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Geophysical features influence the climate change sensitivity of northern Wisconsin pine and oak forests

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Abstract. Landscape-scale vulnerability assessment from multiple sources, including paleoecological site histories, can inform climate change adaptation. We used an array of lake sediment pollen and charcoal records to determine how soils and landscape factors influenced the variability of forest composition change over the past 2000 years. The forests in this study are located in northwestern Wisconsin on a sandy glacial outwash plain. Soils and local climate vary across the study area. We used the Natural Resource Conservation Service's Soil Survey Geographic soil database and published fire histories to characterize differences in soils and fire history around each lake site. Individual site histories differed in two metrics of past vegetation dynamics: the extent to which white pine (*Pinus strobus*) increased during the Little Ice Age (LIA) climate period and the volatility in the rate of change between samples at 50–120 yr intervals. Greater increases of white pine during the LIA occurred on sites with less sandy soils ($R^2 = 0.45$, $P < 0.0163$) and on sites with relatively warmer and drier local climate ($R^2 = 0.55$, $P < 0.0056$). Volatility in the rate of change between samples was positively associated with LIA fire frequency ($R^2 = 0.41$, $P < 0.0256$). Over multi-decadal to centennial timescales, forest compositional change and rate-of-change volatility were associated with higher fire frequency. Over longer (multi-centennial) time frames, forest composition change, especially increased white pine, shifted most in sites with more soil moisture. Our results show that responsiveness of forest composition to climate change was influenced by soils, local climate, and fire. The anticipated climatic changes in the next century will not produce the same community dynamics on the same soil types as in the past, but understanding past dynamics and relationships can help us assess how novel factors and combinations of factors in the future may influence various site types. Our results support climate change adaptation efforts to monitor and conserve the landscape's full range of geophysical features.

Key words: climate change; conserving the stage; fire; forest composition change; geophysical features; landscape context; pine and oak forests; pollen records; sand plain; soils; vegetation; Wisconsin, USA.

Introduction

Managing natural resources under the prospect of centuries of persistent climate change requires a long-term, strategic view that adapts management goals and approaches to the effects of both shifting climate baselines and increased variability. Spatial assessment of landscape sensitivity to climate variability (e.g., Beeson et al. 2001) can inform climate change adaptation because the landscape scale is the scale at which spatial patterns of vulnerability can be detected and relevant ecological and socioeconomic contexts can be accounted for (Davison et al. 2012). Ecological processes also generally occur at spatial scales that cross jurisdictions, and landscape-level understanding can inform cross-boundary management in a changing world.

Paleoecological studies can benefit natural resource management by substantially expanding knowledge about how specific landscapes responded to past climate variability (Birks 1996, Gillson and Willis 2004, Willis et al. 2007). These studies generally use environmental proxies, such as pollen, charcoal, diatoms from lakes, amoeba communities from peat, or carbonate deposits from lakes and caves, each of which can give a highly site-specific signal over long time periods (Hotchkiss et al. 2007, Hobbs et al. 2011, Ireland and Booth 2011, Barrett et al. 2013). Sets of paleorecords from sites along environmental gradients, such as proximity to large

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water bodies (Henne and Hu 2010), differences in soil types (Ewing 2002, Oswald et al. 2003), differences in land use history (Gaudin et al. 2008), or differences in extant vegetation feedbacks (Davis et al. 1998, Lynch 1998, Barrett et al. 2013), can elucidate the effect of landscape context on the response of local vegetation to past changes in land use, climate, and disturbance regimes. Paleoecological studies can integrate empirical information from many sources to determine past responses to actual climate variability and suggest where and how to focus monitoring, management, and research.

In this study, we analyze pollen and charcoal records of forest change from twelve lakes on a sandy, glacial outwash plain in northwestern Wisconsin, USA. Around each lake, we characterized soils, modern climate, and differences in past fire regime to answer the following questions: Do the pollen-based histories of forest composition change differ among sites? Do observed landscape patterns in geophysical factors or climate correspond to differences in past variability in forest composition?

Answers to these paleoecological questions are relevant to resource management on a broad range of landscapes.

