

Trait–environment relationships remain strong despite 50 years of trait compositional change in temperate forests

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Abstract. Temperate North American forest communities have changed considerably in response to logging, fragmentation, herbivory, and other global change factors. Significant changes in the structure and composition of seemingly undisturbed Wisconsin forest communities have occurred over the past 50 years, including widespread declines in alpha and beta species diversity. To investigate how shifts in species composition have affected distributions of plant functional traits, we first compiled extensive data on understory plant species traits. We then computed community-weighted trait means and functional diversity metrics for communities in both the 1950s and 2000s. We examined how trait values and diversity varied across environmental gradients and among Wisconsin's four main ecoregions. Trait means and diversity values reflect conspicuous gradients in species composition, soils, and climatic conditions. Over the past 50 years, values of most traits have changed as communities shifted toward species with higher leaf nutrient levels and specific leaf area, particularly in the southern ecoregions. Trait richness and diversity have declined, particularly in historically species- and trait-rich unglaciated southwestern Wisconsin. Reductions in within-site trait diversity may be diminishing the ability of these forest communities to resist or resiliently respond to shifts in environmental conditions. Despite changes in trait and community composition, trait–environment relationships measured directly via fourth-corner analysis remain strong for most plant traits. Nevertheless, accelerating ecological change (including climate change) could outstrip the ability of plant species and traits to match their environment, particularly in more fragmented landscapes.

Key words: *ecoregion; fourth-corner analysis; functional diversity; overstory; succession; trait–environment relationship; understory; upland forest; Wisconsin, USA.*

INTRODUCTION

Plant communities around the globe are shifting in species composition in response to multiple global changes, including invasive species, herbivory, and habitat fragmentation, with corresponding changes in the distribution of plant traits (Lavorel and Garnier 2002, Hobbs et al. 2009, Clavel et al. 2011). However, the mechanistic links that underlie these changes remain obscure. Species traits determine fitness in specific environments (Shipley et al. 2006), reflecting species' responses to abiotic factors like temperature, moisture, soil nutrients, and light availability (MacGillivray et al. 1995, Cunningham et al. 1999, Rijkers et al. 2000, Lacourse 2009). Traits also tend to be correlated with biotic factors affecting the abiotic environment such as succession and invasion by ecosystem engineers (Aubin et al. 2009, Chabrerie et al. 2010). It remains unclear,

however, how global changes are altering the strength of regional trait–environment relationships.

Systematic shifts in plant traits also affect ecosystem functions, including water uptake, litter decomposition, and biomass production (Cornelissen and Thompson 1997, Diaz et al. 2004, Cornwell et al. 2008, Suding et al. 2008). Processes at the ecosystem scale reflect a complex set of interactions among the species present, their relative abundances, and their trait values (Garnier et al. 2004, Epps et al. 2007). Declines in species diversity within communities can, but need not, reduce the range of traits present there. Declines in functional diversity, in turn, may decrease the efficiency of light, water, and nutrient use, with important implications for the return of carbon and nutrients to the soil (Hooper et al. 2005, Suding et al. 2008, Flynn et al. 2011). These alterations, in turn, could feed back to produce further changes in community composition.

The variety and relative abundance of traits in a community affect how the system can respond to future biotic and abiotic global changes. Recent research suggests that functional diversity affects community

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responses to changes in environmental conditions (Reich et al. 2001, Reich et al. 2004, Craine 2005, Wright et al. 2006, Cadotte et al. 2011, Sterk et al. 2013). Functional redundancy and complementarity can lead to either resistance or resilience to change (Peterson et al. 1998, Hooper et al. 2005, O’Gorman et al. 2011, Steudel et al. 2011). Although the species that contribute most to biomass typically drive ecosystem processes (Laughlin 2011), rare species can make a system more resilient to global changes (Walker et al. 1999).

Prior to European settlement, forest composition across Wisconsin reflected a distinct climatic gradient, differential fire regimes, and soil characteristics that varied with glacial history and topology (Curtis 1959, Rhemtulla et al. 2007). By the mid-20th century, forests in southern Wisconsin were dominated by oaks (*Quercus*) while those in the north ranged from hemlock–deciduous on mesic soils to pine–deciduous on drier soils (Curtis 1959). Since then, forests across the state have transitioned toward more uniform composition reflecting fire suppression, deer overabundance, and habitat fragmentation (Rooney et al. 2004, Rogers et al. 2008, Amatangelo et al. 2011). Many Wisconsin forests are now dominated by maple (*Acer*), ash (*Fraxinus*), and other mesic species (Rogers et al. 2008, Amatangelo et al. 2011, McEwan et al. 2011; Johnson et al., *in press*). These changes in Wisconsin forest overstories often strongly affect understory community composition, yet the linkages between over- and understories have weakened (Rogers et al. 2008, Amatangelo et al. 2011, Sonnier et al. 2014).

The understory is a critical, but often overlooked, component of temperate forests supporting the majority of taxonomic diversity in temperate forests and influencing the regeneration of overstory trees (Gilliam 2007). The understory can also contribute substantially to both annual productivity and up to 60% of nitrogen uptake (Yarie 1980, Olsson and Falkengren-Grerup 2003, Moore et al. 2007). As a result, changes in understory composition can have important implications for both site richness and ecosystem function. Over the past 50 years, shrubs and weedy dicot species (including nonnative invaders) have increased in relative abundance while remnant savanna species have declined in southern upland Wisconsin forests (Rogers et al. 2008). In the north, graminoids and some ferns are increasing while evergreen and biotically pollinated species are decreasing (Rooney et al. 2004, Wiegmann and Waller 2006, Amatangelo et al. 2011). Upland forests in both regions have declined in native species density (Rooney et al. 2004, Rogers et al. 2008). These changes reflect earthworm and plant invasions, habitat fragmentation, deer overabundance, fire suppression, and succession (Rooney and Waller 2003, Bohlen et al. 2004, Hale et al. 2006, Nowacki and Abrams 2008, Nuzzo et al. 2009, Rogers et al. 2009, Rooney 2009).

