Landscape Ecol
DOI 10.1007/s10980-012-9805-5

RESEARCH ARTICLE

Comparison of historical and current forest surveys for detection of homogenization and mesophication of Minnesota forests

Brice B. Hanberry · Brian J. Palik · Hong S. He

Received: 16 April 2012 / Accepted: 1 October 2012

Abstract Intense harvesting and slash fires during the late 1800s and early 1900s led to homogenization throughout the Great Lakes region via the conversion from tamarack, pine, and spruce forests to aspen forests, which are supported by the forest products industry. Subsequently, mesophication occurred in the eastern United States due to fire suppression, transforming oak woodlands to mixed mesophytic forests. We explored both homogenization and mesophication at a regional scale by quantifying changes in community composition and density between historical General Land Office survey points and current USDA Forest Analysis and Inventory plots for Minnesota's Laurentian Mixed and Eastern Broadleaf Forest provinces. We used the Morisita plotless density estimator and applied corrections for surveyor bias to estimate density for historical forests and we used known densities of FIA plots to predict current densities with random forests, an ensemble regression tree method, and terrain and soil predictor variables. Of the 43 ecological units used in the analysis, only one current community was similar to its historical counterpart. Within the Laurentian Mixed Forest province, forest density of primarily mature aspen stands is reduced slightly today compared to the tamarack-dominated forests of the past. Conversely, in the Eastern Broadleaf Forest province, forest densities have increased compared to historical pine and oak woodlands, due to increases of densely growing, fire-sensitive species. Ordinations of functional traits and structure showed substantial changes between current and historical communities as well as reduced differentiation among current communities compared to their historical counterparts. Homogenization in the Laurentian Mixed Forest is occurring by transition from early-successional to late-successional species, with associated changes in forest ecosystems, and homogenization and mesophication in the Eastern Broadleaf Forest are occurring by transition from disturbance-stabilized genera of open forest ecosystems to non-disturbance-dependent genera of dense forests. Despite different starting points of historical forest ecosystems in the Laurentian Mixed Forest and Eastern Broadleaf Forest, we found homogenization and mesophication to be interrelated in the convergence of composition and densities along a common trajectory to dense forests composed of late-successional species in Minnesota.

Keywords Aspen · Drought · Historical ecology · General Land Office · Succession · Tamarack

Electronic supplementary material The online version of this article (doi:10.1007/s10980-012-9805-5) contains supplementary material, which is available to authorized users.

B. B. Hanberry (✉) · H. S. He
Department of Forestry, University of Missouri,
203 Natural Resources Building, Columbia,
MO 65211, USA
e-mail: hanberryb@missouri.edu

B. J. Palik
USDA Forest Service, Northern Research Station,
Grand Rapids, MN 55744, USA

Published online: 09 October 2012

Introduction

Olden and Rooney (2006) defined biotic homogenization as a replacement process by which the genetic, taxonomic, or functional similarities of regional biotas increase over time. In the context of forest ecosystems, regional taxonomic homogenization occurs with loss of spatial differentiation in species compositions that formerly existed along environmental gradients (Foster et al. 1998; Fuller et al. 1998; Oswald et al. 2007). Concurrent with taxonomic homogenization, life history traits may either confer new advantages or conversely disadvantages under anthropogenic conditions, resulting in functional homogenization (McKinney and Lockwood 1999; Olden and Rooney 2006).

Homogenization of mixed forests, which have become primarily broadleaved at the expense of conifers, in the Great Lakes region of the Unites States has occurred by loss of spatially differentiated communities and also, though not strictly homogenization, simplification of structural complexity (Palik and Pregitzer 1992; White and Mladenoff 1994; Friedman and Reich 2005; Schulte et al. 2007; Rogers et al. 2008). After intense harvesting and repeated slash fires during the late 1800s and early 1900s, mixed coniferous forests transformed into aspen forests (Cole et al. 1998; Friedman and Reich 2005). Aspen, an early-successional species with strong post-disturbance sprouting ability, replaced late-successional spruce and disturbance-stabilized pines in the presence of an altered fire regime that first occurred too intensely, destroying aerial seed sources and advance regeneration, then was absent later due to fire suppression (Bergeron and Brisson 1990; Palik and Pregitzer 1992). Aspen also became a preferred species for paper and pulp, unlike other pioneer species such as birch and tamarack, and thus benefited from current harvesting practices, unlike pine and perhaps tamarack that were removed through selective logging/high-grading without replacement (Pinto et al. 2008).

Mesophication is another process that has influenced regional forest composition. Mesophication of broadleaf forests throughout the eastern United States is occurring via replacement of fire-stabilized oaks and pine by fire-sensitive species, specifically shade-tolerant mesophytic species (Nowacki and Abrams 2008). Oak savannas probably covered around 2 million hectares of Minnesota, but disappeared within 20–40 years after Euro-American settlement, due to fire suppression and agricultural conversion (Nuzzo 1986). Without fire, fire-sensitive species successfully invaded oak forest ecosystems and out-competed oaks, which allocate more resources to below-ground root growth to survive fire and drought (Crow 1988; Abrams 1990). A positive feedback loop developed, whereby increasing shade and moisture in forests further facilitate highly competitive mesophytic trees over oaks (Grimm 1983; McCune and Cottam 1985; Nowacki and Abrams 2008).

The patterns of homogenization and mesophication constitute changes in forest composition, and these processes also may establish changes in forest structure and function. We quantified historical and current forests through General Land Office (GLO) and USDA Forest Service Forest Inventory and Analysis (FIA) surveys respectively for the entire extent of Minnesota's forested provinces (Fig. 1). We then explored the following questions: How have current forests changed in community and structure compared to historical forests? What changes occurred by ecological province and within ecological provinces? Do changes in composition of trees by transition class (i.e., shade-intolerant pioneers, disturbance-stabilized oaks and pine, and shade-tolerant mesic species, which indicate different community and structure) and leaf class (i.e., needled vs. broadleaved) reflect homogenization and mesophication? How are homogenization and mesophication related and how are changes in Minnesota's forested provinces related? To our knowledge, this is the first study to compare communities and densities from historical and current trees surveys in Minnesota's forested provinces and examine both homogenization and mesophication concepts for these functional classes across a large spatial scale.

Methods

Overview

We analyzed historical and current communities, densities, and NMS ordinations for sub-regional ecological units within each province (see Appendix in electronic supplementary material for detailed overview of task flow). Communities were designated by dominant trees in the ecological unit. We estimated

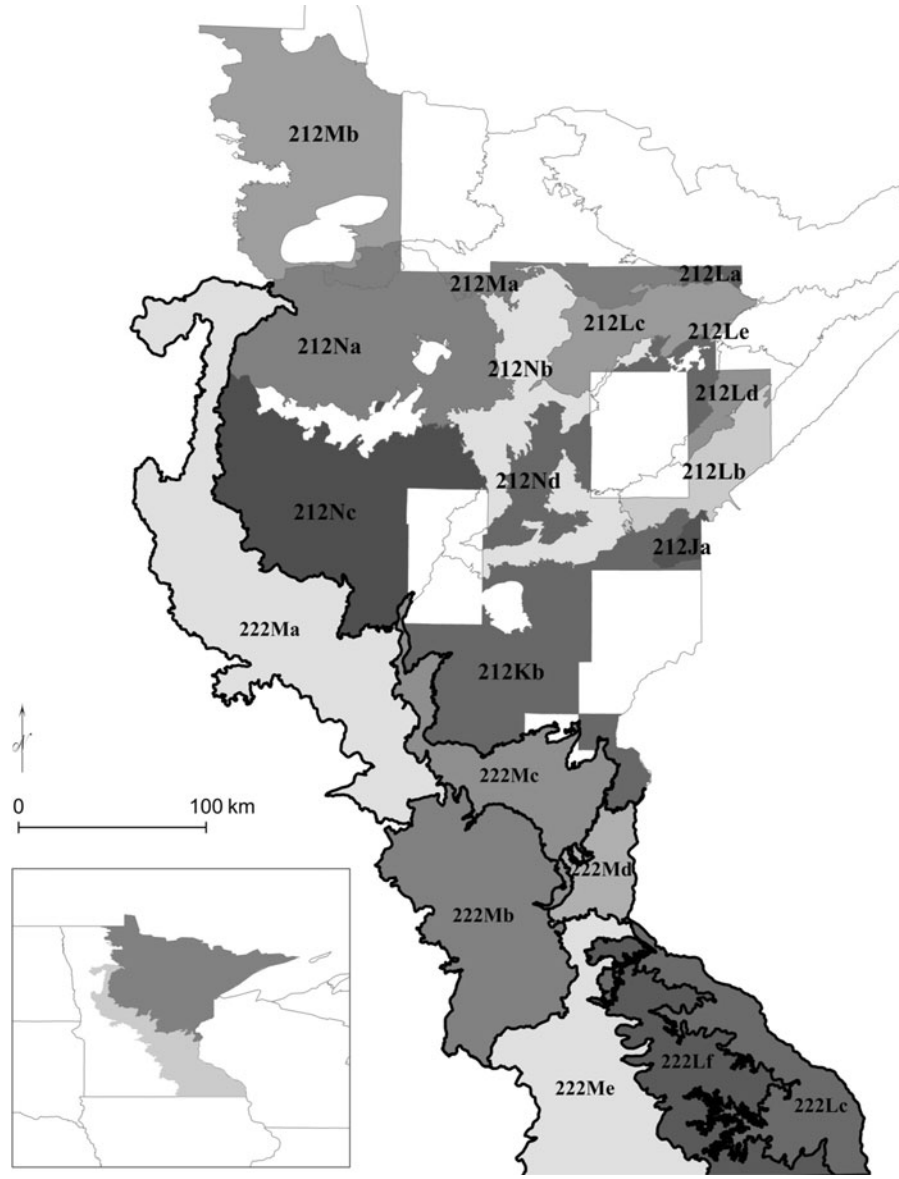


Fig. 1 Ecological subsections (*darkly outlined*) within the Eastern Broadleaf Forest province (222 prefix) and the Laurentian Mixed Forest province (212 prefix)

