



Converging forest community composition along an edaphic gradient threatens landscape-level diversity

Kathryn L. Amatangelo^{1*}, Mark R. Fulton², David A. Rogers³ and Donald M. Waller¹

¹Botany Department, University of Wisconsin - Madison, 430 Lincoln Drive, Madison, WI 53706, USA, ²Biology Department, Bemidji State University, 1500 Birchmont Drive NE, Bemidji, MN 56601-2699, USA, ³Biological Sciences Department, University of Wisconsin - Parkside, 900 Wood Road, Kenosha, WI 53141-2000, USA

ABSTRACT

Aim Plant communities across the temperate zone are changing in response to successional processes and human-induced disturbances. Here, we assess how upland forest under- and overstorey community composition has changed along an edaphic gradient.

Location Northern Wisconsin, USA.

Methods Forest sites initially sampled in the 1950s were resampled for overstorey composition and diversity, basal area, and understorey composition and diversity. We used clustering methods to identify groups of stands based on overstorey composition, and we used similarity indices, ordination and diversity indices to evaluate changes in species abundance and overall community structure.

Results Sites clustered into four overstorey groups along the edaphic gradient: 'hemlock' sites dominated by hemlock in 1950, 'mesic' sites dominated by northern hardwoods, 'dry' sites with a significant pine inclusion in the canopy and diverse 'dry-mesic' sites in the middle. Collectively, forests gained maple, ash and cherry while losing pines, birches and red oaks. The hemlock forest sites gained hardwoods, while the dry-mesic sites shifted towards a more mesic hardwood composition. Only the driest sites have remained relatively stable in species composition.

Main conclusions These trends reflect both 'mesification' and homogenization among northern forests. Highly diverse mid-gradient and mesic hemlock-dominated stands are transitioning to maple dominance. Fire suppression may be favouring invasions of more mesic plants into historically drier sites, while high deer abundance likely limits hemlock regeneration. If current trends continue, maples will dominate the majority of northern forests, with significant losses of local native species richness and substantial shifts in understorey composition.

Keywords

Bray–Curtis ordination, fire suppression, homogenization, overstorey–understorey linkages, succession, Wisconsin forests.

*Correspondence: Kathryn L. Amatangelo, Department of Ecology and Evolutionary Biology, Brown University, Box G, Providence, RI 02912, USA.
E-mail: kamatang@gmail.com

INTRODUCTION

Human impacts can have lasting effects on landscape composition well after land-cover perturbations. Alterations of disturbance regimes in concert with habitat degradation can lead to a loss of ecosystem diversity. There is growing evidence for the homogenization of northern Great Lakes forests via conifer loss (Frelich & Lorimer, 1985; Rhemtulla *et al.*, 2007; Schulte *et al.*, 2007; Nowacki & Abrams, 2008). Northern

Wisconsin forests were historically dominated by conifer and mixed conifer-hardwood stands (Schulte *et al.*, 2007). Because of intense deforestation and resultant fires after Euro-American settlement, old growth forest types decreased in abundance and were replaced by early successional forest types (Rhemtulla *et al.*, 2007). In the 1950s, after major clear cutting and 50–90 years of subsequent regrowth, J.T. Curtis and colleagues at the University of Wisconsin Plant Ecology Lab (PEL) identified a continuum of Northern Wisconsin forest

types that had developed along edaphic and disturbance gradients (Stearns, 1949; Brown & Curtis, 1952; Curtis, 1959). Wet forests developed in low-lying areas, where high-moisture soils supported cedar and hemlock swamps. Upland soils with moderate moisture supply were dominated by mesic northern hardwoods with or without abundant hemlock. On the dry end of the gradient on well-drained outwash upland sands, pine-dominated forests with higher light availability occurred. Fire-dependent pines maintained dominance on sites experiencing regular fires (Mladenoff *et al.*, 2008).

As disturbance regimes shifted away from pre-Columbian ('natural') conditions, so did the factors limiting species distributions and thus the relation of community composition to edaphic gradients. Curtis (1959) postulated that in the absence of disturbance, uninterrupted succession in dry forests on sandy soil in northern Wisconsin would initially lead to white pines invading jack pine stands and eventually a 'climax' mesic maple-dominated forest. This successional sequence occurs as fire-sensitive, shade-tolerant species such as maples and basswood enter the system, setting up a positive feedback loop involving dense shade, higher humidity and highly decomposable foliage (Mladenoff, 1987). Over time, edaphic conditions also shift as soils retain more moisture and nutrients. This favours faster growing, light-competitive species, further favouring mesic, deciduous species. This process has been termed 'mesification' (Nowacki & Abrams, 2008; Rogers *et al.*, 2008). Its rate and the stability of any successional 'endpoint' could depend on initial community composition, local edaphic variables, and/or changing climatic conditions (Pastor & Post, 1988; Kucharik *et al.*, 2010). Such uninterrupted successional sequences were once rare in northern forests, reflecting recurring fire and climatic changes over millennia. However, since the 1920s, fire suppression coupled with recovery from intensive logging has tended to shift oak-pine stands towards more maples and other hardwoods across the Northeast (Nowacki & Abrams, 2008).

Successional processes also interact with human-induced disturbances at the mesic end of Curtis's (1959) upland continuum. Here, cooler, wetter forests composed of cedar (*Thuja occidentalis*) and hemlock (*Tsuga canadensis*) tend to dominate in the absence of large disturbances. In recent decades, however, overabundant deer have limited the regeneration of both cedar and hemlock, in combination with other factors (Anderson & Katz, 1993; Waller & Alverson, 1997; Rooney & Waller, 1998; Rooney *et al.*, 2000, 2002). In northern Wisconsin, deer densities and impacts have increased markedly over the last 40 years (Alverson & Waller, 1997; Rooney *et al.*, 2002, 2004b). Their selective browsing can alter successional trajectories, favouring maple- or cherry-dominated forests that can persist for long periods, especially in the absence of fire (Côté *et al.*, 2004). The second-growth hemlock stands typically found in northern Wisconsin are particularly vulnerable to browsing pressures because of a combination of regional factors that already limit regeneration, including limited seed sources and reductions in coarse woody debris (Mladenoff & Stearns, 1993).

As overstories homogenize across Wisconsin, understory communities traditionally associated with hemlock- or pine-dominated stands are also at risk. Small evergreen herbs and sub-shrubs that thrive in coniferous understories are often outcompeted by taller, deciduous herbs as growing conditions improve (Givnish, 1982). Northern Wisconsin forest understory communities have indeed experienced homogenization (Rooney *et al.*, 2004b) along with losses of palatable, biotically pollinated and dispersed herbs and growing graminoid dominance (Wiegmann & Waller, 2006). These changes probably reflect high deer abundance as well as earthworm invasions and landscape fragmentation (Rooney *et al.*, 2004b). The marked increase in graminoid species could reflect increased deer herbivory on palatable forb species and/or changing climatic conditions (Rooney & Waller, 2008; Rooney, 2009).