Here we investigate how changes in the composition of Wisconsin forest understory communities translate

into shifts in the plant functional traits present among the species found at these sites. We capitalize on the detailed surveys of forests undertaken in the 1950s and 2000s to evaluate how community trait values and diversity have changed over the last 50 years. We also explore how the linkages between traits and environmental gradients have changed during this interval. Knowing the landscape’s environmental patterns and trends in community composition allow us to make specific predictions regarding trait–environment relationships and how these may be changing. Northerly sites should have trait profiles consistent with slower, more cold-tolerant growth. The observed loss of uncommon species and increases in habitat generalists lead us to expect statewide declines in trait diversity. In southern Wisconsin, increases in shade-tolerant herbs that have edged out many grasses and sedges suggest that we should expect thinner leaves and foliage less resistant to decay (Rogers et al. 2008). These shifts are likely to be more significant in southeastern Wisconsin where fragmentation, urbanization, and community changes have all been more severe (Rogers et al. 2009). Because succession has driven substantial changes in many forests, and overstory–understory linkages are still present (Rogers et al. 2008, Amatangelo et al. 2011), we expect stands that have experienced the largest successional changes in the overstory to show the largest changes to understory trait metrics. Given ground-layer homogenization occurring statewide, we also expect trait–environment relationships to have weakened.

METHODS

We focus here on 151 upland forest sites spanning Wisconsin and part of the western upper peninsula of Michigan, including sites that range from “dry-mesic” to “wet-mesic” in Curtis’s original site designations (Curtis 1959, Rogers et al. 2008, Amatangelo et al. 2011; Fig. 1). Curtis and his students sampled the understory composition (herbs, shrubs, and seedlings) of these forests between 1949 and 1953 (1950 time period). The Waller group resampled these sites between 2000 and 2004 (2000 time period). Although Curtis did not permanently mark sample plots, the Waller group was able to accurately relocate sites using the original maps and site descriptions. Curtis-era sampling used 20 1-m² quadrats evenly spaced around square or L-shaped transects (Waller et al. 2012). Similar methods were replicated in the 2000s around three to four such transects, yielding data from at least 80 quadrats. Sampling in the 2000s in the north also occasionally used 120 quadrats placed on three L-shaped transects. All species within each quadrat were recorded, providing frequency data for each species at each site.

We used the total frequencies for each species across time periods and sites to identify the 195 most abundant species, which represent 94.5% of the plant occurrences and 56% of the species present across these sites in both time periods (Rooney et al. 2004, Rogers et al. 2008,

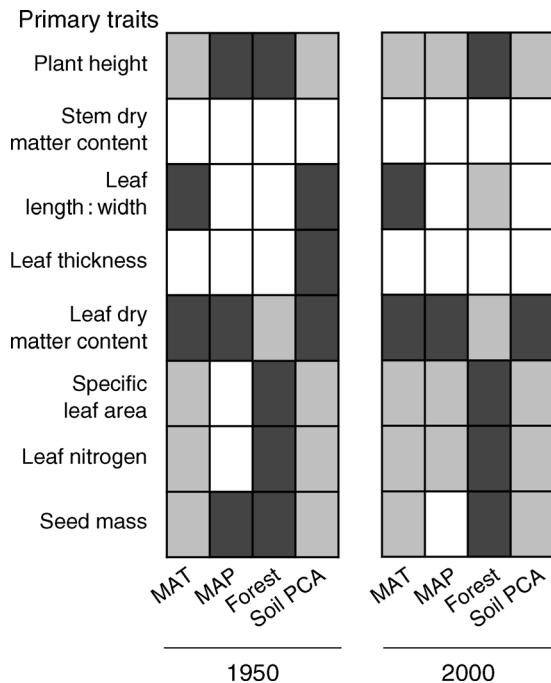


FIG. 1. Fourth-corner results for primary traits and environmental variables in upland forests of Wisconsin and Michigan, USA. Dark gray shows significant negative correlations ($P < 0.05$); light gray shows significant positive correlations ($P < 0.05$). Here, “1950” is a time period with climate data averages from 1944 to 1953; “2000” is a time period with climate data averages from 1996 to 2005. Soil data were collected in the 2000s; landscape data are from 1991 to 1993. MAT is mean annual temperature; MAP is mean annual precipitation; PCA is principal components analysis. “Forest” represents percent cover of forest within 2 km of each site.