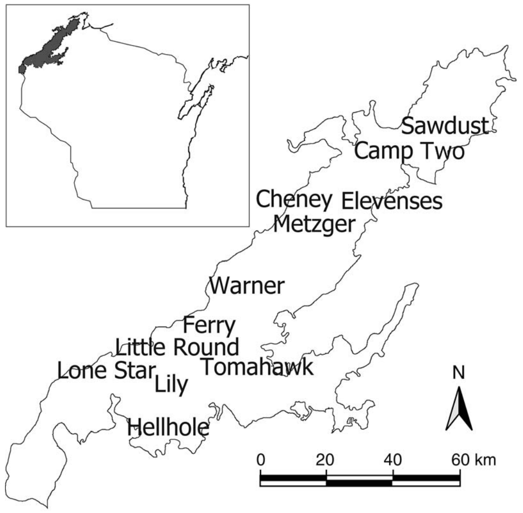

FIG. 1. The forests in this study are located in northwestern Wisconsin, USA, on a sandy glacial outwash plain (inset). Study sites range across three major variations in soils, from an area with more wetland soils and lakes in the southwest, through an area of very sandy soils in the center, to a mosaic of sandy and more fertile soils in the northeast close to Lake Superior.

METHODS

Study area

The study area is the northwestern Wisconsin, USA, sand plain (NWSP), a distinct ecological landscape under Wisconsin's Wildlife Action Plan (WDNR 2005). The sand plain is a linear band of pitted glacial outwash approximately 180 km long, 15–40 km wide, and 450 000 ha in area, and it stretches from the Bayfield peninsula (which extends northeast into Lake Superior) southwest to the St. Croix River on the Minnesota border (Fig. 1). This region's climate is humid continental and is influenced by lake-effect precipitation from Lake Superior, especially in the northeastern section. The topography is flat to gently rolling, and streams are rare. Seepage lakes are most common in the southwest where the water table is highest. Soils across the sand plain are generally nutrient-poor sands with low water-holding capacity, but the northeastern and southwestern sections have finer-textured loamy sands and sandy loams (Radeloff et al. 1999). Coarse, well-drained soils make the entire landscape susceptible to drought and recurring fires, and therefore, favor more open forests dominated by pines and oaks that tolerate drought and reestablish quickly after fire (Curtis 1959, Radeloff et al. 1999).

The sand plain is a mosaic of different land owners and management goals, and includes numerous Conservation Opportunity Areas under Wisconsin's Wildlife Action Plan (WDNR 2005). The landscape is primarily managed by private industrial and county landholders for pulp paper production, but the Wisconsin Department of Natural Resources, the U.S. Forest Service, and county forest programs manage several areas with prescribed fire to promote open, shrubby barrens communities. U.S. Forest Service ownership includes a small portion of the northeastern end of the landscape managed as part of the Chequamegon-Nicolet National Forest, and U.S. National Park Service ownership includes the Namekagon and St. Croix Rivers and shorelands, which border and bisect the landscape, respectively, and are managed as the St. Croix National Scenic Riverway.

Animal species of special concern to wildlife managers are the Karner blue butterfly (*Lycaeides melissa samuelis*), which finds suitable habitat in the oak and pine barrens on the southwestern end of the landscape (USFWS 2003), the Sharp-tailed Grouse (*Tympanuchus phasianellus*), which requires large areas of early successional habitat (Sample and Mossman 1997, Niemuth and Boyce 2004, Niemuth 2006), and Kirtland's Warbler (*Dendroica kirtlandii*), which has recently expanded its range from Michigan into the more dense jack-pine-dominated forests of Wisconsin and has been observed in the northern and central portions of the sand plain (WDNR 2013).

Characterizing climate periods

In this paper, we compared the rate and magnitude of vegetation changes at sites in different landscape contexts to the climatic periods of the Little Ice Age (LIA; 700–75 yr BP) and the time period before the LIA (2000–700 yr BP), which includes the Medieval Climate Anomaly (MCA; 1100–700 yr BP). Dates are presented as calibrated years before the year 1950 (calendar yr BP),

Table 1. Climate, soils, and fire frequency metrics for each site in the northwestern Wisconsin, USA, sand plain.