Most historical studies of long-term shifts in forest communities used witness trees from the mid-19th century. On such a long time scale, it is impossible to tease apart the effects of initial clearcuts and succession from modern factors such as invading species. Our resampling of the sites surveyed by J.T. Curtis and colleagues 50 years ago allows us to investigate more recent trends in northern forests. Here we examine 50-year shifts in the composition of forest canopies, how these vary along an edaphic gradient, and how these canopy shifts in turn influence changes observed in the understory. We specifically ask: are the magnitude and direction of shifts in overstorey community composition consistent along the edaphic gradient, or are drier sites less susceptible to change? How have canopy changes influenced the understory? If associations between over- and understory species are more tightly coupled towards the dry end of gradients (Michalet *et al.*, 2003), even small overstorey changes on dry sites could cause large changes in the understory. We also test whether the composition of the understory has shifted towards more deciduous species in response to reduced overstorey conifer abundance on both ends of the upland forest gradient.

METHODS

Data collection

In the late 1940s and early 1950s (1950 period), J.T. Curtis and colleagues sampled stands in northern Wisconsin (Brown & Curtis, 1952). They quantified canopy composition in each stand using the random pairs method (Cottam & Curtis, 1956) at a series of 40 points spaced 25 m from each other in a grid, for a total of 80 trees sampled per site. At alternating points (20 total), they delineated 1-m² quadrats noting each vascular plant species present. These data were converted to frequency based on the fraction of quadrats occupied.

Stands were relocated and resampled in 2000 and 2004 (Rooney *et al.*, 2004b; Wiegmann & Waller, 2006). Lacking permanent markers, exact 1950s quadrat locations could not be re-located. In 2000, 35 study stands were resampled using three 20 × 20 m plots spaced sequentially 20 m apart and at least 50 m from all edges. The diameter and identity of all trees

>2.5 cm DBH were noted across all three plots (1200 m² total). The understorey was sampled within 120 1-m² quadrats distributed along six 1 × 20 m strip transects located along the first and second sides of each plot, scoring the presence of all vascular plant species < 2.5 cm DBH. In 2004, 31 additional stands were relocated and resampled for both herbs and trees using Curtis' original method, for a total of 66 stands resampled (Fig. 1). We also resampled trees in 30 of the 35 sites sampled in 2000 using Curtis' original method.

We also collected soil samples from the top 10 cm of the A horizon at three locations within 62 of the 66 sites. These were pooled and sent to the University of Wisconsin Soil Analysis lab for analyses of nutrient content (N, P, Ca, Mg, Na and K), pH and texture (Soil and Forage Analysis Lab 2010). Texture analysis was performed using the hydrometer method (Bouyoucos, 1962). Soil pH was measured in a 1:1 soil:solution ratio using a pH meter. For those soils with a pH below 6.6, a Sikora buffer solution with a pH of 7.70 ± 0.01 was added and the Sikora-pH measured. To evaluate total nitrogen, soils were digested with sulphuric and salicylic acid followed by flow injection analysis. Available K, Ca, Na and Mg were extracted with ammonium acetate and analysed by atomic absorption. Plant-available soil P was extracted with sulphuric acid, and the concentration was determined colorimetrically after reaction with a sulphuric-molybdate. We assume that soil texture during the 2000 period sampling reflects 1950 period texture, but accept that community compositional shifts may have caused changes in other soil variables (Van Breeman & Finzi, 1998). Average climate data from 1961 to 1990 (New *et al.*, 2002) for Wisconsin were downloaded and interpolated using the Spline function in ARCGIS 9.1 to estimate mean annual temperature (°C) and growing season precipitation (mm). We

also downloaded potential evapotranspiration (PET) data from NNRI (White & Host, 2008). The distance between each site and the nearest open water feature (m) was calculated from Wisland data (see Rogers *et al.*, 2008 for methods on digitization of sites).

Data analysis

Analyses of the tree data were based on the random pairs data from the 61 sites at which it was collected in 2000 and 2004. Tree counts in the other five sites sampled using the three 20 × 20 m plots ranged from 56 to 116 versus the 79 to 81 trees measured using the random pairs method. Because of this difference in methods and potential biases with the random pairs method (Cottam & Curtis, 1956; Bryant *et al.*, 2004), we performed all overstorey analyses, except for *G*-tests that require count data, on relative basal area and relative density. Because identification techniques differed between periods, we synchronized taxonomy by combining all species in the red oak group (*Quercus rubra*, *velutina* and *ellipsoidalis*) and combined *Fraxinus pennsylvanica* with *F. americana*. We included all overstorey species present in at least two sites. To replicate the original intensity ($n = 20$) and dispersion of understorey quadrats sampled in the 1950 period, we sub-sampled every sixth quadrat from the 2000 period sampling data. These data were also taxonomically synchronized to ensure consistency in taxonomic names and identification quality (see Wiegmann & Waller, 2006). Taxa were only included if they had > 1% frequency throughout the entire study (i.e. were present in 26+ quadrats across both periods). We estimated understorey abundance as frequency of occurrence across quadrats.

Although Northwoods forest communities exist along a continuum, we clustered sites into groups based on initial overstorey composition in order to evaluate whether differing starting conditions led to alternate trajectories or magnitudes of change. Relative basal areas of the overstorey species were calculated and arcsine square root transformed to improve normality before clustering and ordinations. We used Ward's clustering for all 66 sites in 1950 (Ward, 1963; Mccune & Grace, 2002). Ward's clustering on 1950s tree data separated the 66 sites into four distinct groups that explained 50% of the overstorey variation – 14 mesic hemlock sites ('hemlock'), 16 mesic hardwood sites ('mesic'), 19 hardwood 'dry-mesic' sites, and 17 pine-hardwood 'dry' sites. We performed indicator species analysis on the groups using PC-ORD 5.0. We also corrected *P*-values using the false discovery rate (FDR) method owing to the large number of statistical tests (Waite & Campbell, 2006).

To identify significantly increasing or decreasing species within and across groups, we used single classification *G*-tests and replicated tests for goodness-of-fit (Sokal & Rohlf, 1995). The single-classification *G*-statistic tests for a change in a particular species at a given site. Replicated goodness-of-fit tests were applied to all sites at once for overstorey and understorey frequency data. The G_{total} statistic for a species tests for changes in frequency in either direction across all sites.