Amatangelo et al. 2011). We then measured a set of traits on all of these species, termed “primary” traits. On a subset of the 104 most abundant species (accounting for 82.4% of plant occurrences and 25% of species found) we also measured foliar carbon chemistry and additional nutrient levels. While it would be ideal to measure values for all traits on each species, the sampling constraints we faced forced us to focus on the most abundant species. Minor species with distinctive trait values could potentially alter the community trait spectrum and thus bias our results. However, we found no conspicuous differences in trait values between the more and less common species measured (K. Amatangelo, *unpublished data*). Although we could match most taxa to particular trait values, the 1950s surveys identified sedges (*Carex* spp.) only to genus. Of the 28 *Carex* species we identified in the 2000s, 11 were sampled for traits (representing 89% of *Carex* occurrences in the 2000s). For consistency, we lumped *Carex* to the generic level in both time periods and averaged trait values across the 11 sampled species. Interspecific variation in *Carex* traits was maximally variable for leaf dry matter content ($CV = 194\%$) and minimally variable for leaf length : width ($CV = 62.4\%$).

Trait values and diversity

We measured primary traits on 12 individuals (four individuals from each of three sites). For woody species we sampled individuals < 3 m in height. Plant height for all species was measured vertically from the ground to maximum (unstretched) leaf height. We collected young, fully expanded leaves and measured two leaves per individual. For species with markedly different basal and cauline leaves we measured one of each. We measured lamina leaf thickness using an Ames Pocket Thickness Gauge (B. C. Ames, Framingham, Massachusetts, USA), avoiding major veins. We then removed petioles and scanned the leaves on a flatbed scanner. These images were then analyzed for area, length, and width using Image J (Schneider et al. 2012). We measured leaf length and width on the whole blade prior to scanning for large and compound leaves. Leaves were weighed, dried for at least 48 hours at 60°C , and reweighed for specific leaf area (SLA) and leaf dry matter content (LDMC) calculation. On woody plants, we also measured the previous year’s twig growth. Twigs were weighed, dried for at least 48 hours at 60°C , and reweighed for stem dry matter content (SDMC). To quantify seed mass we collected at least 75 seeds (five seeds from each of five individuals at each of three sites; see Plate 1) for each species, and dried and weighed them. We averaged trait values across all individuals, providing one value per species. Although some within-species variation exists for most traits, this is small relative to among-species variation (D. Waller, *unpublished data*). We pooled the leaf material we used for the analyses of SLA and analyzed these for nitrogen content on a Flash EA Analyzer (Thermo Scientific, Waltham, Massachusetts, USA). For carbon chemistry and extended nutrient analyses performed on the 104 most abundant species, we sent leaf material pooled across sites to the University of Wisconsin–Madison Plant and Soil Analysis Lab to obtain one value per species for leaf P, K, Ca, Mg, ash, neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin content.

Of many possible metrics of functional diversity, we chose to use the metrics designed by Vileger et al. (2008): functional richness, functional evenness, and functional divergence. These metrics are orthogonal (Mouchet et al. 2010) and span several aspects of trait diversity. Functional richness is the volume of functional space occupied at a site. Functional evenness measures the regularity of the distributions of traits within that volume. Functional divergence measures how the abundances of the traits are distributed, where a high divergence value means that the most abundant species have extreme trait values (toward the edge of the trait volume). We calculated these functional diversity metrics using means for just the primary traits that we had for most species, standardizing the data to mean 0 and unit SD, and using Euclidean distances in the f-Diversity software package (Vileger et al. 2008, Casanoves et al. 2010, Laliberte and Legendre 2010).



PLATE 1. Seeds from temperate forest understory species vary widely in size and shape. Photo compilation: Sarah Friedrich.

Site information

We compiled data on a variety of environmental and biotic factors we expected to correlate with plant traits across these sites. We downloaded monthly precipitation and average temperature data from the PRISM database (PRISM Climate Group 2004), extracting values for all Wisconsin sites and averaging across 10 years associated with each time period: 1996–2005 for the 2000 time period sample and 1944–1953 for the 1950 time period sample. We estimated forest and urban land cover within 2 km of each site from land cover layers digitized from aerial photos of Michigan in 1991 (*available online*)⁶ or Wisconsin in 1993 (Wisconsin Department of Natural Resources 1998). We used soil data from 144 of the 151 sites based on pooled samples collected in the 2000 time period from the top 10 cm of the A horizon from three locations analyzed at the Wisconsin Soil Analysis lab for N, P, Ca, Mg, Na, K, pH, and texture.

We also used U.S. Environmental Protection Agency (EPA) Site Level III Ecoregions (“ecoregions”) to discriminate among four ecoregions with distinct environmental and vegetative characteristics (Appendix A). Our sites fell into the Southeastern Wisconsin Till Plains (51), North Central Hardwood Forests (15), Driftless Area (34), and Northern Lakes and Forests (52)

ecoregions. To assess the effects of forest succession on understory traits we calculated overstory basal area (BA, m²/ha) and the proportion of overstory individuals in the genus *Acer* at each site in both time periods. Maples (*Acer* spp.) have increased in the overstory in both southern and northern forests, reflecting statewide “mesification” (Rogers 2006, Amatangelo et al. 2011). They also represent extreme late-successional values in Curtis’s (1959) Continuum Index.

Analyses

We compared climate variables between time periods using paired *t* tests. We applied principal components analysis (PCA) to reduce the dimensionality of our soil variables to one axis (soil PCA), which explained 52.3% of soil data variation (additional axes had low explanatory power).

To examine associations of traits with environmental variables, we performed direct analyses using the fourth-corner method (Legendre et al. 1997, Dray and Legendre 2008). This method analyzes the relationships between species traits and environmental variables through the link of three data matrices: species abundances at each site, measurements of environmental variables at each site, and trait values for each species. We used the “fourthcorner” function in the *ade4* package in R (R Development Core Team 2012), using the sequential approach with models 2 and 4 and 9999 permutations (Dray and Legendre 2008, ter Braak et al.