			Temperature (°C)							No. fire events/500 yr		Fire peak magnitude (pieces·cm^{-2}·event^{-1})	
Lake	Lat.	Long.	Coldest month	Warmest month	Ppt. (mm)	Snow-fall (mm)	Sand (%)	CEC	Soil drainage index	Pre-LIA	LIA	Pre-LIA	LIA
Sawdust	46.571	91.272	−11.6	19.3	772	174.7	90.2	3.52	4.50	3.9	3.6	14.5	0.2
Camp Two	46.502	91.411	−11.9	19.3	765	163.2	88.6	5.11	4.29	3.8	4.7	1.8	4.8
Elevenses	46.382	91.496	−12.0	19.5	766	161.5	93.6	0.97	4.96	4.7	5.7	12.97	2.77
Cheney	46.382	91.701	−12.2	19.6	758	154.0	95.5	0.95	4.98	4.7	5.7	9.05	5.72
Metzger	46.318	91.688	−12.1	19.7	759	151.5	95.8	0.87	4.97	7.2	7.4	2.3	2.23
Warner	46.121	92.039	−12.5	20.3	749	137.2	93.6	1.13	5.00	4.1	4.2	14.3	2.53
Ferry	46.013	92.125	−12.6	20.6	746	133.1	91.4	0.84	4.69	0.9	2.1	0.08	5.39
Little Round	46.013	92.226	−12.6	20.6	748	135.5	93.2	1.03	4.96	12.4	8.2	6.72	0.99
Lone Star	45.932	92.365	−12.7	20.7	745	133.3	84.0	2.57	4.28	7.2	3.1	5.56	1.7
Tomahawk	45.924	91.961	−12.5	20.6	744	126.4	89.1	1.38	4.01	3.5	4.4	14.9	0.44
Lily	45.901	92.272	−12.7	20.7	746	132.1	80.3	7.80	2.10	4.5	3.3	8.25	4.53
Hellhole	45.787	92.219	−12.6	20.9	747	129.7	89.0	1.53	2.72	5.4	4.1	6.59	9.27
Maximum	46.571	92.272	−11.6	20.9	772	174.7	95.8	7.80	5.00	12.4	8.2	14.9	9.3
Minimum	45.787	91.272	−12.7	19.3	744	126.4	80.3	0.84	2.10	0.9	2.1	0.1	0.2

Notes: Abbreviations: Lat. and Long. are latitude (°N) and longitude (°W); Ppt. is precipitation; CEC is cation exchange capacity; LIA is Little Ice Age; the pre-LIA period is 2000–700 yr BP; the LIA period is 700–75 yr BP. Soil variables are calculated as area-weighted averages of individual soil bodies within 5 km of the lake site. The soil drainage index is a distance and area weighted index of the area in different drainage classes.

which is the convention for years before the present (BP). The date for the shift between the two climate periods was chosen based on regional paleohydrologic and vegetation studies. The timing of the transition is similar to the transition to the LIA in Europe (Matthews and Briffa [2005] use 650 yr BP), with any local differences in timing contained within the locally defined LIA period. Widespread evidence for a climatic transition between 700–600 yr BP is found in the western Great Lakes region. Paleohydrological records based on testate amoebae indicate that this region experienced severe droughts before 700 yr BP corresponding to droughts occurring throughout the central and western U.S.A. (Booth et al. 2006, Tweiten et al. 2009), with less frequent or severe droughts occurring after 700 yr BP. The transition to LIA climate is represented at many sites on this sand plain by a decline in jack/red pine (*Pinus banksiana* Lamb./*Pinus resinosa* Ait.) and an increase in white pine (*Pinus strobus* L.) between 600 and 700 yr BP (Hotchkiss et al. 2007). Other pollen studies in the region also have an increase in more mesic taxa at about this time, which indicates cooler, moister conditions (McAndrews 1968, Swain 1978, Gajewski et al. 1985, Umbanhowar 2004, but see Shuman et al. 2009).