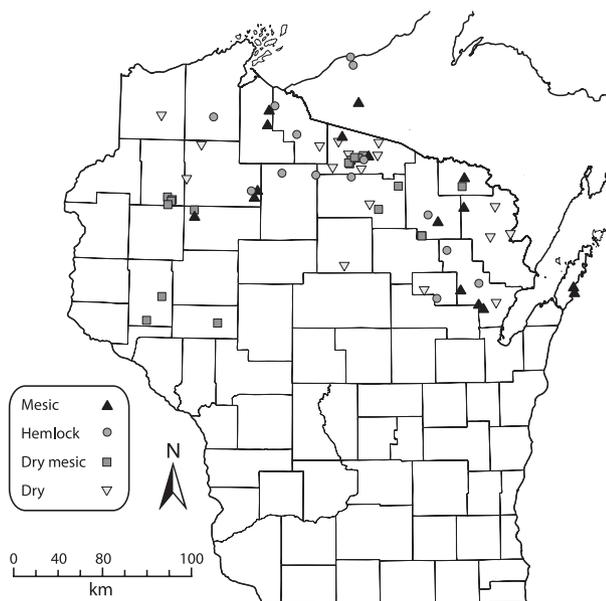


Figure 1 Locations of 66 forest stands sampled in both 1950 and 2000 time periods. Symbols indicate site groups determined by Ward's clustering of 1950 period overstorey relative basal area.

The G_{pooled} statistic combines data from all sites, testing for overall net increases or decreases in frequency. We classified overstorey species as ‘increasers’ or ‘decreasers’ if their changes were large enough and consistent enough to result in significant G_{total} and G_{pooled} test statistics (after the FDR P -value correction for multiple hypothesis tests). We then computed G_{het} values for these species among the four overstorey groups to determine whether groups were responding heterogeneously across the gradient. As our herbaceous ‘increasers’ and ‘decreasers’ generally matched those presented by Wiegmann & Waller (2006), we only discuss understorey species with a significant G_{het} among groups.

We compared understorey plant diversity within and among overstorey groups using the exponential of Shannon entropy ($\exp(H')$, Jost, 2006; Ellison, 2010). We calculated $\exp(H')$ for raw frequency data both for all sites combined and for each overstorey group, and used paired t -tests to test for significant changes across time. We also performed a mixed-model ANOVA on diversity values within understorey strata, with time period, overstorey groups and their interaction as fixed effects and site as a random effect. This allowed us to test for different diversity trajectories between overstorey groups.

We calculated matrices of Bray–Curtis similarities among sites using either transformed abundance (understorey) or relative basal area (overstorey) data. To evaluate changes in among-site similarity within groups, we also calculated Bray–Curtis site similarity values within each plant habit (shrubs, seedlings, herbs, and overstorey) for each period. We then used paired t -tests to test for changes between the two periods. Finally, we used Mantel tests to compute correlations between the similarity matrices for each of the four plant habits in order to evaluate connections between plant habits within and across forest types in each time period.

To visualize and quantify differences in overstorey and understorey composition among groups and time periods, we performed Bray–Curtis ordinations on all sites in both time periods in PC-ORD 5.0 using Sørensen distance measures and city-block axis projection geometry. Ordinations were performed on log-transformed abundances (herbs) or arcsine-square root transformed relative basal area (overstorey). We used Bray–Curtis ordination as it has been shown to effectively represent long gradients, particularly when the endpoints are chosen using the variance-regression method (Ward, 1963; Beals, 1984; Causton, 1988; Mccune & Grace, 2002). It is also insensitive to outliers. In our analyses, the first Bray–Curtis axis always captured the main mesic-dry gradient in the data. Unlike non-metric multidimensional scaling, Bray–Curtis ordination also provides a sequence of ordination axes in order of importance (rather than a configuration that may need to be rotated for interpretation), reducing uncertainty over the optimality of the solution. Finally, the ability to subjectively select axis endpoints makes it easy to examine specific hypotheses (Mccune & Grace, 2002), as described elsewhere.

We also sought to quantify relationships between environmental and biotic variables and these ordination descriptions

of the overstorey and herbaceous communities. We therefore first correlated individual environmental variables with the primary ordination axes. Because of the number of soil variables, we also used principal components analysis (PCA; performed in JMP 7.1 – SAS Institute, Cary, NC, USA) to analyse covariation among the log-transformed soil variables and to extract a primary axis to represent variation among the sites in soil conditions. This succeeded in reducing dimensionality as the first principal component axis (SoilPCA) explained 52.4% of the variation, and we correlated SoilPCA with the primary ordination axes. In addition to these analyses of the environmental variables, we also tested relationships between the over- and understorey by computing correlations between the first two overstorey Bray–Curtis axes (oBC1 and oBC2) and the axes obtained from the herbaceous ordination. To quantify shifts in the mean locations of overstorey and herbaceous communities within each forest-type group, we calculated mean change vectors for the sites within each group in ordination space. We then translated the 1950 endpoints to zero and calculated means and standard errors for each of these score changes.

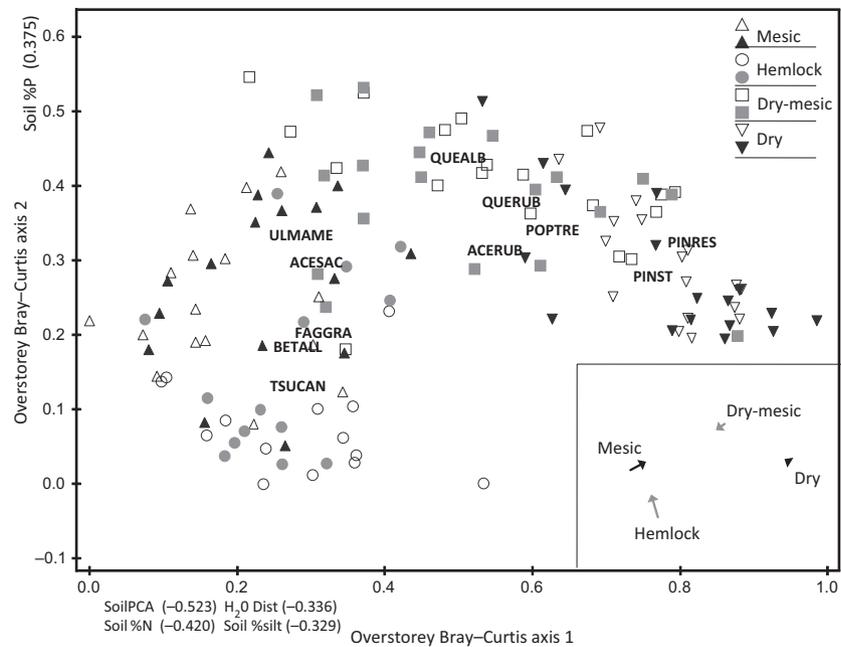
To further test the mesification hypothesis, we calculated changes in ordination axis scores between periods along the mesic-dry (axis 1) and hemlock-hardwood (axis 2) gradients. For data on each of the four plant habits (overstorey, seedlings, shrubs, herbs), we ran Bray–Curtis ordinations on 1950 period data. Using the first axis endpoints from these ordinations (thus defining the main gradient in terms of the 1950 data), we performed an ordination of the data from both time periods, allowing us to calculate changes in ordination scores over time. Changes in axis scores over time were plotted against 1950 scores with calculated regression lines. We selected quadratic models of change when the chi-square term was significant.