⁶ <http://www.mcgi.state.mi.us/mgdl/>

TABLE 1. ANOVA results for community-weighted site means and variances for primary traits in upland forests of Wisconsin and Michigan, USA, for two time periods (1950, 2000) and four ecoregions (see Fig. 2).

Index	R^2	Time period			Ecoregion			Time period \times ecoregion		
		F	df	P	F	df	P	F	df	P
Seed mass	0.473	8.55	1, 148	0.0040	21.46	3, 148	<0.0001	3.84	3, 148	0.0111
Height	0.389	4.66	1, 148	0.0325	4.11	3, 148	0.0078	2.89	3, 148	0.0377
SLA	0.646	12.6	1, 148	0.0005	85.20	3, 148	<0.0001	4.73	3, 148	0.0035
LDMC	0.757	54.6	1, 148	<0.0001	51.17	3, 148	<0.0001	13.5	3, 148	<0.0001
SDMC	0.544	0.41	1, 148	NS	1.69	3, 148	NS	1.56	3, 148	NS
Leaf % nitrogen	0.789	8.51	1, 148	0.0041	118.27	3, 148	<0.0001	3.48	3, 148	0.0176
Leaf length : width	0.607	12.5	1, 148	0.0005	60.5	3, 148	<0.0001	38.8	3, 148	<0.0001
Leaf thickness	0.354	0.34	1, 148	NS	27.0	3, 148	<0.0001	0.69	3, 148	NS

Notes: Here, "1950" is a time period with climate data averages from 1944 to 1953; "2000" is a time period with climate data averages from 1996 to 2005. Analyses were performed on log-transformed data. Abbreviations are: SLA, specific leaf area; LDMC, leaf dry matter content; SDMC, stem dry matter content; NS, not significant.

2012). We analyzed the species abundance and climate data separately for the 1950 and 2000 time periods. Since we had only trait, soil, and forest cover measurements for the modern time period, we used these for analyses in both the 1950 and 2000 time periods.

To evaluate how time period affects trait composition, we first calculated community-weighted mean values (CWM) for each trait at each site and time period. We then applied mixed-model ANOVAs using the functional diversity indices or CWM trait values as response variables. We set ecoregion, time period, and ecoregion \times time period as fixed effects and site as a random effect in these models to evaluate whether traits varied across time period or ecoregions. We also performed analyses with time period, 10-year mean annual temperature (MAT), 10-year mean annual precipitation (MAP), soil PCA, percent forest, and the interactions between the environmental variables and time period as fixed effects (again using site as a random effect). Variables were backward selected with a P value >0.05 to leave. To evaluate the effect of successional changes on trait values and diversity, we computed Spearman's non-parametric rank correlations between changes in site basal area (m^2/ha) or proportion of *Acer* in the canopy between 1950 and 2000 sampling periods and changes in community-weighted mean trait values or diversity. To visualize how sites differed in trait composition among ecoregions and across time, we performed a PCA on sites in trait space using our eight primary traits. We first log-transformed all trait data to improved normality and performed all statistical analyses in JMP (SAS 2010) unless specified otherwise.

RESULTS

Wisconsin in the 21st century is warmer and wetter than it was in the mid-20th century. Mean annual temperature (MAT) increased 5.62%, from 6.65° to 7.03°C, and mean annual precipitation (MAP) increased 8.84%, from 776 to 845 mm (both $P < 0.0001$). Climates are significantly autocorrelated between time periods at the same sites ($R^2 = 0.96$ for MAT, 0.391 for MAP; both $P < 0.05$). The first principal components analysis

(PCA) axis of soil variables explains 52.3% of their variation, with larger values reflecting soils of higher nutrient content and greater water-holding capacity. Sites farther to the south are generally warmer, wetter, and more fertile with MAT, MAP, and soil PCA values all increasing except in the unglaciated (Driftless) area, where values remained high throughout (Appendix A). Forest cover within 2 km of each site is high for most northern sites and low in southeast Wisconsin (Appendix A).

All foliar traits were significantly associated with at least one environmental variable (Fig. 1; Appendix B). Stem dry matter content, however, was alone in not being associated with any measured environmental variable. Foliar nutrient levels (N, P, Ca, Mg, K) were positively associated with increased soil fertility (both individual soil variables and soil PCA) and warmer, wetter climates. Leaf nutrient levels declined with increasing forest cover (Fig. 1; Appendix B), which could reflect the poorer soils common in northern Wisconsin. Specific leaf area, seed mass, and plant height followed the same trend (Fig. 1). In contrast, leaf dry matter content (LDMC), leaf thickness, and leaf length:width ratio increased in colder, drier, sandier sites. Association significances and strengths between traits and environmental variables were often similar between time periods (Fig. 1; Appendix B). The four ecoregions differed in their site mean foliar traits in ways that reflect these responses to environmental gradients (Table 1, Fig. 2; Appendix C). In the 1950s, plant height, specific leaf area, leaf percent N, foliar nutrients (P, Ca, Mg, K), lignin, and ash were all larger in southern ecoregions, while LDMC, leaf thickness, and length:width ratio were larger in the northern ecoregions (Fig. 2). Fiber (acid detergent fiber [ADF] and neutral detergent fiber [NDF]) varied across the state (Appendix C).