Characterizing landscape context: climate and soils

Modern climate data (1961–1990) were interpolated to latitude, longitude, and elevation of each lake (Table 1), following the method in Whitmore et al. 2005 (J. Williams and P. Bartlein, *personal communication*). The soil attributes of the landscape surrounding each lake were characterized using the Natural Resource Conservation Service's Soil Survey Geographic (SSURGO) database (NRCS 2010). The variables examined included soil type, pH (water extract and $CaCl_2$ extract), cation exchange capacity (CEC), calcium carbonate content, available soil water in the top 50 cm, drainage class, slope gradient, fractions of clay, silt, and sand, percent organic matter, and soil bulk density. SSURGO data were extracted for each lake site within a buffer area with a 5-km radius using the program ARCMap 10 (ESRI 2011). The soil variables for each buffer area were consolidated as area-weighted averages of the values in each SSURGO soil type (MUSYM in the SSURGO database). After preliminary screening of soil variables with ordination analysis, we chose soil drainage class as the best representative of the many co-variable soil attributes.

Pollen assemblages in lake sediments reflect the composition of the surrounding vegetation in a distance-weighted manner (Prentice 1985, Sugita 1993). To best capture the relationship between pollen assemblage and the surrounding environment, we created a distance-weighted measure of soil drainage. Soil groups in the SSURGO database are each assigned a drainage class (NRCS 2010) ranging from poorly drained to excessively well drained; these classes were used to create a soil drainage index ranging from 1 (all somewhat poorly drained soils) to 5 (all excessively drained soils). For each site, we created a series of concentric, circular buffer areas with the outer diameter of the rings at 0.5 km, 1 km, 1.5 km, 2.5 km, and 5 km. Within each circular buffer area, we determined the percentage of the total buffer area in each drainage class. This value was multiplied by a weighting factor (1/distance to site at the midpoint of the buffer ring) so that the influence of information from more distant buffers decreased in proportion to their distance from the site. This data transformation made the soil drainage data commensurate with how pollen data represent vegetation at different distances from the sampling site.

Characterizing fire regimes

Fire history for each lake site was derived from previously published charcoal records with some unpublished additions using the same methods (Fig. 1). Previously published records include Ferry Lake (Lynch et al. 2006, 2011, 2014, Hotchkiss et al. 2007, Jensen et al. 2007); Warner Lake (Tweiten et al. 2009, Lynch et al. 2011); Hellhole Lake (Hotchkiss et al. 2007); Lily, Lone Star, and Tomahawk Lakes (Hotchkiss et al. 2007, Lynch et al. 2011); Sawdust, Camp Two, Elevenses, and Metzger Lakes (Lynch et al. 2011); and Little Round and Cheney Lakes (Lynch et al. 2014).

Chronologies were based on 3–10 AMS (accelerator mass spectrometry) radiocarbon dates at each site. AMS samples consisted of 3–6 mL of organic sediment, treated with HCl, KOH, and bleach to remove organic material other than pollen (Brown et al. 1989, Regnell 1992, Richardson and Hall 1994). Bayesian age-depth models for each core were constructed using OxCal 4.1 (Bronk-Ramsey 1995). Individual sample ages were estimated by linear interpolation between midpoints of 95% probability distributions for each date. Age-depth profiles are linear for most sites and are shown in Hotchkiss et al. (2007), Tweiten et al. (2009), or Lynch et al. (2011).

The charcoal was analyzed in samples representing contiguous 5-cm intervals. Organic matter was bleached contiguous 5-cm intervals with hydrogen peroxide, and the samples were sieved for charcoal pieces greater than 125 μmol. The charcoal counts combined with the age model were used to calculate charcoal accumulation rates (CHAR). Large fluctuations in CHAR above a background level indicate a fire event (Long et al. 1998). We used the CharAnalysis program (Higuera et al. 2009) to determine background levels based on a 500-yr lowess smoothing curve, and we defined CHAR peaks based on a local peak-threshold criterion (Higuera et al. 2010, Kelly et al. 2011). The number of peak events per 500 yr (fire frequency) was determined for the time period of the Little Ice Age (LIA; 700–75 yr BP) and the period before the LIA (2000–700 yr BP). The relative intensity of fire events can be determined with a measure of peak magnitude; i.e., the number of particles/cm^2 per fire event (Higuera et al. 2009). The average peak magnitude of fire events was also determined for the LIA (700–75 yr BP) and the period before the LIA (2000–700 yr BP).