historical densities using the Morisita estimator and then adjusted estimates for spatial patterns and surveyor bias. We estimated current densities using known densities at plots and then predicted density using random forest regression trees and 16 predictor variables. We lastly ran ordinations of density and either leaf type of transitional class.

Historical data

In 1812, the United States GLO developed the Public Land Survey System of townships that measured 9.6 km on a side and contained thirty-six 1.6 km^2 (1 $mile^2$) sections (White 1983). Surveyors recorded species, distance, bearing, and diameter for two to four trees every 0.8 km at the corners and middle of each section line. We selected trees surveyed mostly between 1847 and 1908, from the Laurentian Mixed Forest and Eastern Broadleaf Forest provinces of Minnesota (Fig. 1) in the GLO dataset (J. Almendinger, Minnesota Department of Natural Resources, http://deli.dnr.state.mn.us). Due to limited sampling of smaller diameter trees, we selected trees with diameter (DBH) $\geq$ 12.7 cm.

Current surveys

Every 5 years, the USDA Forest Service FIA surveys nationwide long-term plots, spaced about 2,500 ha apart, to monitor current forest conditions. Each plot contains four 7.31 m radius subplots, configured as a central subplot surrounded by three outer subplots. We used data from the latest complete cycle of 2004–2008. We selected live trees with a DBH $\geq$ 12.7 cm due to limited sampling of smaller diameter trees in GLO and FIA surveys.

We grouped some tree species in FIA surveys to parallel documentation of these species in GLO surveys (which often did not distinguish similar species). The groupings were as follows: ashes (*Fraxinus nigra*, *F. pennsylvanica*, *F. Americana*), birches (*Betula papyrifera*), elms (*Ulmus americana*, *U. rubra*, *U. thomasii*), maples (*Acer rubrum*, *A. saccharum*, *A. saccharinum*), aspens (*Populus tremuloides*, *P. grandidentata*, *P. balsamifera*), red oaks (*Quercus nigra*, *Q. ellipsoidalis*, *Q. rubra*), white oaks (*Quercus alba*, *Q. macrocarpa*), spruces (*Picea mariana*, *P. glauca*), cherries (*Prunus* spp.), hickories (*Carya cordiformis*, *C. ovata*), and walnuts (*Juglans cinerea*, *J. nigra*).

Community rules

In the Laurentian Mixed Forest, we developed communities for GLO and FIA data in 47 ecological units based on subsection and land type associations, such as moraines or plains (designated by Cleland et al. 1997; see Table 1 for complete list). In the Eastern Broadleaf Forest, our ecological units for communities were seven subsections due to limited number of FIA survey plots. We set a minimum count of at least $\geq$200 trees per ecological unit to determine each community type. To classify dominant species in a community, while limiting communities to no more than five species yet allowing for species representation, percent composition of species had to be $\geq$12 % per ecological unit in the Laurentian Mixed Forest and $\geq$10 % per ecological unit in the Eastern Broadleaf Forest. To make comparisons easier, we labeled communities by dominant species, regardless of actual frequency, in the same order for both historical and current communities. The order that we listed dominant species in community was based on descending mean percent composition for all combined GLO and FIA trees at the province level. That is, aspen had the combined greatest percent composition in the Laurentian Mixed Forest province and thus was the first species listed for any ecological unit with aspen composition $\geq$12 %, regardless of any species with greater frequency.

Historical density

To prepare GLO data, we converted link distances to meters (i.e., one link equals 0.20 m) and added the radius of the tree diameter to the distance. We retained survey points with 2–4 trees per point, excluding any non-systematic points. Due to variability of density estimates when there was a clustered spatial pattern for points with four trees (Hanberry et al. 2011), we removed the most distant tree to convert points with four trees into points with three trees.

We calculated density with the Morista estimator (Morisita 1957), based on the area of circles around trees. The Morista estimator is

$$\lambda = \frac{(q-1)}{\pi n} \sum_{i=1}^{n} \frac{q}{\sum_{j=1}^{q} r_{ij}^2} \quad (1)$$

where λ (density) is the number of trees/unit area, q is the number of quadrants with surveyed trees (2, 3, or 4), n is the number of plots, and r is the survey point-to-tree distance. We estimated density by the number of trees per survey point for all survey points within an ecological unit. To provide an initial reliable density estimate (at least $\pm$20 %) for each ecological unit, we set the minimum number of survey points at 200 for survey points with two trees and at 50 for survey points with three trees (Hanberry et al. 2011). There were four ecological units (see JaLakePlain, JaTillPlain, LaMoraine, MaRidge in Table 1) in the Laurentian Mixed Forest that had density estimates based on fewer than 200 survey points; all other initial density estimates probably were within $\pm$5 or 10 % of actual densities. We then produced a low and high value based on adjustment for potential spatial patterning (clustered or regular patterns; Hanberry et al. 2011), which we carried into the low and high corrections for surveyor bias.

Due to GLO survey instructions to surveyors for tree selection (e.g., trees of moderate diameter; White 1983), surveyors potentially did not select the nearest

Table 1 Communities (any species ≥10 %) and densities (trees/ha) of historical (GLO) and current (FIA) forests (trees ≥12.7 DBH) by ecological unit (subsection and land type) in the Laurentian Mixed Forest

Ecological unit	GLO community	FIA community	GLO density			FIA density		
			Mean	Low	High	Mean	Low	High
JaLakePlain	Tamarack-spruce-white_pine		391	272	471			
JaTillPlain	Spruce-birch-fir-white_pine	Aspen-birch	404	281	487	367	276	458
KbDrumlinPlain	Aspen-tamarack	Aspen-ash	369	237	460	391	329	453
KbLakePlain	Tamarack-maple		424	266	540			
KbMoraine	Tamarack-birch	Aspen-maple-ash	358	228	453	386	331	441
KbPeatlands	Tamarack	Aspen-maple-ash	512	340	625	399	350	448
KbSandPlain	Tamarack-red_pine		304	195	379			
KbTerraces	Aspen-tamarack		321	199	410			
KbTillPlain	Tamarack-birch	Aspen-maple-ash	463	299	578	385	331	440
LaBedrock	Spruce-birch-jack_pine	Spruce-cedar-ash	492	324	604	379	322	435
LaMoraine	Spruce-birch		547	402	622			
LaTillPlain	Spruce-birch		422	281	517			
LbBedrock	Spruce-birch-fir		486	278	675			
LbMoraine	Tamarack-spruce-birch	Aspen	517	315	681	418	339	498
LbSandPlain	Tamarack-spruce-birch-white_pine	Aspen-spruce-cedar-maple-fir	699	414	942	454	364	545
LbTillPlain	Spruce-birch-fir	Aspen-maple-ash-fir	473	293	615	518	415	620
LcMoraine	Tamarack-spruce-birch	Aspen-spruce	539	350	669	331	243	419
LcRange	Birch	Birch-maple	528	335	671	314	259	370
LcSandPlain	Tamarack-spruce-birch-jack_pine	Aspen-spruce-fir	376	245	466	348	253	443
LcTillPlain	Tamarack-spruce-birch-white_pine	Aspen-cedar	480	307	599	395	328	462
LdDrumlinPlain	Tamarack-spruce-birch	Aspen-spruce-birch-cedar-fir	511	325	650	400	329	472
LeMoraine	Tamarack-spruce-birch-jack_pine		399	250	511			
LeTillPlain	Spruce-birch-jack_pine		598	380	754			
MaPeatlands	Tamarack-spruce		635	420	771			
MaRidges	Tamarack-spruce-jack_pine		475	324	583			
MaTillPlain	Aspen-tamarack-spruce	Aspen-spruce-cedar-ash	521	341	643	407	328	485
MbLakePlain	Aspen-tamarack-spruce-cedar	Aspen-tamarack	468	308	574	372	308	436
MbPeatlands	Tamarack-spruce	Aspen-tamarack-spruce-cedar	596	383	747	460	359	561
MbRidges	Tamarack-spruce-jack_pine	Aspen-tamarack-spruce-cedar-jack_pine	397	263	485	378	274	481
MbTillPlain	Aspen-tamarack-spruce	Aspen-tamarack-spruce	446	292	550	343	279	406
NaLakePlain	Tamarack-cedar	Aspen-tamarack-cedar-ash	585	396	702	427	337	518
NaMoraine	Tamarack-birch	Aspen	398	277	461	404	314	494
NaPeatlands	Tamarack-red_pine	Tamarack-cedar	344	240	402	369	287	451
NaSandPlain	Tamarack-jack_pine-red_pine	Aspen-red_pine	309	203	379	463	384	543
NaTillPlain	Aspen-tamarack-white_pine	Aspen	369	249	442	416	334	498
NbDelta	Birch-maple-white_pine	Cedar-maple	592	381	732	465	333	596
NbDrumlinPlain	Aspen-tamarack-birch	Aspen-maple-ash	429	266	554	396	332	461
NbLakePlain	Tamarack-spruce-birch	Aspen-tamarack-fir	442	283	553	379	303	455