Community-weighted trait means for 11 of 16 traits changed significantly between the sampling periods (Table 1; Appendix C). Plant height, LDMC, seed mass, NDF, and ADF decreased, while specific leaf area (SLA), length:width, and most foliar nutrients (N, P,

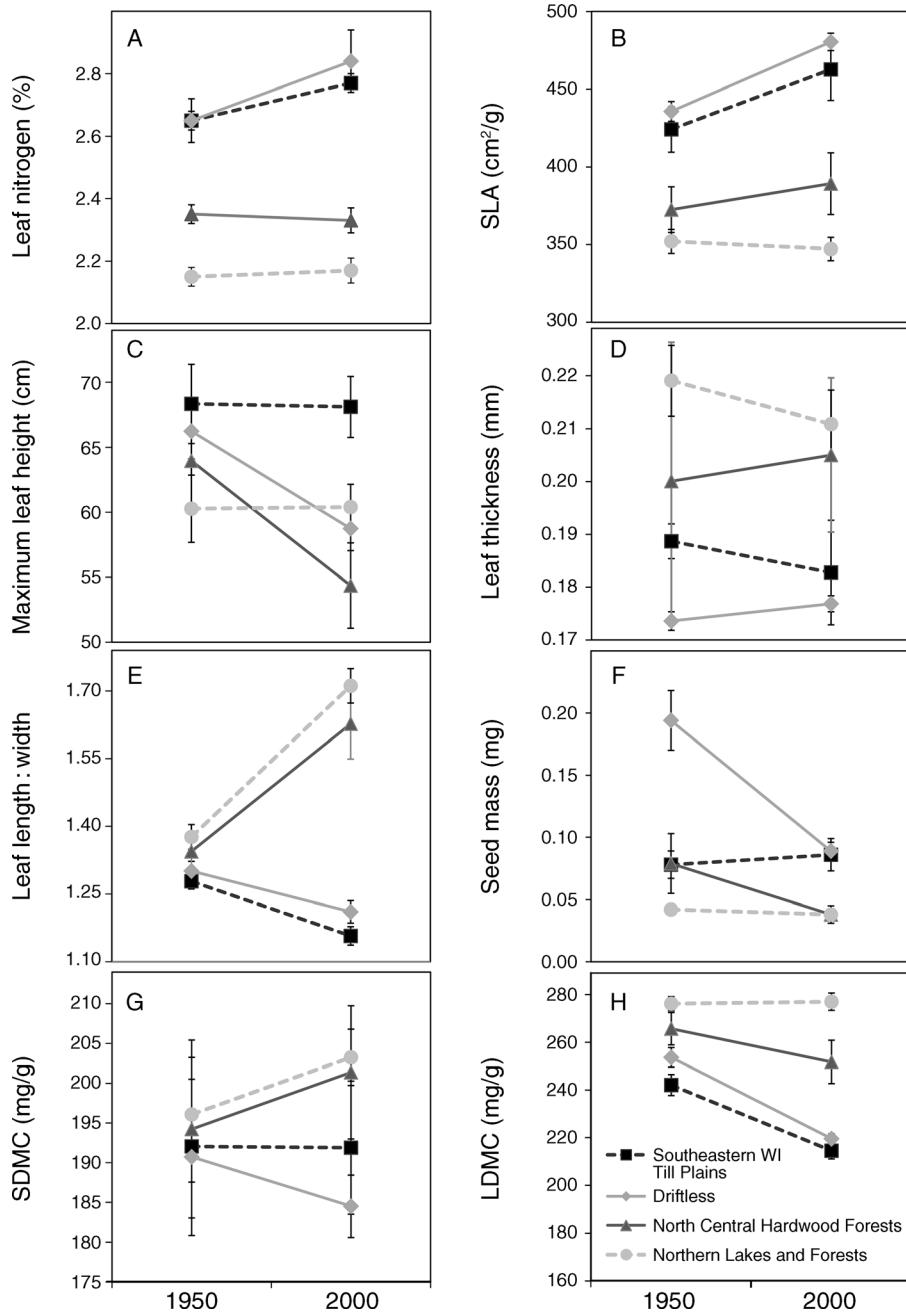


FIG. 2. Community-weighted traits (mean \pm SE) across four ecoregions and two time periods, 1950 (1944–1953) and 2000 (1996–2005). Abbreviation are: SLA, specific leaf area; LDMC, leaf dry matter content; SDMC, stem dry matter content; WI, Wisconsin.

Mg, K) all increased (Fig. 2). These responses, however, were all region specific as shown by the significant time period \times ecoregion interactions for all traits. Leaf length:width ratio and stem dry matter content (SDMC) remained similar across ecoregions in the 1950s but increased in northern ecoregions while decreasing in the south, accentuating differences that were originally small (Fig. 2). Leaf N and SLA also became more strongly differentiated from somewhat

higher values in the south in the 1950s to still higher levels by the 2000s. Leaf height and LDMC declined in some but not all ecoregions, also causing divergence. More southerly ecoregions experienced greater decreases in LDMC. In contrast, a sharp decline in mean seed mass in the Driftless area resulted in convergence for this trait. Leaf thickness appeared to converge in a parallel way between the two ecoregions within the north and south regions (Fig. 2). The PCA of sites in trait space

