indices, regardless of calculation methods, the strongest effects were for the maximum historical proportion of the landscape in agriculture (positive effect; see Figure 1a,c; Supporting Information Figures S2.1 and S2.2) and the area of the town (positive effect; Supporting Information Tables S2.1–S2.3). This was also true for taxon richness when controlling for the number of individuals (Supporting Information Table S2.3; Figure S2.2). The effects of the environmental principal components analysis axis (negative) and





**FIGURE 1** Changes in diversity indices between historical and contemporary time periods, with diversity indices calculated after fixing taxon richness as constant over time within towns. (a,c) The relationship between changes in Shannon diversity (a) or Simpson diversity (b) and the maximum historical proportion of the town in agriculture. (b,d) Histograms for Shannon diversity (b) and Simpson diversity (d), with vertical red lines showing the mean change over time. The black lines show the slopes of the linear relationships; the 95% confidence intervals around predictions are shown in grey. Changes in diversity were modelled using linear mixed-effect models, with ecoregion as a random effect and a spatial correlation structure (see main text). Diversity indices were expressed as Hill numbers

**FIGURE 2** The relationship between geographical distance and Bray–Curtis dissimilarity in composition (calculated after fixing taxon richness as constant over time within towns) in both the historical (blue) and the contemporary (red) time periods. Each data point is for a pair of towns in a given time period. Locally weighted polynomial regression was used for each time period separately. Confidence intervals were estimated by nonparametric bootstrapping. The difference between the historical and contemporary curve and its associated confidence interval (using the bootstrap replicates) is shown in grey



growing degree days (positive) were significant in some but not all models; in no cases did the warming or N-deposition variables have significant effects (Supporting Information Tables S2.1–S2.3).

Bray–Curtis dissimilarity increased with geographical distance for both time periods (Figure 2). For nearby towns (< c. 125 km apart), dissimilarity was greater in the contemporary than the historical dataset, whereas the opposite was true for towns further apart (Figure 2). The same pattern held whether fixing richness constant across time (Figure 2) or using the raw data (Supporting Information Figure S2.3).

## 4 | DISCUSSION

This study represents a novel contribution to ongoing debates about biodiversity change (Blowes et al., 2019; Cardinale et al., 2018; Gonzalez et al., 2016; Primack et al., 2018; Vellend, Dornelas, et al., 2017) via the use of a dataset with a baseline that captures conditions preceding especially intense human impacts unambiguously, in addition to having a larger spatial grain than most previous studies (i.e., entire towns rather than study plots). Under the hypothesis that land-use history has increased environmental heterogeneity (specifically, spatial variation in past disturbance intensity and timing), we predicted: (a) an overall increase in landscape-scale tree diversity, and (b) a positive effect of the extent of historical agricultural land use on diversity change. The results did not support the first prediction, with small average declines, increases or no significant change in diversity, depending on the index of diversity or method of calculation. Either our hypothesis linking land use to heterogeneity and diversity is false, or additional processes counter the hypothesized positive effects, as discussed further in subsequent paragraphs. Regardless, our observed distributions of diversity change centred close to zero (Figure 1b,d) are consistent with meta-analyses of biodiversity time series reporting mean trends either indistinguishable from zero (Blowes et al., 2019; Dornelas et al., 2014; Vellend et al., 2013) or only weakly non-zero relative to variation among studies (e.g., positive in the case of Elahi et al., 2015).

Our results supported the second prediction, with a positive effect of the maximum historical coverage of agricultural land on diversity change (Figure 1a,c). Although it is difficult to pinpoint precise underlying mechanisms, these results nonetheless suggest that extensive human disturbance followed by forest recovery can increase landscape-scale diversity. At higher values of historical agricultural land coverage, the predicted diversity change was positive (Figure 1a,c), similar to the overall increase in landscape-scale tree diversity observed over the past c. 200 years in nearby Québec, Canada (Danneyrolles et al., 2021). More surprising was negative predicted diversity change at low values of historical agricultural land coverage (Figure 1a,c). Taken together, these results suggest that there is one or more factors causing diversity to decline, which is countered by positive effects of more extensive land use (perhaps via heterogeneity). Our interpretation of the results in Figure 1, speculative but informed, is as follows. Across much of this region, clearing

of old-growth forests via agriculture and logging, with subsequent succession, has favoured increased dominance by maples (*Acer* spp.; see Thompson et al., 2013); increased dominance depresses diversity. [Note that even in landscapes with little agriculture, most forests have been logged historically and impacted by pathogens, such as beech bark disease. Fire suppression might also contribute to a decrease in tree diversity in some parts of the study region (Nowacki & Abrams, 2008, 2015).] At the same time, different specific forms of agriculture (e.g., crop versus pasture) and spatial variation in the timing of succession should increase locality-to-locality variation in species composition, and therefore landscape-scale diversity. These opposing forces could result in minimal diversity change, on average (Figure 1b,d), and a positive effect of the extent of past agricultural land use (Figure 1a,c).