Table 1 continued

Ecological unit	GLO community	FIA community	GLO density			FIA density		
			Mean	Low	High	Mean	Low	High
NbMoraine	Aspen-tamarack-birch	Aspen-maple-ash	537	351	663	423	348	499
NbTillPlain	Tamarack-spruce-birch	Aspen-fir	529	345	654	407	308	507
NcDrumlinPlain	Aspen-tamarack	Aspen-jack_pine-white_oak	350	229	432	373	302	445
NcMoraine	Aspen-jack_pine-red_pine-white_pine	Aspen-maple	313	205	387	365	309	421
NcSandPlain	Jack_pine-red_pine	Aspen-jack_pine-red_pine	210	137	259	383	330	436
NcTillPlain	Aspen-birch-white_pine	Aspen-tamarack-birch-maple	465	301	578	394	320	467
NdLakePlain	Tamarack-spruce	Aspen-ash	442	293	539	364	273	454
NdPeatlands	Tamarack-spruce	Aspen-tamarack-ash	608	402	741	379	292	466
NdTillPlain	Aspen-tamarack-spruce-birch	Aspen-spruce-fir	421	273	526	372	314	430
Mean values			457	297	569	395	318	473

Listed species order is the same for both GLO and FIA communities, regardless of frequency. Missing values for FIA community and density occur due to <200 trees for current forests

trees, which would produce a distance rank from the survey point of 1. Selection of more distant trees will result in underestimated densities. We adjusted density estimates by assuming that surveyors selected trees within a range of mean distance rank from 1.4 to 1.95 (a reasonable range of surveyor bias; Hanberry et al. 2012). Using a rank-based method, we estimated a low value, assuming trees selected had a mean rank of 1.4, and a mean value, assuming trees selected had a mean rank of 1.8. Using a complementary method to correct for surveyor bias in quadrants, azimuth, and species and diameter, we estimated density to reach a target rank of 1.8 for mean values and a target rank of 1.95 for high values. We found the frequencies for quadrant location, quadrant configuration, and azimuth by ecological unit and corrected for non-random frequencies by determining the adjustment quotient based on frequencies in regression equations (Hanberry et al. 2012). Azimuth was not recorded for at least 95 % of points in the Eastern Broadleaf Forest province and for some ecological units in the Laurentian Mixed Forest province. For missing azimuths in the Laurentian Mixed Forest province, we used mean values from ecological units with azimuths (but not for the Eastern Broadleaf Forest). For azimuth and species and diameter corrections in the Eastern Broadleaf Forest province and species and diameter corrections in the Laurentian Mixed Forest province, we adjusted density estimates based on correction values from simulations to reach a target rank of 1.8 for mean values and a target rank of 1.95 for high values.

We then averaged the two mean values from the two complementary methods and retained the low value from the rank-based method and high value from the bias method. We did not use a simple mean to produce one density estimate from the density estimates from points with two trees versus three trees. We took into account (1) the type of survey point by multiplying the count of points with three trees by two, giving these more accurate points (Hanberry et al. 2011) twice the weight of points with two trees and (2) the total number of points for each type of point by using a frequency weight, the count of points over the total count of points. We multiplied each density estimate by the frequency weight and summed the two values to determine the mean density by ecological unit.

Current density

We selected accessible FIA plots that were 100 % forestland and contained at least two trees. We calculated trees per acre, which we later converted to trees per hectare, using the provided expansion factor of 6.02, where one tree represents the inverse of the plot area in acres; 1/(4 * 0.042), and summed the values for each plot. To predict density for a continuous area based on discrete plots, we used random

forests regression trees (Breiman 2001; Cutler et al. 2007) with the randomForest package (Liaw and Wiener 2002) in R statistical software (R Development Core team 2010).

To predict density, we chose 16 predictor variables: ecological subsection and bedrock geology, seven soil variables, and seven DEM (digital elevation model)-derived topographic variables. The seven soil variables from Soil Survey Geographic; Natural Resources Conservation Service (SSURGO, http://soildatamart.nrcs.usda.gov) were (1) drainage class, (2) hydric soil presence class, (3) mean water holding capacity (cm/cm), (4) pH, (5) organic matter (%), (6) clay (%), and (7) sand (%) to either the soil profile depth or to a restriction depth and weighted by component percentage. The seven variables from a 30 m digital elevation mode were (1) elevation (m), (2) slope (%), (3) transformed aspect ($1 + \sin(\text{aspect}/180 * 3.14 + 0.79)$; Beers et al. 1966), (4) solar radiation (700–1,900 in 4 h intervals on summer solstice for re-sampled 60 m DEM), (5) topographic roughness (Sappington et al. 2007), (6) wetness convergence (T. Dilts, http://arcscripts.esri.com), and (7) topographic position index. We then calculated the mean value for each topographic variable by a unique prediction zone.

The SSURGO soil polygons were discrete spatial units but each unique prediction unit was based on a zone of soil map unit (i.e., soil polygons with similar soil characteristics), land type association, and geology, resulting in spatially disjunct predictions units with a mean area of 210 ha in the Laurentian Mixed Forest province, and a mean area of 146 ha in the Eastern Broadleaf Forest province. Due to lack of soils surveys in seven counties (Cook, Crow Wing, Isanti, Koochiching, Lake, Pine, and part of St. Louis) in the Laurentian Mixed Forest province, five subsections (Glacial Lake Superior Plain/Ja, St. Croix Morain/Jd, Border Lakes/La, Toimi Uplands/Ld, Laurentian Uplands/Le) had reduced areas.

We adjusted each predicted density estimate to determine the mean density by ecological unit. To provide a range of values that incorporated both uncertainty and variation, we calculated the standard deviation of the density estimates within each ecological unit and produced a low and high value based on the mean density by ecological unit $\pm$ the standard deviation (about 45 and 72 trees/ha in the Eastern Broadleaf Forest and Laurentian Mixed Forest provinces, respectively).

Ordination by functional trait and density

Nonmetric multidimensional scaling (NMS) is a method to graphically represent species composition along axes based on a (dis)similarity matrix; distance between graphed points represents degree of (dis)similarity. We chose the Sorensen/Bray-Curtis distance measure to represent differentiation within and between ecological units historically and currently based on functional traits and density. Although density does not directly represent taxonomic or functional homogenization, changes in structure occur in conjunction with changes in species composition and functional traits. Fire removes woody biomass of fire-sensitive species and thus without fire, composition shifts to species with different functional traits and density increases. We therefore incorporated structure into functional homogenization, resulting in a functional and structural examination of homogenization.

We analyzed functional traits of leaf class (needled or broadleaved) for the Laurentian Mixed Forest and transitional class for both provinces separately and in combination. There were three transitional classes: early-successional, late-successional, and disturbance-stabilized. We defined early-successional, shade-intolerant pioneers by shade tolerance <2.0 (Niinemets and Valladares 2006) and representative of early-successional forest ecosystems produced by stand-replacing fires. We defined later-successional species with greater shade tolerance by shade tolerance ≥ 2.0 and representative of late-successional forest ecosystems. In contrast, disturbance-stabilized species of pine and oak are fire-tolerant and not transitional given a continuous ground fire regime, thus pine and oak represent stable oak and pine savannas and woodlands.

We removed one ecological unit the Laurentian Mixed Forest, the sand plain in the Nc subsection due to extreme dissimilarity with other ecological units. Based on pre-testing, we chose 2-dimensional solutions (ecodist package in R by Goslee and Urban 2007). We checked that all stress values, a measure of distance between original space and ordination space, remained under 0.1.