Characterizing forest history

Analysis of forest composition change over the past 2000 years is based on pollen assemblages using 1-mL samples at 50–120 yr resolution. Each record was limited to data within the past 2000 years, excluding modern data after 75 yr BP when the area was impacted by logging, farming, and development. Pollen was extracted from sediment using standard methods (Faegri and Iversen 1989). Pollen percentages were based on the sum of 25 common upland pollen types (Table 3). Variability among all samples from all lake sites was characterized by nonmetric multidimensional scaling (NMS; Prentice 1980) using squared-chord distance as a distance measure (Overpeck et al. 1985). Analysis was conducted with the R statistical environment (R Development Core Team 2009) using the vegan (Oksanen et al. 2010) and MASS packages (Venables and Ripley 2002). A two-dimensional NMS solution was chosen as the best trade-off between reduced model stress and additional dimensions. Thus, each pollen sample has a pair of coordinates in the two-dimensional pollen composition space. Correlations between soils, climate variables, or individual pollen types and each of the two-dimensional NMS scores were determined with permutation tests (1000 permutations).

The NMS scores were used to calculate the volatility of the rate of change between samples. The rate of change between samples is the distance traveled in the two-dimensional NMS space to arrive at each sample divided by time between samples. Large changes in NMS space over short time periods represent spikes in the rate of change between samples. The coefficient of variation (CV) of all the rate-of-change shifts in each pollen record is a measure of the volatility in the rate of change in that record.

A second metric of temporal variability reflects the pollen percentage of white pine (*Pinus strobus* L.), a pollen type that increased substantially over the study period, particularly at the time of LIA climate changes (Hotchkiss et al. 2007). A white pine ratio was calculated for each individual lake record as the average percentage of white pine pollen in LIA-aged samples divided by the average white pine pollen percentage in the preceding time period from 2000 to 700 yr BP. The coefficient of variation of rate of change and the white pine ratio were compared to the soil drainage index, temperature in the warmest month, and LIA fire frequency with linear regression. All data were standardized to the mean value of each time series before plotting and regression calculations.

RESULTS

Do different sites have different histories of change?

Forest histories varied across the landscape but also show a major trend in species composition through time. Nonmetric multidimensional scaling (NMS) reveals two major compositional trends across all the pollen samples (Fig. 2). The first NMS axis explains 59.5% of the original variability among samples and corresponds to a compositional gradient from samples with higher jack/red pine pollen to samples with higher percentages of oak, grasses, alder, and herbaceous species (Table 2). The second NMS axis explains 36.8% of the original variability and shows a strong association with white pine pollen (Table 3). The second NMS axis is also strongly associated with samples from the Little Ice Age (LIA) climate period, as indicated in Fig. 2; these samples cluster toward the bottom of the diagram near