The hypothesis linking land use to heterogeneity and diversity essentially invokes increased within-landscape beta diversity to explain increased landscape-scale “alpha” diversity. Consistent with this idea, we found that nearby towns are now more dissimilar in composition (increased beta diversity) than they were before European settlement, whereas more distant towns (anything beyond c. 125 km) are now more similar in composition (Figure 2). The latter is often referred to as “biotic homogenization” (Baiser et al., 2012; FINDERUP NIELSEN ET AL., 2019), and our results point to a clear scale dependence of biotic homogenization versus differentiation. As reported previously (Thompson et al., 2013), there has been, on average, biotic homogenization across the north-eastern USA, as there has been across other regions (Baiser et al., 2012; Danneyrolles et al., 2021; Vellend, Baeten, et al., 2017). However, at smaller scales the opposite is true. We have indirect support for locality-to-locality biotic differentiation within landscapes, and direct evidence of differentiation between nearby landscapes, at the same time as we see biotic homogenization at larger scales. As with so many other topics in ecology, scale seems to be a crucial component of context when evaluating whether human activities have caused biotic homogenization versus differentiation. Human activities might represent a homogenizing force in general at some scales (large), but the opposite at other scales (small).

At least two features of our study are relevant to evaluating the potential generality of conclusions. First, the data focus only on forests and only on the trees in those forests. Crop fields, pastures and urban areas are important landscape elements both historically and at present, and herbaceous plants contribute most of the regional plant diversity. Crop fields and, to a lesser degree, pastures involve the elimination of trees, and therefore almost certainly led to loss of tree diversity at the local scale (e.g., typical plots of c. 100–1,000 m<sup>2</sup>). However, in all but a few landscapes forest cover has been ≥ 20% throughout the entire study duration; therefore, there is no a priori reason to expect consequent loss at the landscape scale. In a study of birds in southern Ontario, Canada, maximum species richness was observed at an intermediate proportion of natural land cover; there was very little trend between 20 and 80% natural land cover, but a c. 20% decrease in richness when natural land cover decreased to 0% or increased to 100% (Desrochers et al., 2011). For

herbaceous plants across both forest and non-forest habitats, one might expect even stronger effects of land use on heterogeneity seen from a “plants-eye view”, given strongly contrasting conditions in forests versus fields. In other words, one might expect a stronger positive effect of land use on landscape-scale plant diversity in a study including all types of land cover and plant species. The observed increase in total plant diversity within regions of Denmark over the past 140 years is consistent with this idea (Finderup Nielsen et al., 2019).

The second notable feature of our study is the massive increase in forest cover since the mid-19th century in this region, which contrasts with many other regions where forest cover has seen a net decline (Hansen et al., 2013). It is possible that without this recovery phase, forest tree diversity would have seen more pronounced declines in this region. That said, in many parts of the globe disturbances in mature forests create landscapes with an increasingly heterogeneous mix of past disturbance regimens and successional stages (Southgate, 2019), such that the hypothesis linking land use to heterogeneity and diversity at the landscape scale might be relevant in many different places. If human disturbance were to stop, the increased heterogeneity might be ephemeral (albeit long lasting given the longevity of trees), and future consequences of disturbances (or lack thereof) will depend on whether those disturbances continue to create environmental heterogeneity. Other forms of disturbance (e.g., strip mines) might create environmental heterogeneity, but not in a way that enhances diversity if disturbed sites support little life at all. Overall, although we can draw confident conclusions only about the region under study, there are indications that the underlying processes might apply more broadly. The effect of human land use on plant biodiversity is not universally negative, but instead it is highly context dependent and, possibly, positive in general at the landscape scale when it leads to increased environmental heterogeneity as perceived by the organisms that live there.

## ACKNOWLEDGMENTS

Estimates of N deposition were obtained via S. Simkin, E. Allen, C. Clark and W. Bowman's Working Group: United States Geological Survey Powell Center Working Group on Diversity and N Deposition. Constructive feedback from M.V.'s laboratory group, two anonymous reviewers and Allen Hurlbert helped to improve the manuscript.

## DATA AVAILABILITY STATEMENT

The original forest dataset HF210 is in the Harvard Forest Data Archive: <https://harvardforest.fas.harvard.edu/harvard-forest-data-archive>. All data and code are available at: [https://github.com/mvellend/WT\\_FIA\\_TreeDiv](https://github.com/mvellend/WT_FIA_TreeDiv)

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## BIOSKETCH

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## SUPPORTING INFORMATION

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

**How to cite this article:** Vellend M, Thompson JR, Danneyrolles V, Rousseu F. Changes in landscape-scale tree biodiversity in the north-eastern USA since European settlement. *Global Ecol Biogeogr*. 2020;00:1–8. <https://doi.org/10.1111/geb.13248>