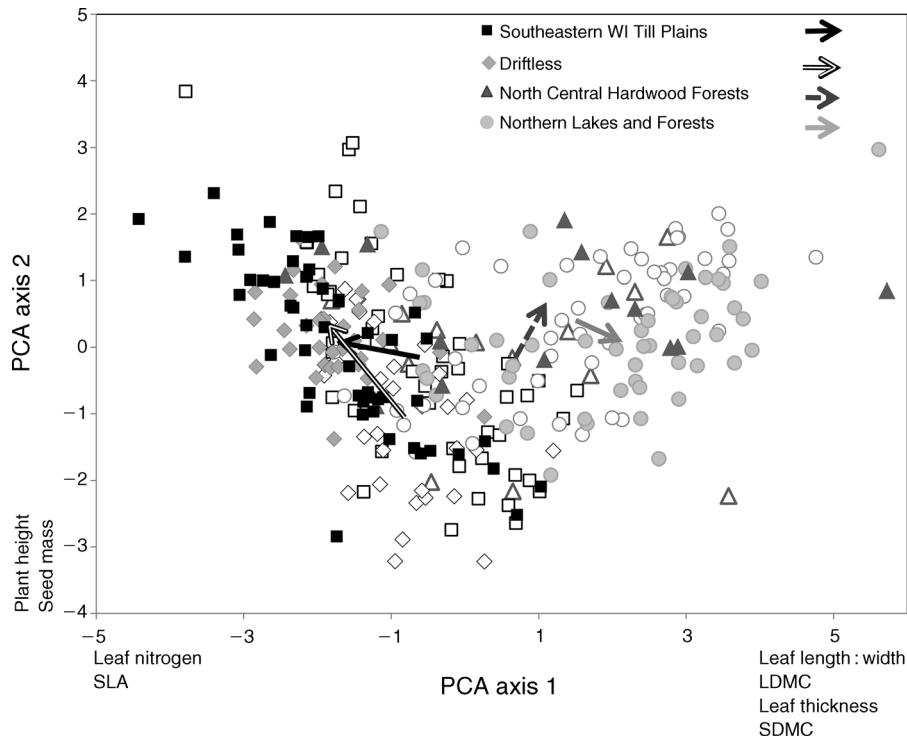


FIG. 3. Principal components analysis (PCA) of sites based on community-weighted means of eight traits. Symbols indicate ecoregions; open symbols are sites in the 1950 time period (1944–1953), and solid symbols are sites in the 2000 time period (1996–2005). PCA axis 1 explains 47.9% of the variation; axis 2 explains 20.2% of the variation. Traits are indicated on the axes where $R^2 > 0.200$; positive correlations with the axes are indicated by placement at maximum x or y values, and negative correlations are indicated by placement at minimum values. Arrows indicate ecoregion means from 1950 to 2000 time periods. Abbreviations are as for Fig. 2.

visually demonstrates these differences in trait divergence among ecoregions, with those in the north moving right while those in the south move left along PCA axis 1. This axis explains 47.9% of the variation and is correlated with the eight primary leaf and stem traits (see axis labels, Fig. 3).

Analyses of variance that focused on measured environmental variables rather than ecoregions show similar results (Appendix D), although time period itself was rarely significant. However, time period interacted with one or more environmental variables to affect trait values for every trait. Most commonly, MAT interacted with time period, although soil fertility also affected leaf nutrient concentrations.

The three multivariate diversity metrics also varied between time periods and across ecoregions (Table 2,

Fig. 4). Functional richness declined in all four ecoregions with a pronounced decline in the Southeastern Wisconsin Till Plains. Functional evenness also generally declined except in the Northern Lakes and Forests ecoregion, where it increased. Functional divergence increased in the Northern Lakes and Forests, stayed steady in the Southeastern Wisconsin Till Plains and North Central Hardwood Forests, and declined greatly in the Driftless area (Fig. 4). Differences in forest cover may explain some of these different trajectories as models for all three metrics showed significant period \times percent forest interaction terms. Sites with low forest cover (often in the Southeastern Wisconsin Till Plains) showed steep declines in functional richness (Fig. 4; Appendix E).

TABLE 2. ANOVA results for diversity metrics.

Index	R^2	Time period			Ecoregion			Time period \times ecoregion		
		F	df	P	F	df	P	F	df	P
Functional richness	0.591	17.12	1, 148	<0.0001	7.15	3, 148	0.0002	5.93	3, 148	0.0008
Functional evenness	0.319	2.60	1, 148	NS	2.41	3, 148	0.0694	7.51	3, 148	0.0001
Functional divergence	0.556	0.98	1, 148	NS	3.70	3, 148	0.0132	10.67	3, 148	<0.0001

Notes: All metrics except functional divergence were log-transformed prior to analysis. NS indicates not significant.

Changes in overstory basal area (BA) and the proportion of maple stems in the canopy were slightly correlated with changes in five functional traits (Appendix F). Increasing basal area is linked to increases in understory SLA and declines in LDMC and leaf length:width. Increasing *Acer* abundance in the overstory corresponds with taller understory plants and thinner leaves. None of these correlations were significant after *P* value correction.

DISCUSSION

Alterations to forest communities induced by exotic invasive species, deer overabundance, habitat fragmentation, and fire suppression have contributed to changing patterns of functional composition over the past 50 years in Wisconsin forests. However, despite considerable shifts in understory community composition and trait means, traits remain strongly associated with abiotic environmental variables within both time periods. Significant trait-environment linkages are found even at paleoecological time scales (Lacourse 2009, Chabrerie et al. 2010, Swenson and Weiser 2010, Laughlin et al. 2011a), but we had expected human-induced global change factors to be weakening trait-environment relationships. Contrary to those expectations, most traits were highly associated with soil, climate, and/or forest cover in both time periods. Leaf thickness alone is losing its association with environmental variables, which may reflect losses of thick-leaved evergreen species in northern ecoregions.