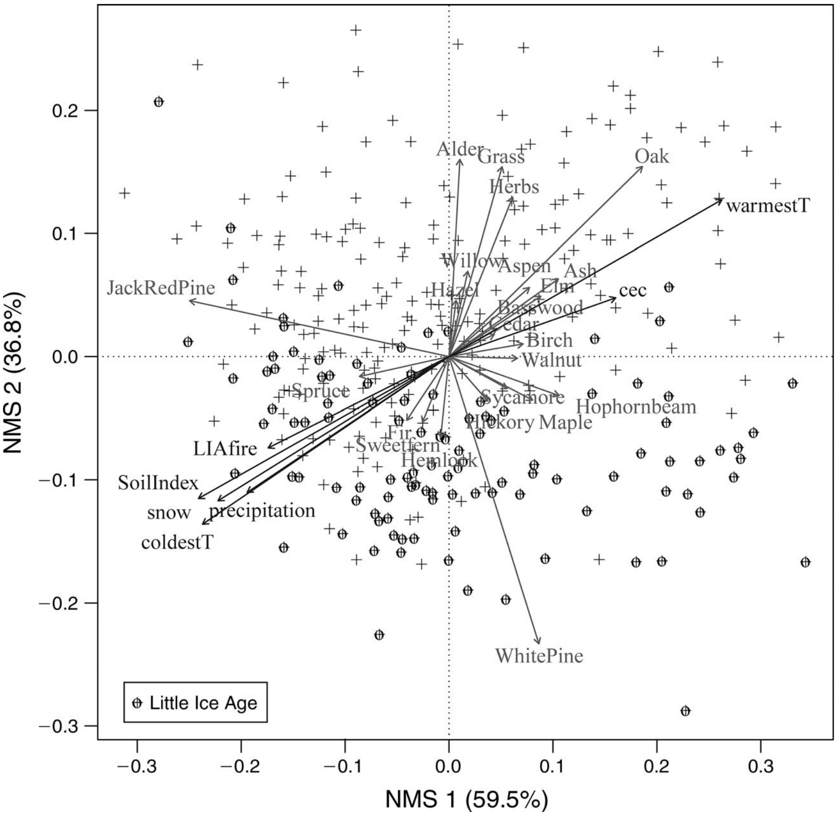

FIG. 2. A nonmetric multidimensional scaling (NMS) ordination of pollen samples, by taxa, from all lake sites over the last 2000 years shows that lake records varied across the landscape (NMS 1 axis, explaining 59.5% of variability), but also changed substantially through time (NMS 2 axis, explaining 36.8% of variability). The NMS 1 axis corresponds to a compositional gradient from samples with higher jack/red pine pollen to samples with higher percentages of oak, grasses, alder, and herbaceous species. The NMS 2 axis shows a strong association with white pine pollen. Samples from the Little Ice Age climate period (700–75 yr BP), indicated with circles, are clustered on the negative end of NMS 2 and are associated with increased pollen percentages of white pine. ColdestT and warmestT, respectively, are the coldest month and warmest month temperatures; SoilIndex is the soil drainage index; LIAfire is the number of fire events per 500 yr during the Little Ice Age.

the samples with higher proportions of white pine pollen.

Individual sites demonstrate different trajectories through this species–composition ordination through time (Fig. 3). Pollen assemblages of some sites, especially Sawdust and Cheney, remain in a constricted zone of ordination space through the 2000-yr record. Assemblages at other sites, such as Ferry, Lily, and Hellhole, traverse a larger area of the ordination space through time. Pollen data from several lakes, such as Little Round, Lily, and Hellhole, make a marked shift toward the negative end of the second NMS axis and remain there through the LIA period. The pattern of distinct trajectories among sites is also illustrated by LIA white pine pollen percentages (Fig. 4). Again, sites such as Warner, Little Round, Lily, and Hellhole all show marked shifts in white pine abundance during the LIA, whereas sites such as Sawdust, Elevenses, and Cheney shift much less.

Individual sites also show differences in how rapidly species composition changes between samples (Fig. 5). The CV of the rate of change between adjacent samples differs among sites but the differences do not correspond to geographic location or climatic period in a straightforward way (Table 2). The most volatile site (Little Round, with a CV of 0.96) and the least volatile site (Lone Star, with a CV of 0.52) are near each other in the southwestern section of the landscape (Fig. 1). Some lakes, such as Camp Two, Elevenses, Warner, and Little Round, have increased rates of change during the Medieval Climatic Anomaly (MCA, 1100–700 yr BP; Fig. 5). Others, such as Sawdust, Cheney, Tomahawk, and Lily, have decreased rates of change during the MCA and increased rates during the LIA. Little Round, Ferry, Warner, and Metzger all show large multiple-sample spikes in rates of change, but these spikes do not appear to align with each other in time or correspond to a particular climate time period.

TABLE 2. Temporal variability metrics for each site in the northwestern Wisconsin, USA, sand plain.

Lake	Variability	
	Rate of change, CV	White pine ratio
Sawdust	0.87	0.98
Camp Two	0.68	1.38
Elevenses	0.70	1.37
Cheney	0.64	1.28
Metzger	0.89	1.10
Warner	0.75	1.85
Ferry	0.66	1.53
Little Round	0.96	1.56
Lone Star	0.52	1.32
Tomahawk	0.65	1.90
Lily	0.65	2.02
Hellhole	0.59	1.96
Maximum	0.96	2.02
Minimum	0.52	0.98

Note: The white pine ratio is the average percentage of white pine pollen in LIA-aged samples divided by the average white pine pollen percentage in the preceding time period from 2000 BP until 700 BP. CV is coefficient of variation.