RESULTS

The Wards grouping and indicator species analyses revealed four clusters of stands with distinct overstorey composition, explaining 49% of the variation in composition. The hemlock forest group was characterized by abundant *Betula alleghaniensis*, *Thuja occidentalis* and *Tsuga canadensis*. In contrast, forests in the mesic group were dominated by *Acer saccharum*, with *Fagus grandifolia*, *Tilia americana*, *Ostrya virginiana*, *Fraxinus americana/pennsylvanica*, *Ulmus americana* and *Ulmus rubra*. Indicators for the dry-mesic group included *Acer rubrum*, *Betula papyrifera*, *Populus tremuloides*, *Populus grandifolia*, *Quercus alba*, *Quercus macrocarpa* and the red oak group. Lastly, the group of dry sites reflected pine dominance by *Pinus resinosa*, *Pinus banksiana* and *Pinus strobus*.

The Bray–Curtis ordination of the overstorey showed a continuum of forest sites along axis 1, with dry sites clustered closely together at high values of axis 1 (Fig. 2). Variability along axis 2 distinguished the coniferous ‘hemlock’ from elm/maple hardwood ‘mesic’ forests (high on axis 2). Hemlock forests generally shifted away from hemlock domination,

Figure 2 Bray–Curtis ordination of 66 sites at two time periods based on relative basal area of 28 overstorey species. Drier sites increase along axis 1. Centroids of representative species are indicated by six-letter codes: TSUCAN, *Tsuga canadensis*; BETALL, *Betula alleghaniensis*; FAGGRA, *Fagus grandifolia*; ACESAC, *Acer saccharum*; ULMAME, *Ulmus americana*; QUEALB, *Quercus alba*; QUERUB, *Quercus rubra/ellipsoidalis/velutina*; ACERUB, *Acer rubrum*; POPTRE, *Populus tremuloides*; PINRES, *Pinus resinosa*; PINST, *Pinus strobus*. Correlations of environmental variables with $r > 0.300$ indicated next to axes. Outline shapes are site locations in the 1950 period, filled in shapes are from the 2000 period. Inset: Mean vectors of change of sites within each group.



plotting closer to hardwood-dominated mesic sites in 2000 than in 1950 in ordination space (Fig. 2 inset).

Few individual environmental variables were correlated with these community ordination axes. Soil silt, soil N, and distance to nearest open water all declined along overstorey Bray–Curtis axis 1 ($r = -0.329$, $r = -0.420$, $r = -0.336$). Soil P ($r = 0.375$) was the only site attribute significantly related to overstorey Bray–Curtis axis 2. Interestingly, the composite soil fertility variable soilPCA [$0.26 \cdot \log \text{pH} + 0.32 \cdot \log \text{OM} - 0.36 \cdot \log \text{Sand} + 0.37 \cdot \log \text{Silt} + 0.22 \cdot \log \text{Clay} + 0.38 \cdot \log \text{N} + 0.13 \cdot \log \text{P} + 0.28 \cdot \log \text{K} + 0.37 \cdot \log \text{Ca} + 0.37 \cdot \log \text{Mg}$] correlated more strongly with ordination axis 1 ($r = -0.523$) than any of its individual components, justifying the PCA. Average climate variables showed no significant correlations with overstorey composition on either axis.

The ordination of understorey herbaceous community composition shows that variation among these communities generally parallels the variation observed among the overstorey communities (Figs 1 & 2). Thus, not surprisingly, the under- and overstorey Bray–Curtis axis scores covaried: overBC1 covaried with both herb Bray–Curtis axes ($r = 0.679$ and $r = 0.603$, respectively), while overBC2 only covaried with herb BC axis 2 ($r = 0.546$). Mean annual temperature, soil N, and the soil PCA all declined along herb BC axis 1 ($r = -0.519$, $r = -0.480$, and $r = -0.717$, respectively), while potential evapotranspiration–precipitation and site latitude showed weaker relationships with axis 1 ($r = -0.368$ and $r = 0.447$, respectively). Sites in all four overstorey forest types moved closer together in 2000 along the hemlock–hardwood gradient – Fig. 3 inset.

In gradient-based analyses, most strata demonstrated mesification and homogenization along two Bray–Curtis axes. All three understorey habits (herbs, shrubs and seedlings) exhibited this trend along the length of 1950 axis 1 (Fig. 4). Herb

and shrub linear fits between 1950 axis 1 scores and the change in axis 1 scores had significant intercepts and slopes (Fig. 4b,c), while the seedling changes were smaller and not significant (Fig. 4d). The overstorey demonstrated a significant mesification trend along the majority of the 1950 axis 1 gradient; however, because of little change at the dry sites a quadratic function best fit the 1950 score–change relationship (Fig. 4a). Overstorey species, herbs and seedlings also exhibited homogenization trends over time along the hemlock–hardwood axis 1950 BC2 (Fig. 5a,b,d). Linear fits between 1950 axis 2 scores and the change in axis 2 scores had significant intercepts and slopes. In the overstorey, hemlock sites had particularly large change scores as they lost hemlocks and shifted towards hardwood species. In contrast to the other habits, shrub communities did not become more similar over time, although there was a significant shift away from species associated with hemlock sites along 1950 axis 2 (Fig. 5c).

Across the northwoods, overstories are losing *Betula* spp., *Pinus* spp., *Quercus* spp., *Ulmus* spp., *Thuja occidentalis* and *Tsuga canadensis* while gaining *Acer* spp., *Carya cordiformis*, *Fraxinus* spp., *Prunus serotina* and *Tilia americana* (Table 1). Twelve of the woody taxa had significant G_{het} scores. Within groups, hemlock sites particularly lost *Thuja* and *Tsuga*, while mesic sites lost *Pinus strobus*, *Tsuga* and *Ostrya virginiana*, but gained red oaks (*Quercus rubra*, *Q. velutina*, *Q. ellipsoidalis*). Sites in the mesic–hardwood group that already contained maples did not proportionally gain as many maples as the other three groups. Maples increased in relative abundance in hemlock and dry–mesic sites enough to replace previous dominants like *Tsuga* and red oaks (Fig. 6). The original dominants in these and the dry sites (*Tsuga*, *Quercus* spp., and *Pinus* spp.) all increased in average girth between time periods. Overstorey species at the mesic sites changed least in proportion abundance and girth between the two time periods.