Results

Community changes from fire-dependent pine and oak

In the Laurentian Mixed Forest province, one community (aspen-tamarack-spruce of the till plain in ecological subsection Mb; Fig. 2) remained the same in historical and current forests of the 36 ecological units with at least 200 FIA trees of DBH $\geq$ 12.7 cm (Table 1). Aspen was the current dominant species in 32 of the ecological units, whereas aspen historically was a dominant species in only 11 of the ecological units. Tamarack (*Larix laricina*), spruces, birches, and the three pines (jack, *Pinus banksiana*; red, *Pinus resinosa*; eastern white, *Pinus strobes*) were the dominant species in the past and were less common currently. Maples, northern white cedar (*Thuja occidentalis*), and balsam fir (*Abies balsamea*; an extremely shade-tolerant species) became more common and ashes in particular, which historically were not a dominant genus, became a dominant genus in 12 ecological units. In GLO surveys, about 45 % of species were early-successional, 23 % of species were disturbance-dependent (pine or oak), and 32 % of species were late-successional. In FIA surveys, about 39 % of species were early-successional, 15 % of species were disturbance-dependent, and 46 % of species were late-successional. For trees <12.7 cm in FIA surveys, 54 % of species were early-successional, 4 % of species were disturbance-dependent, and 42 % of species were late-successional. The proportion of needled-to-broadleaved trees essentially flip-flopped from historical to current times. In GLO surveys, about 65 % of species were needled and 35 % of species were broadleaved. In FIA surveys, about 37 % of species were needled and 63 % of species were broadleaf. For trees <12.7 cm in FIA surveys, about 29 % of species were needled. Change varies by ecological unit for both transitional and leaf class and generally along an east to west gradient as subsections became exposed to fires from western prairies and savannas (Table 3).

No communities were the same as in the past in the Eastern Broadleaf Forest province (Table 2), due to genus additions of elms, boxelder (*Acer negundo*), aspen, maples, American basswood (*Tilia americana*), ashes, or red pine (due to successful plantations) and subtractions of oaks from communities. Historically, white oaks were a dominant taxa in all seven subsections and red oaks were a dominant taxa in all but one subsection. In current forests, white oaks were no longer a dominant taxa in one subsection whereas red oaks were no longer a principal taxa in three of the six subsections it formerly dominated. In current forests, elms, boxelder, aspen, maples, or red pine became dominant species in the five subsections that historically were dominated by white oaks and red

Table 2 Communities (any species $\geq$12 %) and densities (trees/ha) of historical (GLO) and current (FIA) forests (trees $\geq$12.7 DBH) by subsection in the Eastern Broadleaf Forest

Subsection	GLO community	FIA community	GLO density			FIA density		
			Mean	Low	High	Mean	Low	High
Lc\The Blufflands	White_oak-red_oak	White_oak-red_oak-elm	94	61	116	314	275	353
Lf\Rochester Plateau	White_oak-red_oak	White_oak-elm-boxelder	72	46	89	310	284	336
Ma\Hardwood Hills	White_oak-aspen	White_oak-aspen-maple-basswood-ash	303	200	369	357	292	423
Mb\Big Woods	White_oak-red_oak-elm-aspen-basswood	Elm-maple-boxelder-basswood-ash	206	135	251	311	281	340
Mc\Anoka Sand Plain	White_oak-red_oak	White_oak-red_oak-aspen-red_pine	98	64	120	307	230	383
Md\St. Paul-Baldwin Plains	White_oak-red_oak	White_oak-red_oak-red_pine	122	76	154	333	294	372
Me\Oak Savanna	White_oak-red_oak	White_oak-elm-maple-boxelder	77	51	93	295	257	334
Mean values			139	90	170	318	273	363

Listed species order is the same for both GLO and FIA communities, regardless of frequency

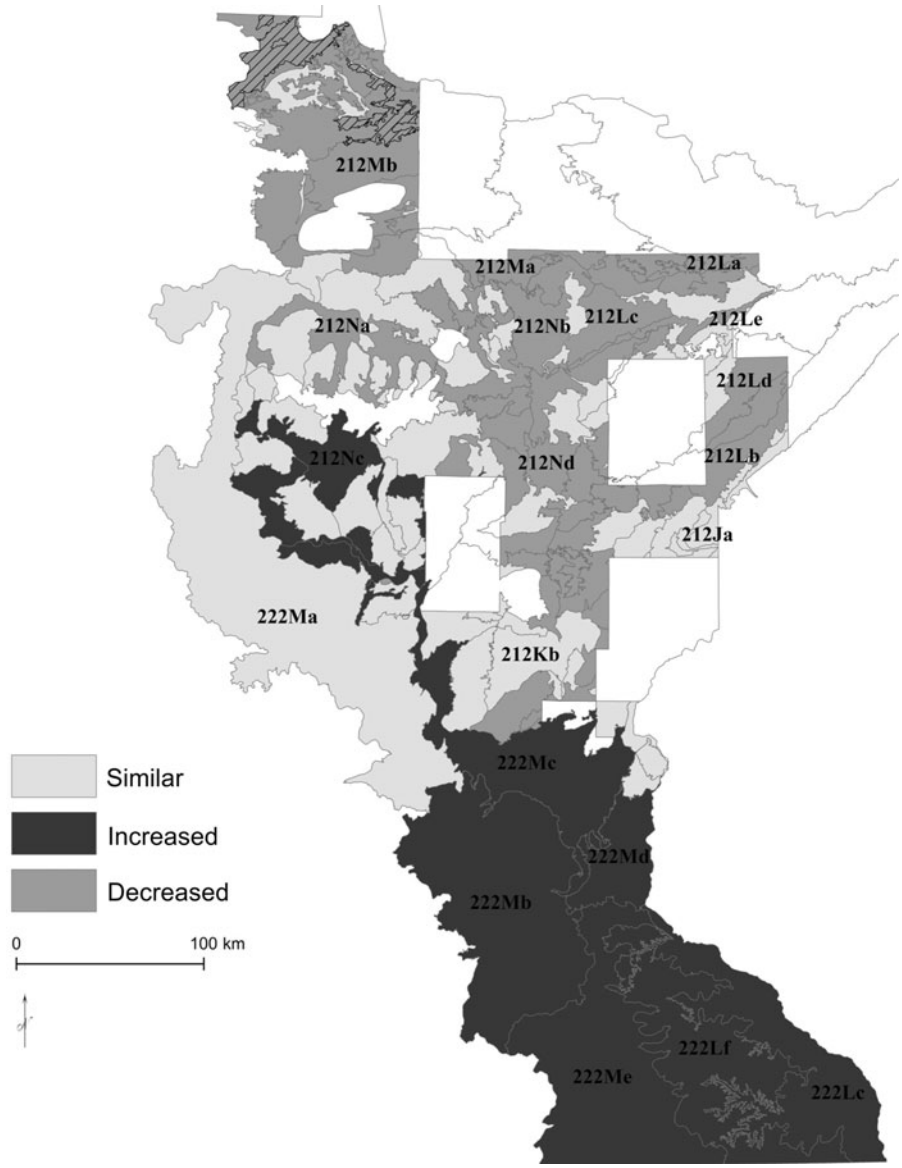


Fig. 2 Changes in tree density (trees ≥12.7 cm DBH) from historical to current forests by ecological unit. Ecological units with "increased" or "decreased" tree density had non-overlapping density ranges, whereas those with "similar" tree densities had overlapping ranges (see Tables 1, 2). All communities have changed except in the striped ecological unit of northern Laurentian Mixed Forest. Land type associations are outlined in the Laurentian Mixed Forest. *Blank areas* did not have soil surveys

oaks only. Boxelder, maples, ashes, and red pine were new dominant species. The few species that were adapted to a continuous fire regime decreased and were replaced by a variety of species; thus, dominant species included about 76 % of trees in GLO communities but only 55 % of trees in FIA communities. In the GLO surveys, about 54 % of species were oaks, 19 % of species were early-successional, and 27 % of species were late-successional. In FIA surveys, about 24 % of species were oaks and 5 % were pines, 18 % of species were early-successional, and 53 % of species were late-successional. For trees <12.7 cm in FIA surveys, 6 % of species were oak and 73 % of species were late-successional. Change varies by ecological subsection, due to variation in firebreaks of lakes and water bodies remaining after glaciation. The ecological subsections of Ma, the Hardwood Hills, and Mb, Big Woods were named accurately based on historical presence of fire-sensitive species.