Does landscape context relate to different histories?

Modern climate varies across the NWSP (Table 1). Average temperature in the warmest month ranges from 20.9°C at Hellhole in the southwest to 19.3°C at Sawdust and Camp Two in the northeast (Table 1). The temperatures in both winter and summer show the cooling effect of Lake Superior. Proximity to Lake Superior also influences total snowfall and total precipitation (Table 1). Soil attributes, by contrast, show a heterogeneous pattern across the NWSP (Table 1). The southwest is more variable among sites in percent sand, cation exchange capacity (CEC), and soil drainage than the central or northeast parts of the landscape. These differences in modern climate and soil attributes correspond to the overall species composition gradient (Fig. 2). The jack pine-dominated vegetation histories occurred in sites with more excessively drained soils, lower CEC, and also cooler summer climate influenced by their proximity to Lake Superior. More oak occurred at sites with less excessively drained soils,

TABLE 3. Association of individual pollen types and environmental variables with the nonmetric multidimensional scaling (NMS) ordination of historical pollen samples from all lakes.

Variables and plant taxon	NMS 1	NMS 2	R^2	P (Pr > r)
Pollen type				
Jack/red pine (*Pinus banksiana*, *P. resinosa*)	−0.98382	0.179159	0.9499	0.000999***
Spruce (*Picea*)	−0.982702	−0.185192	0.1135	0.000999***
Fir (*Abies balsamea*)	−0.618842	−0.785515	0.0637	0.001998**
Sweetfern (*Comptonia peregrina*)	−0.432507	−0.901631	0.0513	0.001998**
Hemlock (*Tsuga canadensis*)	−0.121314	−0.992614	0.0644	0.000999***
Alder (*Alnus*)	0.065149	0.997876	0.38	0.000999***
Hazel (*Corylus*)	0.146273	0.989244	0.0315	0.011988*
Willow (*Salix*)	0.252694	0.967546	0.0759	0.000999***
Grass (Poaceae)	0.314429	0.949281	0.3891	0.000999***
White pine (*Pinus stobus*)	0.347728	−0.937595	0.9127	0.000999***
Herbs	0.427345	0.904089	0.3027	0.000999***
Larch (*Larix laricina*)	0.500905	0.865502	0.0172	0.067932†
Hickory (*Carya*)	0.717417	−0.696644	0.0399	0.002997**
Oak (*Quercus*)	0.769566	0.638568	0.8626	0.000999***
Aspen (*Populus tremuloides*)	0.809012	0.587792	0.1349	0.000999***
Ash (*Fraxinus*)	0.857297	0.514821	0.2223	0.000999***
Elm (*Ulmus*)	0.87396	0.485998	0.1507	0.000999***
Basswood (*Tilia americana*)	0.896404	0.443238	0.0389	0.004995**
Sycamore (*Platanus*)	0.906957	−0.421224	0.0564	0.000999***
Maple (*Acer*)	0.915148	−0.403119	0.1141	0.000999***
Cedar (*Thuja occidentalis*)	0.923305	0.384068	0.0328	0.00999**
Hophornbeam (*Ostrya virginiana*)	0.957766	−0.28755	0.1807	0.000999***
Beech (*Fagus*)	0.980671	−0.195662	0.0174	0.068931†
Birch (*Betula*)	0.9898	0.142464	0.0765	0.000999***
Walnut (*Juglans*)	0.999759	−0.021971	0.0639	0.000999***
Environmental factor				
LIA fire frequency	−0.92003	−0.39185	0.1832	0.000999***
Soil drainage index	−0.90225	−0.43122	0.3656	0.000999***
Total snowfall	−0.8848	−0.46597	0.3233	0.000999***
Total precipitation	−0.86954	−0.49386	0.2554	0.000999***
Temperature, coldest month	−0.86731	−0.49776	0.3831	0.000999***
Pre-LIA fire frequency	0.32538	−0.94558	0.0025	0.704296
Temperature, warmest month	0.89967	0.43658	0.4363	0.000999***
Cation exchange capacity	0.95836	0.28555	0.1434	0.000999***