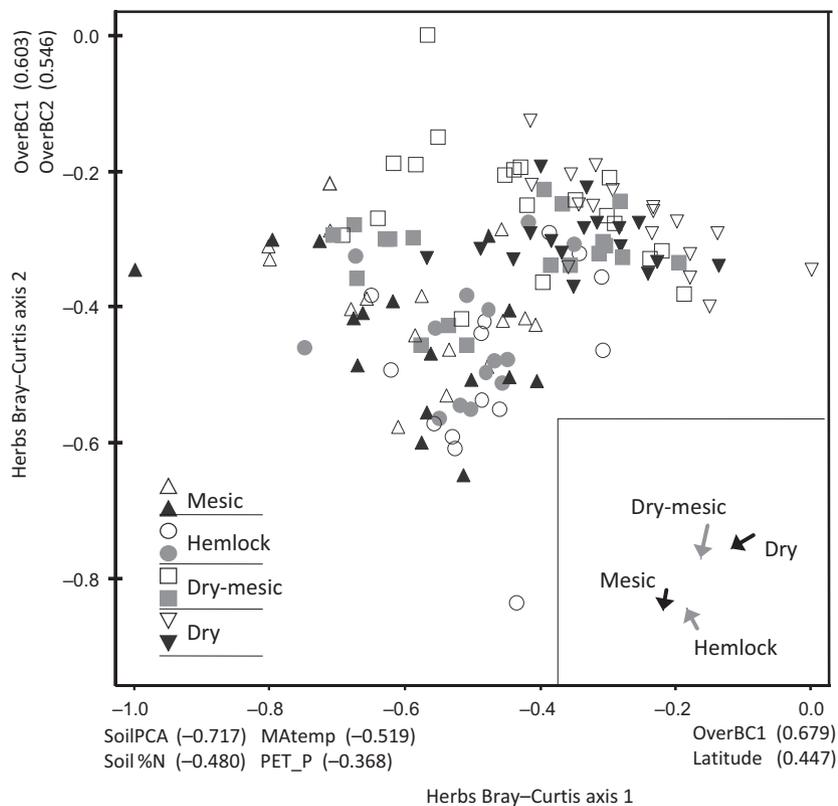


Figure 3 Bray-Curtis ordination of 66 sites at two time periods based on abundance of 65 herbaceous species. Correlations of environmental variables with $r > 0.300$ indicated next to axes. Outline shapes are site locations in the 1950 period, filled in shapes are from the 2000 period. Inset: Mean vectors of change of sites within each groups.

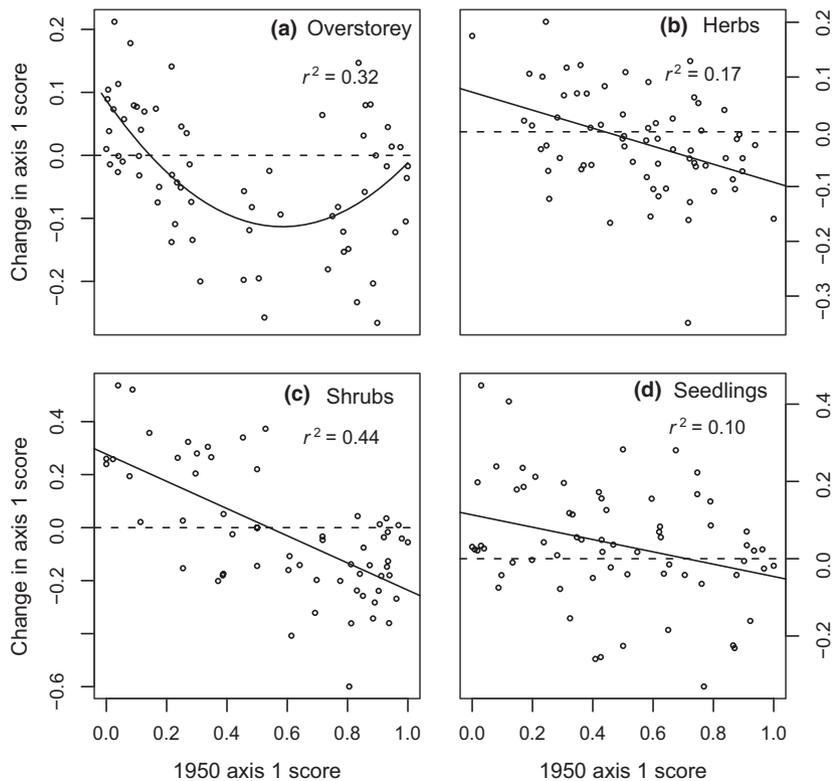


Figure 4 Changes in axis 1 scores (2000–1950) plotted against first axis 1950 Bray-Curtis ordination scores for four vegetation strata. Larger axis 1 scores are drier forests.

The G -test analyses of the understorey herb data identified winner and loser species (significant G_{total} and G_{pooled}) similar to those found by Wiegmann & Waller (2006). Among these,

26 taxa (herbs, shrubs and seedlings) had significant G_{net} scores reflecting heterogeneous responses across sites. We investigated the heterogeneity of these responses across the four overstorey

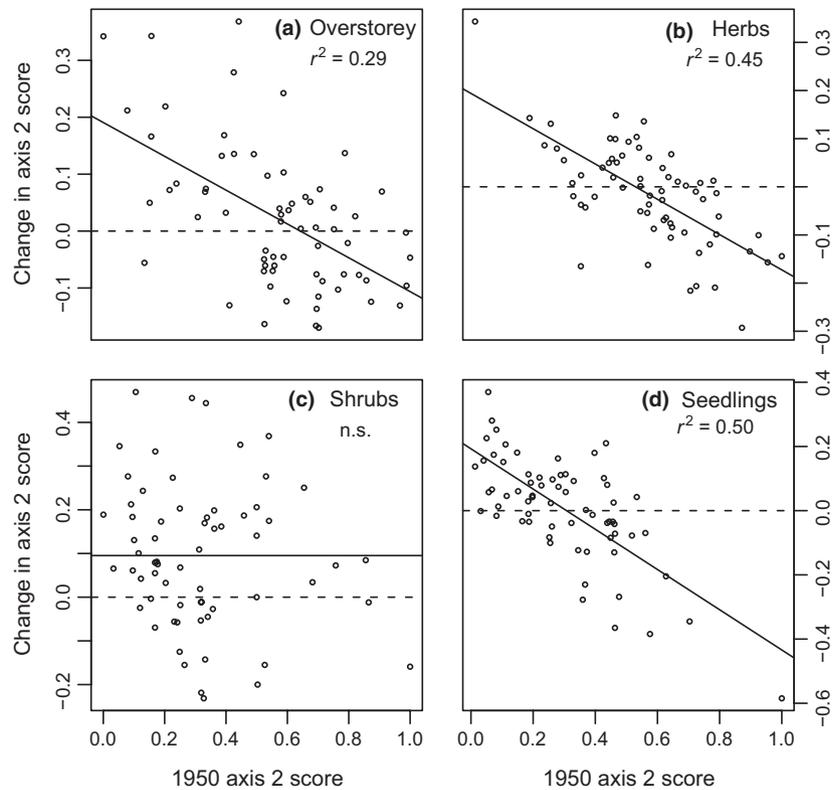


Figure 5 Changes in axis 2 scores (2000–1950) plotted against second axis 1950 Bray–Curtis ordination scores for four vegetation strata. Smaller axis 2 scores are more hemlock-dominated.

Table 1 Directions (– or +) of significant ($P < 0.05$) abundance changes of overstorey taxa based on replicated goodness of fit tests pooled across all sites (significant G_{pool} and G_{total}) or within site groups. Species with significant G_{het} statistics across all sites after P -value correction (“variable response species”) were analysed for significant abundance changes within groups.