Density changes

In the Laurentian Mixed Forest province, historical densities were slightly greater by a factor of 1.15 than

Table 3 Percent disturbance-stabilized (% oak and pine), early-successional (early), late-successional (late), broad-leaved, and needled species of historical (GLO) and current (FIA) forests (trees ≥12.7) by ecological unit of subsection and land type association in the Laurentian Mixed Forest or subsection in the Eastern Broadleaf Forest of Minnesota

Ecological unit	NMS ID	GLO surveys			FIA surveys			GLO surveys		FIA surveys	
		% Oak and pine	% Early	% Late	% Oak and pine	% Early	% Late	% Broadleaf	% Needle	% Broadleaf	% Needle
JaTillPlain	1	34	25	41	4	67	29	32	68	86	14
KbDrumlinPlain	2	27	45	28	19	34	47	65	35	97	3
KbMoraine	3	24	45	32	15	31	54	56	44	74	26
KbPeatlands	4	6	73	21	8	37	55	29	71	88	12
KbTillPlain	5	14	49	37	9	30	61	61	39	89	11
LaBedrock	6	32	36	32	3	21	76	27	73	42	58
LbMoraine	7	11	50	40	7	48	45	37	63	61	39
LbSandPlain	8	24	50	26	5	26	68	34	66	51	49
LbTillPlain	9	11	31	59	8	30	62	31	69	64	36
LcMoraine	10	20	41	39	8	46	46	30	70	59	41
LcRange	11	13	46	40	5	35	60	55	45	86	14
LcSandPlain	12	29	40	31	24	33	43	24	76	40	60
LcTillPlain	13	23	39	38	4	39	57	31	69	61	39
LdDrumlinPlain	14	14	47	39	5	36	58	31	69	50	50
MaTillPlain	15	8	43	49	9	38	53	34	66	55	45
MbLakePlain	16	8	54	38	9	53	38	28	72	48	52
MbPeatlands	17	1	71	28	5	52	43	9	91	38	62
MbRidges	18	27	48	25	21	37	42	12	88	21	79
MbTillPlain	19	1	62	36	4	49	47	31	69	47	53
NaLakePlain	20	16	46	38	4	41	55	28	72	49	51
NaMoraine	21	26	46	28	10	39	51	36	64	66	34
NaPeatlands	22	28	53	19	1	35	64	15	85	19	81
NaSandPlain	23	59	29	12	34	35	31	16	84	56	44
NaTillPlain	24	32	38	30	19	42	39	38	62	75	25
NbDelta	25	19	43	38	14	15	71	52	48	29	71
NbDrumlinPlain	26	5	63	33	2	43	55	53	47	87	13
NbLakePlain	27	23	40	37	9	53	38	24	76	56	44
NbMoraine	28	20	47	33	12	32	56	49	51	70	30
NbTillPlain	29	14	47	39	4	46	51	35	65	63	37
NcDrumlinPlain	30	31	54	14	46	36	18	42	58	70	30
NcMoraine	31	52	36	12	25	42	33	39	61	84	16
NcSandPlain	32	65	26	9	54	31	15	25	75	59	41
NcTillPlain	33	33	46	21	17	54	29	50	50	78	22
NdLakePlain	34	10	54	36	13	36	51	31	69	64	36
NdPeatlands	35	5	69	26	6	47	47	18	82	55	45
NdTillPlain	36	11	56	34	1	33	67	35	65	40	60
Lc	37	87	3	10	30	13	57				
Lf	38	92	4	4	22	13	65				
Ma	39	21	43	35	25	26	49				
Mb	40	32	14	54	13	6	81				
Mc	41	78	17	6	55	21	24				
Md	42	86	10	5	54	18	28				
Me	43	90	5	4	18	9	73				

Ecological units were simplified to NMS IDs for ordinations

current densities for trees with DBH ≥ 12.7 cm (Table 1), however most of the ecological units of subsection and land type association had overlap between historical and current high and low density values (Fig. 2). Historical densities averaged 457 trees/ha ranging by ecological units from 210 to 699 trees/ha whereas current densities averaged about 395 trees/ha ranging by ecological unit from 314 to 518 trees/ha. An exception to decreased density was one of the sand plains of the Nc subsection that historically was dominated by only jack pine and red pine. This ecological unit currently, with aspen as an additional dominant species, had a density estimate of 383 trees/ha (330–436 trees/ha), which was 1.8 times greater than historical density of 210 trees/ha (137–259 trees/ha).

In the Eastern Broadleaf Forest province, densities were about three times greater currently than in the past (Fig. 2). Indeed, not all of the Eastern Broadleaf Forest province was forested historically. Historical densities averaged about 139 trees/ha, ranging by ecological unit from 72 to 303 trees/ha (DBH ≥ 12.7 cm). Four subsections had densities below 100 trees/ha. Current densities were about 318 trees/ha, ranging by ecological unit from 295 to 357 trees/ha. All but one subsection had non-overlapping densities that were lower historically (Fig. 2). Subsection Ma, the Hardwood Hills, had a historical density of 303 trees/ha, whereas currently the mean density was 357 trees/ha.

Ordination

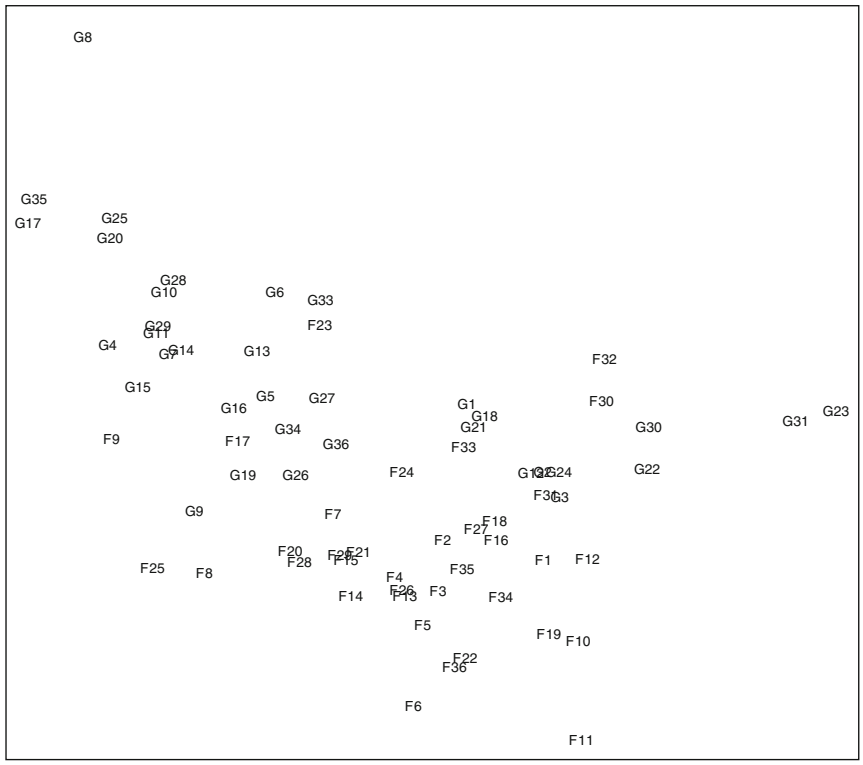
Ordination of ecological units by transitional class and density in the Laurentian Mixed Forest and Eastern Broadleaf Forest and leaf class and density in the Laurentian Mixed Forest show the extent of heterogeneity within historical and current forest composition and change over time. For transitional class in the Laurentian Mixed Forest, mean distance among historical communities was 0.14 ± 0.003, whereas currently it was 0.08 ± 0.001; mean movement over time was 0.14 ± 0.01 (Fig. 3). For leaf class in the Laurentian Mixed Forest, mean distance among the historical communities was 0.13 ± 0.002 compared to 0.09 ± 0.001 currently; mean movement over time was 0.15 ± 0.01 (Fig. 4). For transitional class in the Eastern Broadleaf Forest, mean distance among historical communities was 0.30 ± 0.03, whereas among current communities distance was 0.10 ± 0.007; mean movement by ecological unit over time was 0.42 ± 0.09 (Fig. 5). For transitional class of both forested provinces, mean distance among historical communities was 0.36 ± 0.02, whereas among current communities distance was 0.10 ± 0.003; mean movement by ecological unit over time was 0.26 ± 0.05 (Fig. 6).

Discussion

Patterns in community composition and density

Historically, the Laurentian Mixed Forest province in northeastern Minnesota contained dense forests dominated by pioneer species of tamarack, aspen, and birch that succeeded into spruce, with the exception of pure open pine barrens in the Nc ecological subsection. All but one community type changed due to additions of aspen, maples, cedar, and fir and a new dominant species, ash, and declines in coniferous tamarack, spruce, and the three pines (jack, red, white). In the Eastern Broadleaf Forest province, oaks decreased while a variety of fire-sensitive species increased in all communities. These general trends agreed with compositional changes in the mixed forests of the Great Lakes (Zhang et al. 2000; Friedman and Reich 2005; Schulte et al. 2007) and in broadleaf forests of the eastern United States (Nowacki and Abrams 2008).