Although the relationships between traits and the environment seem stable, there is no guarantee that this will continue if the rate of global change increases. Accelerating ecological change (particularly climate change) could cause disequilibria between traits and the environment going forward (Laughlin et al. 2011a). Over the 50-year interval from 1960 to 2010, Wisconsin experienced substantial warming in many areas of the state along with drying in the north and spotty higher rainfall in the south (Kucharik et al. 2010). Several of these climate shifts appear related to the changes we have observed in plant abundance (D. Waller, unpublished data). Climate change is expected to speed up, and as it does so, species that do not currently extend to northern Wisconsin sites could begin to grow there, assuming that they have the capacity to migrate across the fragmented landscape of southern and midstate forests (Honnay et al. 2002, Rogers et al. 2009, Early and Sax 2011).

Wisconsin forest plant communities have shifted in trait values as well as diversity and composition over the past 50 years, particularly in the two southern ecoregions. These changes reflect a shift toward species with more nutrient-rich, easily decomposable aboveground parts. These trait value shifts reflect shifts in community composition from sedges and grasses to more shade-tolerant, high specific leaf area (SLA), native deciduous forbs (Lusk and Warton 2007, Rogers et al. 2008, Meers

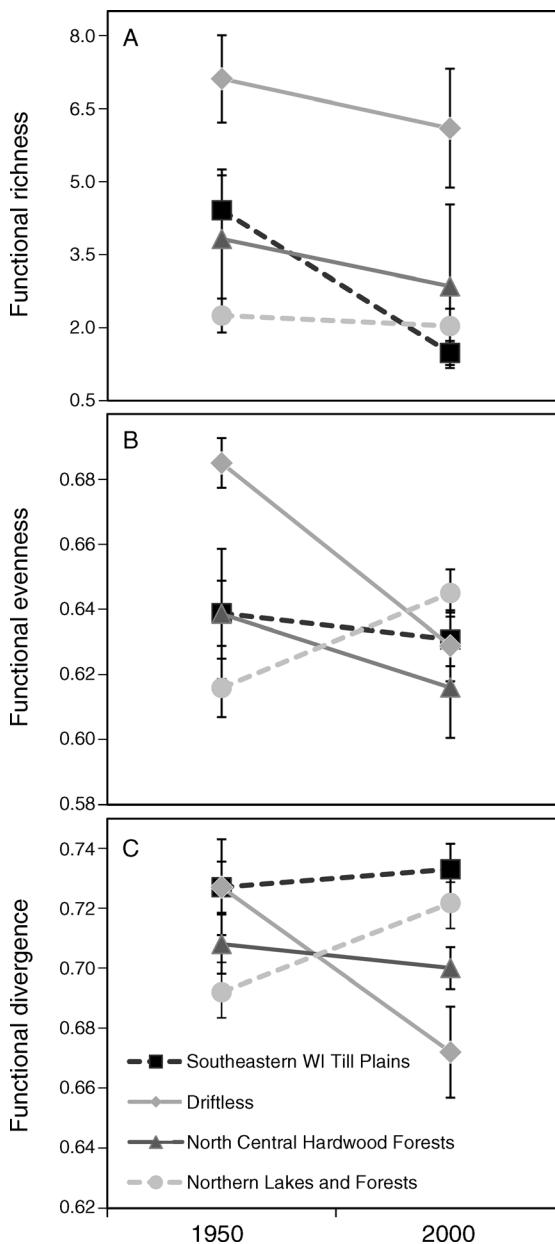


FIG. 4. (A) Functional richness, (B) functional evenness, and (C) functional divergence (all as mean \pm SE) by ecoregion and time period: 1950 (1944–1953) and 2000 (1996–2005). Higher functional richness values indicate a greater volume of occupied trait space. Higher functional evenness values indicate more even distribution of trait values with that volume. Higher divergence values indicate that more abundant species have more extreme trait values.

et al. 2010). This could reflect succession and mesification (transitions toward more shade-tolerant species with thinner leaves), increases in aerial N deposition, or another factor. Increases in SLA and foliar nutrients and declines in leaf dry matter content (LDMC) and recalcitrant carbon will likely increase rates of decomposition (Cornelissen and Thompson 1997, Dahlgren et

al. 2006, Lusk and Warton 2007, Cornwell et al. 2008, Meers et al. 2010, Carlucci et al. 2012, Joner et al. 2012, Siefert 2012). As litter decomposition accelerates so will nutrient release, altering interactions with microbes. Trends in the understory are likely to amplify similar trends in the overstory as oak litter is replaced by litter from maples and other species richer in nutrients and poorer in recalcitrant carbon (Finzi et al. 1998, Lovett et al. 2004, Rogers et al. 2008). Invasions by earthworms and their increasing abundance could accelerate these trends (Bohlen et al. 2004, Hale et al. 2005). Increases in the rate of nutrient cycling and available nutrients could drive further changes in species composition. Many exotic species, for example, have high rates of uptake and thrive in nutrient-rich environments (Ehrenfeld 2004, Lake and Leishman 2004). Exotic species have increased in relative abundance from an average of 1.2% in the 1950s to 8.4% in the 2000s across the southern ecoregions despite few recent disturbances (Rogers 2006).