Species	Pooled	Hemlock	Mesic	Dry-mesic	Dry
<i>Acer spicatum</i>	–				
<i>Betula alleghaniensis</i>	–				
<i>Pinus banksiana</i>	–				
<i>Pinus resinosa</i>	–				
<i>Ulmus americana</i>	–				
Variable Response					
<i>Betula papyrifera</i>	–	+		–	+
<i>Pinus strobus</i>	–		–		–
Quercus red group	–		+	–	+
<i>Thuja occidentalis</i>	–	–			
<i>Tsuga canadensis</i>	–	–	–	+	+
<i>Abies balsamea</i>		+		–	+
<i>Ostrya virginiana</i>		+	–		+
<i>Populus grandidentata</i>				–	
<i>Populus tremuloides</i>		+	+	+	–
<i>Acer rubrum</i>	+	+		+	+
<i>Acer saccharum</i>	+	+		+	+
<i>Fraxinus nigra</i>	+	+	+	+	
<i>Carya cordiformis</i>	+				
<i>Fraxinus americana/pennsylvanica</i>	+				
<i>Prunus serotina</i>	+				
<i>Tilia americana</i>	+				

groups (Table 2). Most understorey species were declining in one or more of the overstorey groups. Hemlock sites lost many herbaceous species typically associated with those overstories, including *Coptis trifolia*, *Cornus canadensis*, and *Mitchella repens*. Dry-mesic sites showed the highest declines in the

understorey species (nine species), while dry sites experienced few large shifts in understorey species abundances.

The understories of mesic and hemlock sites had generally lower alpha-diversity ($\exp(H')$) values than dry and dry-mesic sites (Table 3). Differences in diversity values among groups

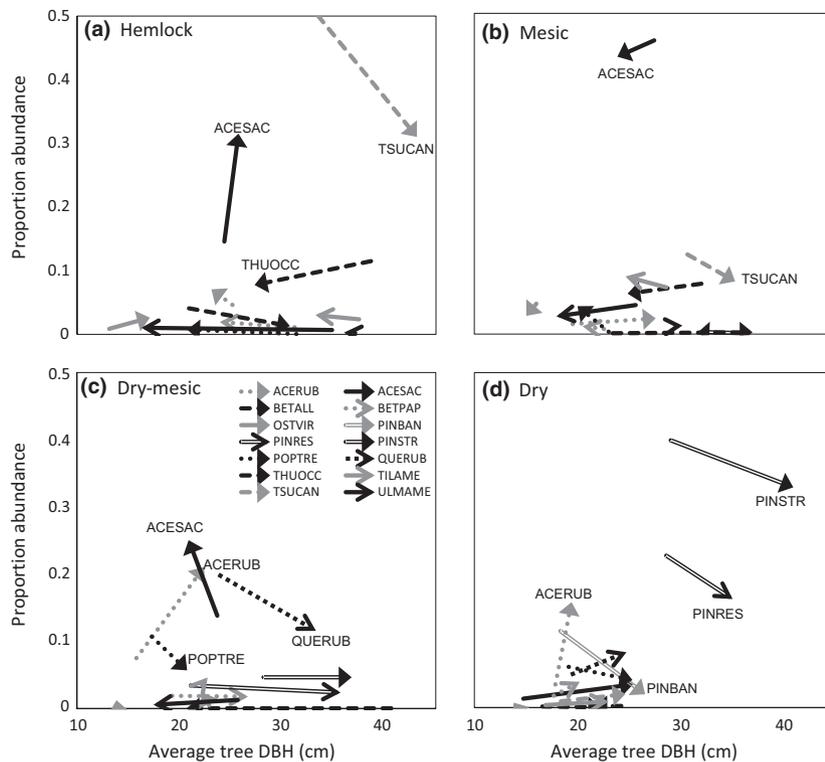


Figure 6 Changes in average diameter at breast height (DBH) and proportion abundance of 12 important overstorey species in each of four site groups. Arrowhead indicates position in 2000 time period; arrows with consistent line types represent species indicators for the same group. Species with > 10% stem abundance in either time period are labelled at the 2000 point.

were significant for shrubs ($F_{3,62} = 21.99$, $P < 0.0001$) and seedlings ($F_{3,62} = 4.66$, $P < 0.01$) but not herbs. Based on paired t -tests, diversity in mesic and dry-mesic sites decreased significantly in the herbaceous layer. The herb layer diversity decrease was significant across all groups based on ANOVA analysis ($F_{3,62} = 11.25$, $P < 0.01$). The interactions between time and group were not significant for any understorey strata.

Average Bray–Curtis similarities varied among the site groups and between time periods (Table 4). Dry sites resembled each other more than other site groups in both time periods. Between time periods, shrub layers became more heterogeneous in all groups, but changes in similarity in tree seedlings, trees and herbs were less consistent. Seedling layers at dry sites experienced significant homogenization (from 35.8 to 53.1 similarity) because of a large, consistent increase in prevalence of *Acer rubrum* seedlings. A similar pattern occurred in the overstorey, where similarity among the dry sites increased, while the other sites showed no change or the opposite trend. Shifts in site similarity in the herbaceous layer were distinct between dry/dry-mesic sites, where similarity declined, and mesic/hemlock sites, where similarity increased.

The Mantel tests comparing similarities among the various component communities indicate that the links between overstorey trees and tree seedlings have weakened considerably since 1950 (from $r = 0.72$ to 0.10, Fig. 7). The links between shrub and seedling community composition have also weakened (from $r = 0.29$ to -0.03). In contrast, overstorey-herb and shrub-herb correlations have remained consistently strong (overstorey: $r = 0.48$ and 0.47 and shrub: $r = 0.60$ and 0.48 in 1950 and 2000, respectively). Mantel tests within overstorey

groups showed similar trends. Exceptions were that tree-herb connections in hemlock and dry sites and tree-shrub connections in mesic sites increased (from non-significant to 0.322, 0.351, and 0.193, respectively).

DISCUSSION

Forests in northern Wisconsin have shifted considerably in both over- and understorey composition over the past 50 years. The magnitude and direction of overstorey change differs along the primary edaphic gradient originally described by Curtis (1959). Overstoreys on both ends of the upland edaphic gradient are losing their formerly dominant coniferous species as these are being replaced by shade-tolerant deciduous species. As conifers decline in abundance at sites where they were historically dominant, individual hemlock and pine trees have grown larger, reflecting an ageing population. This lack of conifer regeneration reflects fire suppression at the dry end of the gradient and deer overbrowsing combined with the legacy effects of logging across much of the region (Mladenoff & Stearns, 1993; Alverson & Waller, 1997; Rooney *et al.*, 2000, 2002, 2004a; Côté *et al.*, 2004; Nowacki & Abrams, 2008). Maples in particular have increased in importance across the gradient and are replacing hemlock, red oaks and pines in the overstorey of many forests. Almost half the canopy in dry-mesic sites is now maples, on par with maple dominance in mesic sites. As a result, hemlock and dry-mesic sites are both converging to more closely resemble mesic hardwood communities. The understorey herb communities associated with these forests are also converging in composition in a parallel

Table 2 Directions of significant ($P < 0.05$) abundance changes of herbs based on replicated goodness of fit tests within groups. Symbols in parentheses are significant at $P < 0.1$ level after correction. Seven of 12 evergreen species and 24 of 50 deciduous species are represented. Species with an (e) next to their name are evergreen.