The replacement of conifers by broadleaf species in the Laurentian Mixed Forest and conversion from fire-stabilized oaks to fire-sensitive species in the Eastern Broadleaf Forest were accompanied by changes in density. Where historical communities contained tamarack, aspen, birch, and spruce, forests became less dense, at around 0.85 of historical densities. Where the historical community was pine in the Nc ecological subsection, current aspen and pine forest density was 1.8 times greater than historical density. Other historical communities that contained pine, such as the Na Sand Plains, also tended to increase in density, as well as communities in the ecological subsections of Na and Nc. These western subsections probably experienced more frequent fire return intervals due to exposure to fires originating in the drier western portion of the state. Because the spatial extent in the study was larger than simply pine forests (i.e.,



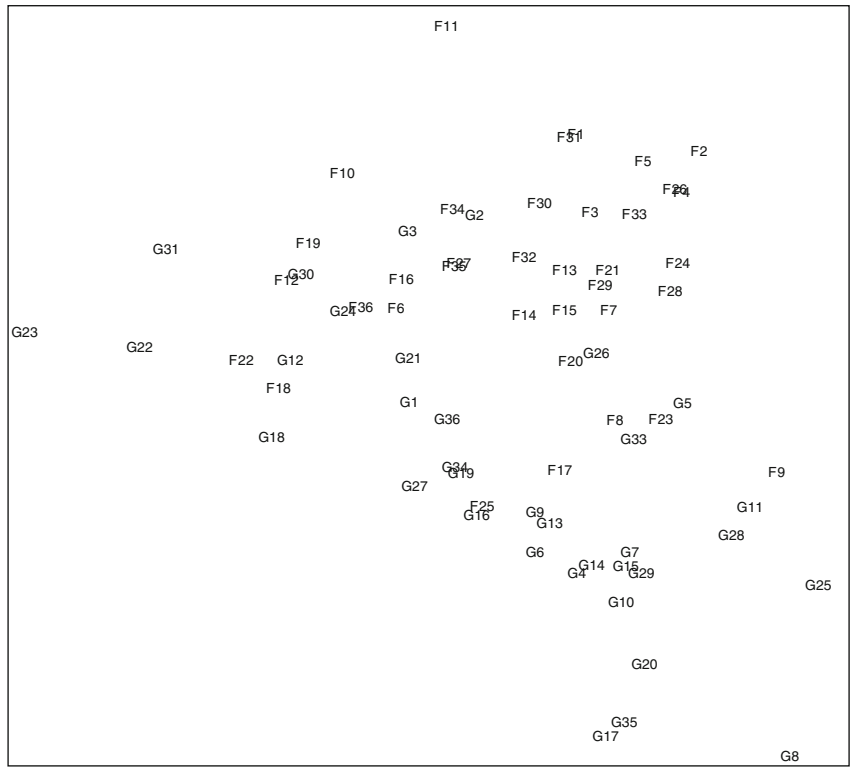
Ordination distance of transitional class and density among ecological units

Fig. 3 Ordination of ecological units by historical and current percent transitional class and densities in the Laurentian Mixed Forest province. Historical ecological units have prefix of *G* whereas current ecological units have prefix of *F*. Refer to Table 3 for NMS ordination ID number

includes tamarack, aspen, spruce, and birch as well), the difference will be magnified when comparing historical open pine barrens and woodlands with mixed pioneer and mesophytic species, which grow in denser forests. Lastly, where historical communities were oak in the Eastern Broadleaf Forest province, densities of current forests that included dominant American basswood, ashes, aspen, boxelder, elms, and maples were about three times greater than historical open forest ecosystems. Subsections with greater number of water bodies that acted as firebreaks changed less than subsections with more flammable conditions.

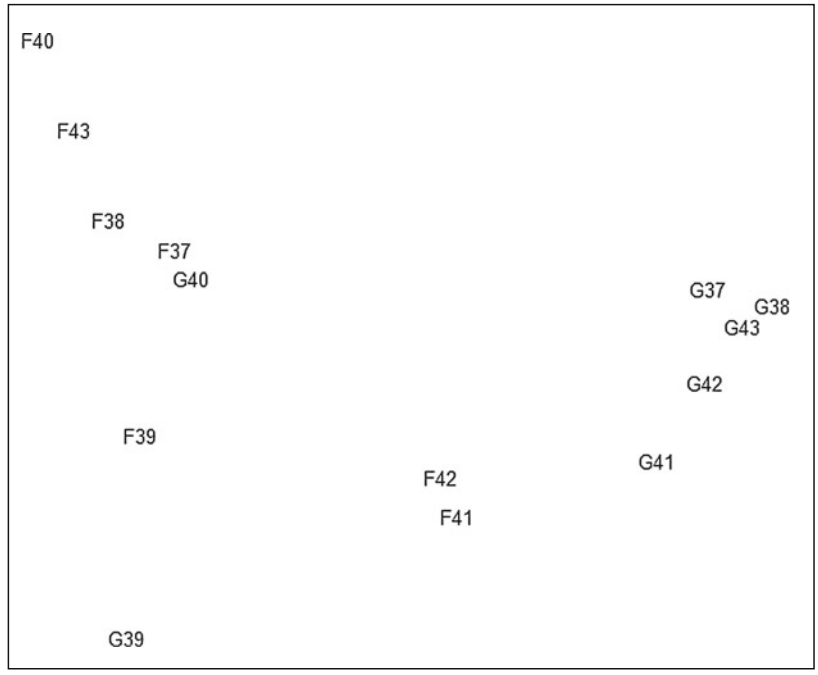
In regions with a continuous ground fire regime, such as the Eastern Broadleaf Forest province of Minnesota, increased density in contemporary forests is typical due to prevention of woody biomass development by fires in historical open forest ecosystems (e.g., Zhang et al. 2000). We believe that decreases in density between historical mixed pioneer species and spruce forests compared to contemporary aspen-dominated forests have not been quantified in other studies. Less frequent, stand-replacing fire regimes of the Laurentian Mixed Forest (Frelich and Reich 1995) did not provide enough time for developmental stages to occur in dense, closed forests, whereas self-thinning (Shenoy et al. 2011) and current silvicultural practices may explain reduced densities in present-day aspen forests.

Results may have been affected by bias in GLO surveys, small samples sizes in the FIA surveys, and analysis decisions. The GLO surveys contain surveyor bias and species misidentification. Additionally, GLO surveys are not complete and may over-represent dominant species, whereas FIA surveys are complete but sparse in number. Turnover in community may reflect our community designation thresholds and densities may reflect, among other factors, our assumptions about the amount of surveyor bias. However, overall trends are consistent within this study and align with other research (e.g., Palik and Pregitzer 1992; White and Mladenoff 1994; Friedman and Reich 2005; Schulte et al. 2007; Rogers et al. 2008).



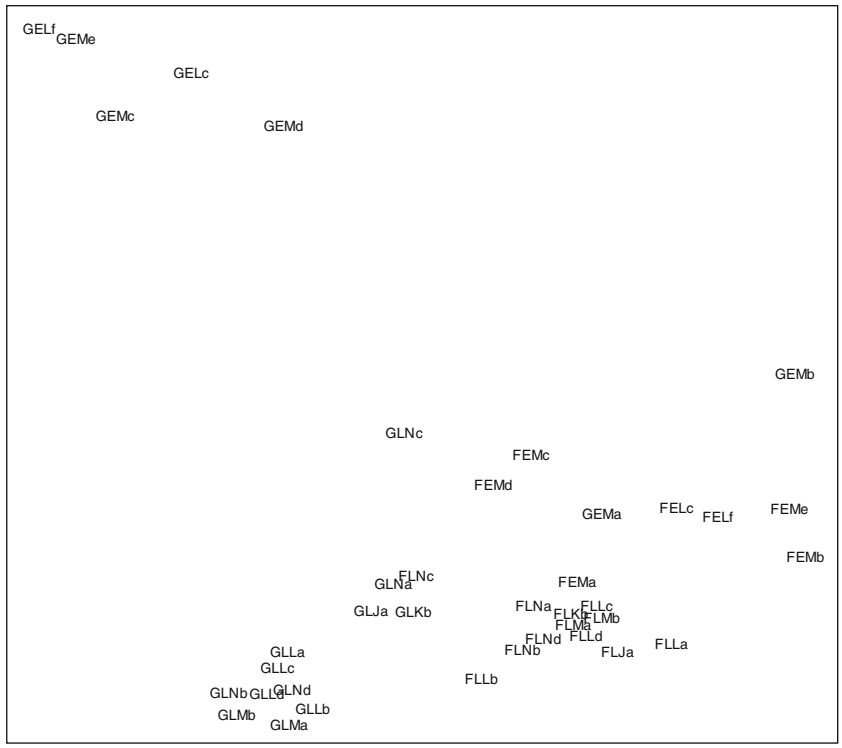
Ordination distance of leaf class and density among ecological units

Fig. 4 Ordination of ecological units by historical and current percent leaf class and densities in the Laurentian Mixed Forest province. Historical ecological units have prefix of *G* whereas current ecological units have prefix of *F*. Refer to Table 3 for NMS ordination ID number



Ordination distance of transitional class and density among ecological subsections

Fig. 5 Ordination of ecological subsections by historical and current percent transitional class and densities in the Eastern Broadleaf Forest province. Historical ecological subsections have prefix of *G* whereas current ecological subsections have prefix of *F*. Refer to Table 3 for ecological subsection acronyms



Ordination distance of transitional class and density among ecological subsections

Fig. 6 Ordination of ecological subsections by historical and current percent transitional class and densities in the Eastern Broadleaf Forest and Laurentian Mixed Forest provinces. Historical ecological subsections have prefix of *G* whereas current ecological subsections have prefix of *F*. Eastern Broadleaf Forest ecological subsections have prefix of *E* whereas Laurentian Mixed Forest ecological subsections have prefix of *L*

Homogenization and mesophication

Throughout our entire study area, the primary trend was increased abundance of less common indigenous species offset by decreased abundance of formerly common tree species. Increased species evenness was most evident in pine and oak ecosystems, which were dominated formerly by one genus, and often one species, that was fire-tolerant. Despite increased representation by numerous species and decreased dominance by the most abundant species, functional types may better characterize landscape changes in forest ecosystem types, and presumably ecosystem functioning, than species richness. Plant functional classes are groupings of plants with similar responses to and effects on environmental conditions (Díaz and Cabido 2001) and correspond with forest ecosystem types.