Sites in the Driftless ecoregion originally had and continue to maintain higher species and trait richness than sites in other parts of Wisconsin despite steep declines in other functional diversity metrics (Rogers 2006). High species and functional richness probably reflects Driftless sites' topographic diversity, high soil fertility, and distinct disturbance history, all factors that contribute to species and trait richness. They could also reflect higher phylogenetic diversity (Mouchet et al. 2010). However, the variety of plant traits present also reflects the environmental filtering and competition processes that occur during community assembly (Keddy 1992). A high functional richness implies weak environmental filters and/or strong competitive filters, making it complicated to disentangle these by looking solely at functional richness (Ackerly and Cornwell 2007). Driftless sites in the 1950s also had the highest functional evenness and high functional divergence that have since eroded steeply. These metrics suggest that competitive filtering favored a radiation of trait forms under the original conditions that have since declined in response to the loss of particular trait complexes (Mouchet et al. 2010). These should be examined in more detail to gain insights into what is driving these ecological changes.

The general decreases in functional diversity apparent in most ecoregions may be diminishing the ability of these forest communities to resist, or resiliently respond to, shifts in environmental conditions. Rare species may be particularly able to respond quickly to disturbances that change the environmental filters in an ecosystem (Walker et al. 1999, Thompson et al. 2010). Yet rare species have declined the most in these forests over the past 50 years (Rooney et al. 2004, Rogers et al. 2008). As plant communities in the Southeastern Wisconsin Till Plains and Driftless ecoregions converge in trait profiles they could also be converging in ecosystem function, potentially reducing the diversity of processes and

ecosystem services across the landscape (Olden et al. 2004, Clavel et al. 2011).

In contrast to the shifts observed in the southern ecoregions, trait means remained steadier in the Northern Lakes and Forests sites between the 1950s and 2000s. This seems surprising given that many sites have lost evergreen shrubs and conifer seedlings and saplings while gaining grasses and sedges (Amatangelo et al. 2011). However, this transition from evergreen to deciduous species was already well underway by 1950 (Stearns 1949). The increases in leaf length : width ratio and declines in foliar Ca observed in the Northern Lakes and Forests region probably reflect the linear leaves and very low leaf Ca of grasses and sedges (Broadley et al. 2003). Wiegmann and Waller (2006) noted similar shifts toward ferns, monocots, and abiotically pollinated and small-seeded species. Other factors such as invasive earthworms may also be altering forest floor nutrient relations, but these have not yet appreciably affected trait spectra. Two of the factors implicated in changing trait profiles in the south, increasing exotic species and landscape fragmentation, are still rare in the north. Exotic species averaged 2.0% of the total understory frequency in the 2000s (Rooney et al. 2004). However, if global changes accelerate as predicted, they are likely to increase their impact on these northern forests, and trait values may change as a result.

Sites in the Northern Lakes and Forests ecoregion have increased in the evenness of trait distributions and functional divergence, despite losing rare species. The increasing abundance of once-rare grasses and sedges in these sites, coupled with decreases in previously dominant evergreen species, has contributed to this more even distribution of life forms (Rooney et al. 2004, Amatangelo et al. 2011). Increasing evenness is also consistent with stronger competitive filtering at these sites (Mouchet et al. 2010) as forests, particularly those in drier sites, get shadier as maples replace oaks, birches, and pines (Amatangelo et al. 2011). Nonetheless, continued deer overabundance and fire suppression may eventually reduce functional diversity in these northern forests.

Across the state, canopies are closing as *Acer* species increase in dominance. This process of forest mesification provides shadier environments, favoring thinner and larger leaves for understory deciduous species (Lusk and Warton 2007). However, the relationships we found between overstory structure and trait changes were often weak, in contrast to another study investigating long-term structural changes on understory forest traits (Laughlin et al. 2011b). This may reflect the weakening of overstory-understory linkages at these Wisconsin sites (Rogers et al. 2008, Amatangelo et al. 2011). Changes in overstory structure and composition could eventually act to shift understory trait values, but this process may be slow and thus not yet evident. This could change as forest composition continues to converge as

once-dominant species like *Quercus* spp., *Pinus* spp., and *Thuja occidentalis* fail to recruit into the overstory.

CONCLUSION

We observed strong shifts in within-site trait composition and diversity through time. These parallel the conspicuous shifts in species composition and diversity that have occurred at these sites over the past 50 years. How trait composition and diversity change, however, appears to vary across landscapes that differ in disturbance history and environmental conditions. Changes in both diversity and trait values were largest in the smaller and more fragmented southern forests, suggesting that these forests may have lower functional resilience to further changes in climate and landscape conditions. Additionally, the strong associations we found between plant traits and environmental conditions across ecoregions suggest that forests may face increasing disequilibria as climate and other environmental changes accelerate.

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SUPPLEMENTAL MATERIAL

Appendix A

Maps of environmental variables quantified at each site, including climate, soil, and vegetation cover data ([Ecological Archives E095-157-A1](#)).

Appendix B

Results of fourth-corner analyses for plant traits and environmental variables in two time periods ([Ecological Archives E095-157-A2](#)).

Appendix C

Foliar chemistry trait community-weighted site means presented and analyzed by ecoregion and time period ([Ecological Archives E095-157-A3](#)).

Appendix D

Multiple linear regression results for all traits included in the study ([Ecological Archives E095-157-A4](#)).

Appendix E

Multiple linear regression results for functional diversity metrics ([Ecological Archives E095-157-A5](#)).

Appendix F

Rank correlations between changes in community-weighted trait mean values and changes in overstory structure and composition between the 1950 and 2000 time periods ([Ecological Archives E095-157-A6](#)).