Species	Pooled	Hemlock	Mesic	Dry-mesic	Dry
<i>Circaea alpina</i>	–				
<i>Epigaea repens</i>	–				
<i>Fragaria virginiana</i>	–				
<i>Gaultheria procumbens</i> (e)	–				
<i>Mitella diphylla</i>	–				
<i>Pyrola</i> sp.	–				
<i>Uvularia sessilifolia</i>	–				
Variable response					
<i>Cornus canadensis</i> (e)	–	–			
<i>Coptis trifolia</i> (e)		–			
<i>Lycopodium obscurum</i> (e)		–	+		
<i>Mitchella repens</i> (e)	–	–	–		
<i>Streptopus roseus</i>	–	(–)	–	–	
<i>Anemone quinquefolia</i>			–		
<i>Galium triflorum</i>			–		
<i>Aralia nudicaulis</i>	–		–	–	
<i>Amphicarpaea bracteata</i>	–			–	
<i>Aster macrophyllus</i>	–			–	
<i>Clintonia borealis</i>	–			–	
<i>Luzula</i> sp.	–			–	
<i>Polygala paucifolia</i> (e)	–			–	
<i>Viola</i> sp.				–	
<i>Pteridium aquilinum</i>	–				–
<i>Lycopodium clavatum</i> (e)				–	+
<i>Smilacina racemosa</i>	+	+			
<i>Arisaema triphyllum</i>	+				
<i>Athyrium filix-femina</i>	+				
<i>Carex</i> sp.	+				
<i>Dryopteris carthusiana</i>	+				
<i>Oryzopsis asperifolia</i>	+				
<i>Schizachne purpurascens</i>	+				
<i>Trientalis borealis</i>	+				

Table 3 Means and standard errors of the exponential of Shannon's entropy ($\exp(H')$) for understory habits.

	Hemlock	Mesic	Dry-Mesic	Dry
Herbs				
1950	13.5 (1.45)	14.1 (1.11)	16.8 (1.12)	14.2 (0.96)
2000	12.3 (1.16)	11.7 (1.16)†	13.9 (1.17)*	13.9 (1.03)
Seedlings				
1950	3.03 (0.31)	2.68 (0.22)	4.17 (0.35)	3.17 (0.28)
2000	3.04 (0.37)	3.17 (0.31)	3.91 (0.32)	3.28 (0.20)
Shrubs				
1950	2.44 (0.44)	2.64 (0.35)	5.12 (0.29)	5.71 (0.42)
2000	2.80 (0.33)	2.48 (0.45)	3.94 (0.40)*	4.80 (0.41)†

*Significant differences based on paired t -tests at $P < 0.05$.

† $P < 0.10$.

manner. Because of these parallel changes, the herbaceous layers of these Wisconsin forests remain correlated with the overstorey composition of the forests they inhabit. Ground-layer micro-climates reflect the type and density of forest canopies. These herbaceous communities are equally or more

correlated with climatic conditions (e.g. temperature and precipitation) than with the edaphic conditions that tended to correlate more closely with overstorey community composition. These results suggest that herbaceous species in Wisconsin forests are vulnerable to changing climates, particularly those at the southern (warm and dry) edges of their range (Beatty *et al.*, 2008; Thuiller *et al.*, 2008).

This dependence of understory conditions on overstorey composition is reflected in how herbaceous communities at dry sites changed in response to overstorey changes. On average, these sites have remained fairly stable in overstorey composition despite red maple increasing from 3% to 16% of the canopy. However, dry forest stands varied in their trajectories: seven lost pine dominance, while ten others did not. As a result, dry site herb and shrub communities became less similar as some diverged to resemble more mesic stands. These variable trajectories among dry stands maintained overall diversity across stands as few herbaceous species decreased consistently across all the dry sites. None of the variables we measured predicted whether a dry site would be stable, suggesting that unmeasured variables or stochastic processes affected succession at these sites.

Table 4 Bray–Curtis average similarities (means and standard errors) for transformed abundance (herbs, seedlings, shrubs) and trees (transformed relative basal area) at all sites and within each group. Higher numbers indicate that sites are more similar to each other.

	All	Hemlock	Mesic	Dry-mesic	Dry
Herbs					
1950	36.3 (0.9)	41.9 (1.5)	35.8 (2.0)	43.0 (1.5)	54.9 (1.2)
2000	37.8 (0.8)*	44.7 (1.5)†	36.1 (1.2)	40.7 (1.6)*	49.2 (1.3)*
Seedlings					
1950	36.9 (1.3)	60.5 (2.1)	55.3 (1.8)	49.5 (2.3)	35.8 (2.6)
2000	37.4 (1.1)	47.3 (2.9)*	43.1 (2.6)*	41.5 (2.8)*	53.1 (2.9)*
Shrubs					
1950	23.2 (1.2)	26.8 (4.0)	19.5 (2.3)	36.8 (1.9)	49.2 (1.5)
2000	18.7 (0.9)*	19.5 (1.9)	14.0 (1.8)	23.7 (1.7)*	41.4 (1.8)*
Trees					
1950	29.6 (0.7)	59.4 (1.9)	57.9 (1.6)	42.8 (1.5)	50.2 (1.8)
2000	33.7 (0.6)*	50.3 (2.2)*	47.6 (1.7)*	40.7 (1.5)	56.5 (2.3)*

*Significant differences based on paired *t*-tests at $P < 0.05$.

† $P < 0.10$.

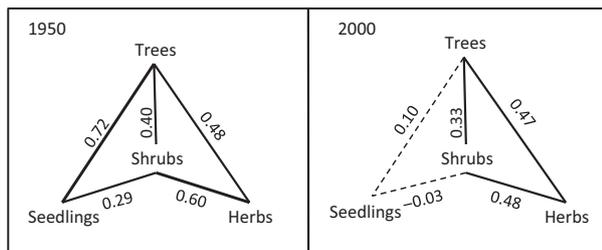


Figure 7 Mantel tests performed on Bray–Curtis similarity matrices. Solid lines indicate significant ($P < 0.05$) positive correlations between strata; dashed lines indicate correlations that are not statistically significant.

In contrast to the dry sites, the initially highly diverse dry-mesic sites experienced substantial declines in diversity. These sites are becoming dominated by mesic hardwoods that cast deep shade. Although succession has not been consistent across sites, overall trends indicate that dry-mesic sites are highly vulnerable to the successional changes that follow fire suppression. Previous researchers have postulated that when such forests occupy relatively fertile soil, they could easily shift to a mesic state (Pastor & Post, 1986; Nowacki & Abrams, 2008). This suggests that these sites will be difficult to restore once they have transitioned to maple dominance.