The question becomes which functional type best represents functional homogenization, because the trait of interest depends on the process of interest. Ordinations for leaf and transitional class both showed change between historical and current communities and reduced differentiation among current conditions versus historical conditions. In the Laurentian Mixed Forest province, the ratio of needled species to broadleaved species essentially reversed, as needled species decreased from 65 to 37 %. Although a swap of a pioneer conifer (tamarack) for a pioneer broadleaf (primarily aspen) is transformative, to some degree this reversal also may be close to a neutral zone between homogenization and differentiation, particularly as tamarack trees are deciduous and self-pruners, similar to broadleaf trees. And though there certainly are differences such as tree architecture between needled and broadleaved species, producing changes in ecosystem functioning including temperature (Shenoy et al. 2011), forest structure and thus to some extent function may remain relatively similar between (1) pioneer species such as aspen and tamarack, (2) disturbance-stabilized species such as pine and oak, and (3) later-successional species of fir and maple compared to differentiation among aspen, oak, and mesic broadleaf forests or among tamarack, pine, and mesic coniferous forests.

Homogenization in the Laurentian Mixed Forest is occurring through convergence in functional groups and structure, in the transition from early-successional

and disturbance-stabilized species, and their respective forest ecosystems, to late-successional species that are competitive for light in mesic forests. Despite increases in aspen, other pioneer species, particularly tamarack, have decreased to a greater extent than aspen has increased. Pioneer and disturbance-stabilized species each have decreased by about 7 % units each (i.e., from 45 to 39 % and 23 to 15 %, respectively), while late-successional, shade-tolerant species have increased about 14 % units, which has resulted in reductions in regional distinctiveness of forest ecosystems. Indeed, continued aspen dominance supported by forestry is preventing greater functional convergence to shade-tolerant species, as has occurred in broadleaf forests, which do not have a large component of pioneer species compared to disturbance-dependent species.

Mesophication in turn is a change in functional groups from disturbance-stabilized to non-disturbance-dependent species, and strictly, shade-tolerant mesophytic species, due to fire suppression (Nowacki and Abrams 2008). Similarly to other oak systems in the Eastern Deciduous Forest biome, open oak woodlands are becoming an artifact of pre-settlement fire regimes in the Eastern Broadleaf Forest of Minnesota (Nowacki and Abrams 2008). Oaks have declined dramatically as fire-sensitive and increasingly shade-tolerant elms, boxelder, maples, American basswood, and ashes have out-competed oaks in the absence of fire. In the Eastern Broadleaf Forest province, disturbance-stabilized species have decreased from 54 to 29 % of species composition, while late-successional species have increased from 27 to 53 %, leaving pioneer species unchanged at about 19 %. Homogenization of functional classes and densities has shifted open forest ecosystems to closed forest ecosystems.

The pattern of homogenization in the Laurentian Mixed Forest of one type of forest ecosystem being replaced by mesic forests of shade-tolerant species resembles mesophication in the Eastern Broadleaf Forest. Our results show convergence of structure and functional classes of both provinces to a common forest type. In contrast, initial forest ecosystems differed; historical forests in the Laurentian Mixed Forest generally were composed of fire-sensitive species that were consumed by stand-replacing fire regimes (Frelich and Reich 1995) unlike open forest ecosystems stabilized by a continuous ground regime in the Eastern Broadleaf Forest. The process of mesophication additionally includes a positive feedback cycle from woody densification that increases moisture and reduces flammability, which is not a distinct outcome given the density of early-successional forest ecosystems in the Laurentian Mixed Forest.

In the Laurentian Mixed Forest province, needled shade-tolerant species have decreased slightly from 24 to 21 % of composition while broadleaved shade-tolerant species increased from 8 to 25 %, indicating that broadleaved species may be the eventual winners between the ecological analogues of shade-tolerant species. Climate change in particular may favor the growth capabilities of broadleaved species over tolerance to stress of needled species (Galatowitsch et al. 2009) and additionally, conifer seedling establishment often relies on exposed mineral soil or decomposing logs for a seedbed (Mladenoff and Stearns 1993). Sprouts also may be more shade-tolerant and drought-tolerant than seedlings and thus vegetative reproduction by broadleaved species may provide a competitive advantage. Ultimately the ability to grow under shaded conditions at different life stages, while compensating for herbivore damage, and the ability to take advantage of canopy gaps created by drought and pathogen probably will determine species composition.

Influence of acute drought declines

A factor that may reverse both increased density and homogenization and mesophication to late-successional species is drought (i.e., the "savannification" concept of Frelich and Reich 2010), which appears to lead to sudden aspen decline across the western United States and Canada (Frey et al. 2004; Worrall et al. 2010) and acute oak decline across the eastern United States and Europe (Andersson et al. 2011; Haavik et al. 2011). Drought alone generally is not severe enough to incite mortality, but with contributing factors such as pathogens or other stressors over time, acute dieback may occur with crown loss in groups of trees rather than individual trees (Mueller-Dombois 1987; Auclair et al. 1996; Klos et al. 2009). Dieback of other species has been reported but perhaps, due to the abundance of aspen and oak, dieback has never occurred at such intensity while spread over widespread areas (Mueller-Dombois 1987; Auclair et al. 1996; Allen et al. 2010).

Drought may lead to acute oak decline, however drought should not lead to chronic oak decreases consistent with transition to fire-sensitive species due to fire suppression. In the past, acute oak decline occurred (Thomas et al. 2002), droughts have been more severe (Swetnam and Betancourt 1998; Stambaugh et al. 2011), and resulting mortality of overstory trees provided ideal conditions for recruitment of advance oak regeneration when fire was present (Mueller-Dombois 1987). Oaks have adaptations that increase water use and efficiency making them more resistant to drought, perhaps particularly as saplings and seedlings, than mesic species (Niinemets and Valladares 2006). In addition to xerophytic leaves and physiological advantages, oaks have a well-developed root system, and indeed, develop the root system early in preference to aboveground growth (Abrams 1990; Klos et al. 2009). Acute oak decline, similarly to oak mortality from fire, is a hazard of balancing drought-prone conditions that occasionally kill oak trees but allow growing space for oak regeneration. The visibility of acute oak decline in broadleaf forests, compared to less widespread acute dieback of mesic species, is greater simply because oaks are more abundant in sites predisposed to drought (Kabrick et al. 2008) and oak forests are more dense and competitive for water than historically. Mesic species lack deep roots and drought adaptations and they should be more susceptible to decline due to drought, which should become more evident as mesic species claim droughty soils (Klos et al. 2009).

Although drought and acute decline are not new to oaks over the past 5,000 years, large extents of acute decline associated with drought may be new to aspen, which has expanded in extent and dominance in the past century, perhaps also in the western United States even without the support of pulp forestry (Kulakowski et al. 2004). Drought combined with pathogens is one form of disturbance that both kills mature canopy trees and initiates tree regeneration, but instead of landscape-wide self-replacement, succession appears to be occurring in some stands in the western United States and Canada (Kulakowski et al. 2004). It is puzzling that drought may have different effects than fire, for although aspen is not tolerant of drought (Niinemets and Valladares 2006) and overstory aspen also is not tolerant of fire, aspen sprouts grow rapidly from persistent root systems and aspen can live on through post-fire sprouting, similar to grasses. Quaking aspen dominance in mixed forests may be transitory, if mature aspen clonal colonies die without replacement stemming from drought.