Mesic sites varied in their susceptibility to change, with hemlock-dominated mesic forests particularly losing the species that thrive in their understories, including several evergreen subshrubs. Over half the evergreen herbaceous species present in the northwoods declined in abundance while none consistently increased. As hemlock sites become more dominated by maples and other hardwoods, soil, light and water relations all shift, reducing their suitability for

habitat specialist understorey plants. In hardwood-dominated mesic sites, species and overall community changes were significant but modest. These shifts may reflect deer herbivory in that previous work in northern Wisconsin found significant shifts from palatable showy species to graminoids and ferns, particularly in sites without hunting (Rooney & Waller, 2003; Rooney *et al.*, 2004b; Wiegmann & Waller, 2006; Rooney, 2009). Although shaded mesic hardwood forests may be the end point of uninterrupted succession in northern Wisconsin forests, forest composition and structure are also not likely to remain stable as the impacts of continuing non-native species invasions and climate change become manifest (Taverna *et al.*, 2005; Von Oheimb & Brunet, 2007; Rogers *et al.*, 2008).

Successional models predict that forest composition will respond to changes in environmental conditions (i.e. climate change) in addition to changes in disturbance regimes. Mechanistic models correctly predict that distinct communities will develop on different soils reflecting how species' physiological requirements interact with edaphic constraints on water and nitrogen availability (Botkin *et al.* 1972; Pastor & Post, 1986; Huston *et al.* 1988). With climate change, a shift from boreal forest to northern hardwoods is predicted on silty clay loam soils regardless of specific climate-change scenarios (Huston *et al.* 1988; Pastor & Post, 1988). A shift to northern hardwoods is also predicted on sandy soils in scenarios where precipitation increases (Post & Pastor, 1996). Spatially variable and occasionally significant climate changes have been documented in Wisconsin over the past 57 years (Kucharik *et al.*, 2010). The sites included in this study are primarily in the north central to north eastern part of Wisconsin (Fig. 1). Across the study region, there has been a 0–150 mm decrease in spring and summer precipitation, while daily maximum temperatures have cooled 0–1.5 °C in summer and fall, likely reducing evapotranspiration and mitigating the drying effects of reduced precipitation (Kucharik *et al.*, 2010, figs 3B,C, 5C,D). Overall, the length of the growing season in northern Wisconsin has increased by from 1 to 4 weeks (Kucharik *et al.*, 2010, fig. 9C). However, because of cooling daytime temperatures, the number of growing degree days (base 10 °C) actually declined in the eastern portion of the study area and significantly increased at only 10 of our westernmost sites (Fig. 1; Kucharik *et al.*, 2010, fig. 8A). Our site types are well dispersed along the climate change gradient with a low probability that our mesification results are a spatial artefact (Fig. 1). Both the direction and spatially variable patterns of recent climate change supports that the trends we have identified are primarily successional rather than climatic-change effects. As future climate changes here are predicted to be greater (Kucharik *et al.*, 2010), we expect successional pathways and changing climates to interact in the future. Additionally, models of forest change with changing climates do not yet incorporate recent results suggesting that several temperate deciduous forest species have substantially increased their growth rates in recent decades in response to increased concentrations of atmospheric CO₂ and/or longer growing seasons and warmer temperatures (Cole *et al.* 2010; McMahon

et al., 2010). Such increases in growth may contribute to the competitive success of deciduous species relative to conifers and thus to mesification trends in this area.

The relative importance of succession and human-induced disturbances varies substantially among the different forest types we identified along the edaphic gradient. Although anthropogenic shifts in conditions are occurring at all sites, shifts on the dry end of the spectrum (mesification) are following the successional hypotheses as predicted by Curtis (1959) and Nowacki & Abrams (2008) in the absence of fire. This suggests that humans are having less impact at these sites. In contrast, changes at the more mesic sites appear to be more attributable to shifts in various biotic factors including deer, earthworms, and pathogens that often have specific effects on different species or functional groups (Rooney *et al.*, 2002, 2004b; Wiegmann & Waller, 2006).

As these changes in Wisconsin's forests continue, we can expect further changes in how soils develop and how under- and overstorey species interact with mammals, birds and surrounding landscape conditions. The loss of hemlock and dry-mesic overstories and some associated understorey plants will clearly diminish landscape-level community diversity. Wisconsin has already lost much of its original prairie-oak woodland-forest mosaic to the south of our study area where associated species including grassland birds have declined drastically (Rhemtulla *et al.*, 2007; Sample & Mossman, 2008). We expect similar consequences within hemlock and pine stands if they continue to transition to maple dominance. For example, bird species that prefer those stands are likely to decline in abundance (Roberts, 2001). Because non-native earthworms prefer mesic, high pH soil, the demise of pine-dominated stands will likely expand habitats for earthworms to thrive, potentially further increasing the impacts of invasive plant species in the region (Rooney *et al.*, 2004a).

There may be opportunities to manage these northern forest types in ways that could slow the successional changes and homogenization they are experiencing. It would make particular sense to address the conspicuous factors affecting patterns of forest regeneration. For hemlock and mesic stands, we suggest providing suitable seed bed conditions (e.g. rotting 'nurse' logs to favour seedlings of hemlocks, yellow birch and several other species) and reducing deer densities and/or browsing impacts to increase the recruitment of hemlock, cedar, yellow birch, northern red oak, white pine and other species (Mladenoff & Stearns, 1993; Rooney & Waller, 1998, 2008; Rooney *et al.*, 2000, 2002). As long as deer populations remain high in the region, large-scale disturbances including logging are likely to result in transitions to more deciduous forest types (Frelich, 2002). Thus, reducing the intensity and frequency of logging in the region would likely slow transitions of mesic conifer forests to more deciduous stands. At the dry end of the gradient, restoring fire may be the only way to prevent further transitions of dry-mesic and mesic sites to a maple-dominance except on the driest sandier soils. In the absence of substantial shifts in forest and wildlife management

like these, we expect the trends of mesification and homogenization observed over the past half-century to continue and accelerate.

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BIOSKETCH

We work as part of the Wisconsin Plant Ecology Laboratory (<http://www.botany.wisc.edu/PEL/>) to analyse the causes and consequences of long-term ecological change. The data collected by the original PEL researchers at >1400 sites in the 1940s and 1950s give us a uniquely detailed baseline for assessing ecological change over 50+ years. We are tracking species invasions, local extinctions, changes in diversity, and shifts in species' local and regional abundances. More broadly, we seek to understand the forces driving ecological change to improve our stewardship of both natural and managed habitats.

Author contributions: K.L.A., D.A.R., M.R.F. and D.M.W. conceived the ideas; D.A.R. collected the data; K.L.A. and M.R.F. analysed the data; and K.L.A. and D.M.W. led the writing.

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