Conclusions

Despite different historical forest ecosystems in Minnesota's broadleaf and mixed forests, species that are succeeding in both provinces are fire-sensitive and late-successional, due to absence of fire disturbance that historically maintained open oak and pine ecosystems and dense, early-successional forests of pioneer species. In the Eastern Broadleaf Forest province, homogenization occurred primarily through mesophication, or transition of disturbance-stabilized oak and pine ecosystems to successional forests of fire-sensitive species that generally are shade-tolerant. In the Laurentian Mixed Forest, pines were the dominant disturbance-stabilized species, but pines were rare relative to oaks in the Eastern Broadleaf Forest. In contrast, pioneer species, which initiate after stand-replacing disturbance, were more abundant in the Laurentian Mixed Forests. Early-successional forests, that historically were self-replacing, currently are succeeding to late-successional forests, despite the importance of aspen to the forest products industry. If aspen collapses due to sudden aspen decline in the Great Lakes region, similarly to western United States and Canada, succession will become increasingly more evident. In addition, in the Laurentian Mixed Forest province, broadleaved trees are succeeding at the expense of conifers to the point where former mixed forests may shift entirely to broadleaved forests.

Homogenization, like fragmentation, results from human influence, making it a convenient term to apply to modern forests compared to pre-settlement forests. However, open oak and pine ecosystems were dominated by few tree species tolerant of a continuous ground fire regime so that any compositional changes will increase local tree species diversity, hence taxonomic differentiation rather than taxonomic homogenization occurs. Closed forest ecosystems furthermore are denser and develop over time, producing more internal canopy heterogeneity and structure than open oak and pine ecosystems and early-successional forest ecosystems. Nonetheless, widespread transitions that increase a variety of shade-tolerant species will be at the expense of unique regional open ecosystems and dense,

early-successional forest ecosystems, ultimately decreasing separation of tree functional classes and forest types and homogenizing the landscape within and among regions. The distinction between the Eastern Broadleaf Forest and Laurentian Mixed Forest has diminished due to convergence along a common trajectory to successional forest ecosystems composed of shade-tolerant species.

Acknowledgments We thank anonymous reviewers for their suggestions. We received funding from the National Fire Plan, USDA Forest Service.

References

Abrams MD (1990) Adaptations and responses to drought in *Quercus* species of North America. Tree Physiol 7:227–238

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kizberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manage 259:660–684

Andersson M, Milberg P, Bergman K-O (2011) Low pre-death growth rates of oak (*Quercus robur* L.)—is oak death a long-term process induced by dry years? Ann For Sci 68:159–168

Auclair AND, Lill JT, Revenga C (1996) The role of climatic variability and global warming in the dieback of northern hardwoods. Water Air Soil Pollut 91:163–186

Beers TW, Dress PE, Wensel LC (1966) Aspect transformation in site productivity research. J For 64:691–692

Bergeron Y, Brisson J (1990) Fire regime in red pine stands at the northern limit of the species' range. Ecology 71: 1352–1364

Breiman L (2001) Random forests. Mach Learn 40:5–32

Cleland DT, Avers PE, McNab WH, Jensen ME, Bailey RG, King T, Russell WE (1997) National hierarchical framework of ecological units. In: Boyce MS, Haney A (eds) Ecosystem management applications for sustainable forest and wildlife resources. Yale University Press, New Haven, pp 181–200

Cole KL, Davis MB, Stearns R, Guntenspergen G, Walker K (1998) Historical land cover changes in the Great Lakes Region. In: Sisk TD (ed) Perspectives on the land-use history of North America: a context for understanding our changing environment. US Geological Survey, Biological Resources Division. Biological Science Report USGS/BRD/BSR 1998-0003, Springfield, pp 43–50

Crow TR (1988) Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—a review. For Sci 34:19–40

Cutler DR, Edwards TC Jr, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ (2007) Random forests for classification in ecology. Ecology 88:2783–2792

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655

Foster DR, Motzkin G, Slater B (1998) Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. Ecosystems 1:96–119

Frelich LE, Reich PB (1995) Spatial patterns and succession in a Minnesota southern-boreal forest. Ecol Monogr 65:325–346

Frelich LE, Reich PB (2010) Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? Front Ecol Environ 8:371–378

Frey BR, Lieffers VJ, Hogg EH, Landhäusser SM (2004) Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. Can J For Res 34:1379–1390

Friedman SK, Reich PB (2005) Regional legacies of logging: departure from pre-settlement forest conditions in northern Minnesota. Ecol Appl 15:726–744

Fuller JL, Foster DR, McLachlan JS, Drake N (1998) Impact of human activity on regional forest composition and dynamics in central New England. Ecosystems 1:76–95

Galatowitsch S, Frelich L, Phillips-Mao L (2009) Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. Biol Conserv 142:2012–2022

Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological data. J Stat Softw 22:1–19

Grimm EC (1983) Chronology and dynamics of vegetation change in the prairie-woodland region of southern Minnesota, U.S.A. New Phytol 93:311–350

Haavik LJ, Stahle DW, Stephen FM (2011) Temporal aspects of *Quercus rubra* decline and relationship to climate in the Ozark and Ouachita Mountains, Arkansas. Can J For Res 41:773–781

Hanberry BB, Fraver S, He HS, Yang J, Dey DC, Palik BJ (2011) Spatial pattern corrections and sample sizes for forest density estimates of historical tree surveys. Landscape Ecol 26:59–68

Hanberry BB, Yang J, Kabrick JM, He HS (2012) Adjusting forest density estimates for surveyor bias in historical tree surveys. Am Midl Nat 167:285–306

Kabrick JM, Dey DC, Jensen RG, Wallendorf M (2008) The role of environmental factors in oak decline and mortality in the Ozark Highlands. For Ecol Manage 255: 1409–1417

Klos RJ, Wang GG, Bauerle WL, Rieck JR (2009) Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. Ecol Appl 19:699–708

Kulakowski D, Veblen TT, Drinkwater S (2004) The persistence of quaking aspen (*Populus tremuloides*) in the Grand Mesa Area, Colorado. Ecol Appl 14:1603–1614

Liaw A, Wiener M (2002) Classification and Regression by randomForest. R News 2:18–22

McCune B, Cottam G (1985) The successional status of a southern Wisconsin oak woods. Ecology 66:1270–1278

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

Mladenoff DJ, Stearns F (1993) Eastern hemlock regeneration and deer browsing in the Northern Great Lakes region: a re-examination and model simulation. Conserv Biol 7: 889–900

Morisita M (1957) A new method for the estimation of density by the spacing method, applicable to non-randomly distributed populations. Seiri Seitai 7:134–144 (in Japanese)

Mueller-Dombois D (1987) Natural dieback in forests. Bioscience 37:575–583

Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol Monogr 76:521–547

Nowacki GJ, Abrams MD (2008) The demise of fire and 'mesophication' of forests in the eastern United States. Bioscience 58:123–138

Nuzzo VA (1986) Extent and status of Midwest oak savanna: presettlement and 1985. Nat Area J 6:6–36

Olden JD, Rooney TP (2006) On defining and quantifying biotic homogenization. Glob Ecol Biogeogr 15:113–120

Oswald WW, Faison EK, Foster DR, Doughty ED, Hall BR, Hansen CS (2007) Post-glacial changes in spatial patterns of vegetation across southern New England. J Biogeogr 34:900–913

Palik BJ, Pregitzer KS (1992) A comparison of presettlement and present-day forests on two bigtooth aspen-dominated landscapes in northern lower Michigan. Am Midl Nat 127:327–338

Pinto F, Romaniuk S, Ferguson M (2008) Changes to preindustrial forest tree composition in central and northeastern Ontario, Canada. Can J For Res 38:1842–1854

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rogers DA, Rooney TP, Olson D, Waller DM (2008) Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89:2482–2492

Sappington JM, Longshore KM, Thompson DB (2007) Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. J Wildl Manag 71:1419–1426

Schulte LA, Mladenoff DJ, Crow TR, Merrick LC, Cleland DT (2007) Homogenization of northern U.S. Great Lakes forests due to land use. Landscape Ecol 22:1089–1103

Shenoy A, Johnstone J, Kasischke E, Kielland K (2011) Persistent effects of fire severity on early successional forests in interior Alaska. For Ecol Manage 261:381–390

Stambaugh MC, Guyette RP, McMurry ER, Cook ER, Mekoc DM, Lupod AR (2011) Drought duration and frequency in the U.S. Corn Belt during the last millennium (AD 992–2004). Agric For Meteorol 151:154–162

Swetnam TW, Betancourt JL (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. J Clim 11:3128–3147

Thomas FM, Blank R, Hartmann G (2002) Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. Forest Pathol 32:277–307

White CA (1983) A history of the rectangular survey system. Bureau of Land Management, Washington, DC

White MA, Mladenoff DJ (1994) Old-growth forest landscape transitions from pre-European settlement to present. Landscape Ecol 9:191–205

Worrall JJ, Marchetti SB, Egeland L, Mask RA, Eager T, Howell B (2010) Effects and etiology of sudden aspen decline in southwestern Colorado, USA. For Ecol Manage 260:638–648

Zhang Q, Pregitzer KS, Reed DD (2000) Historical changes in forests of the Luce District of the Upper Peninsula of Michigan. Am Midl Nat 143:94–110