Notes: Individual factors are related to the axis scores by permutation tests ($i = 1000$) which provide correlation scores listed by each factor and significance values. LIA is Little Ice Age. Significance based on 1000 permutations is indicated by † $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

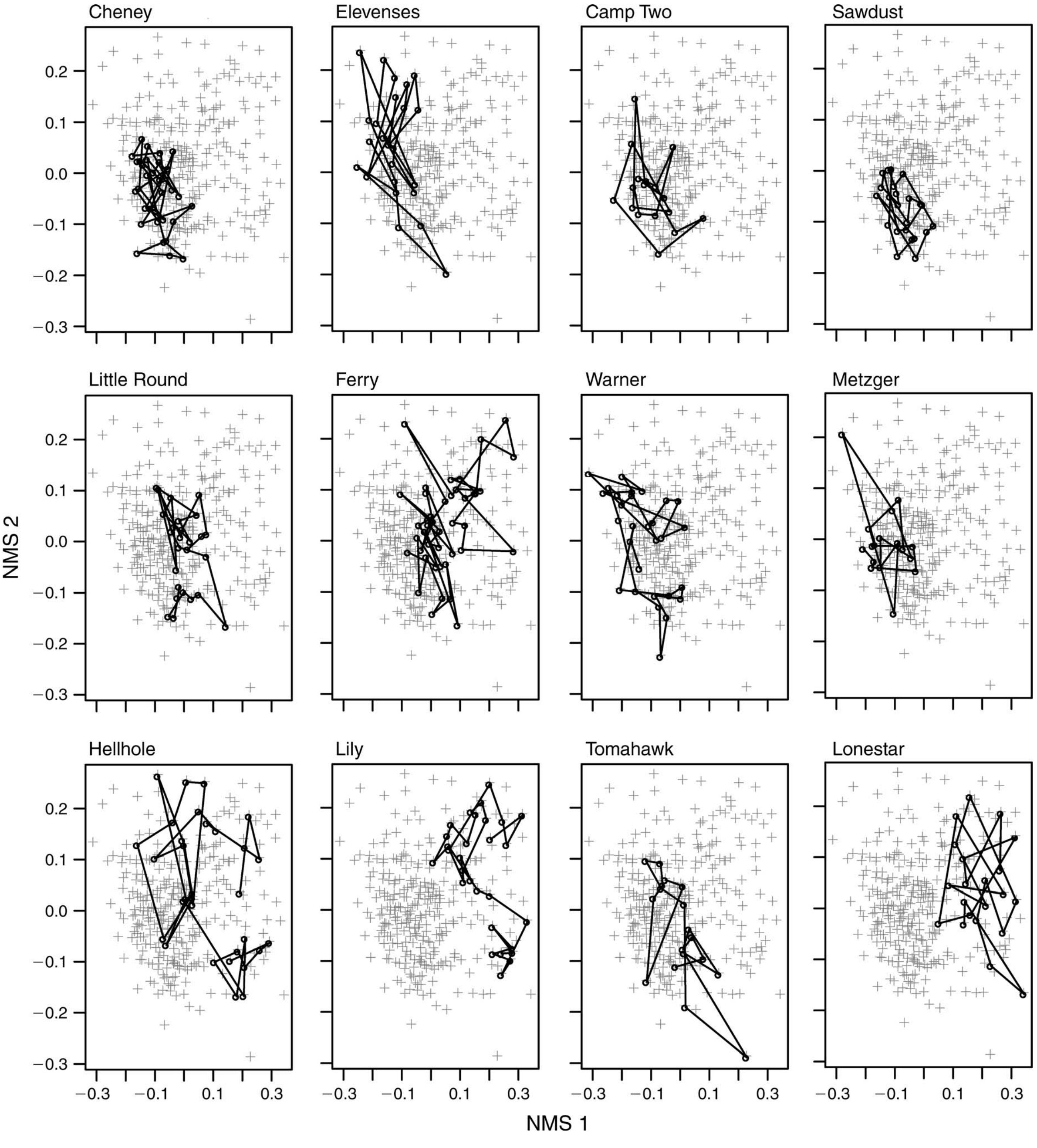

FIG. 3. Individual lake sites differ in the range of compositional variability they show in ordination space over the last 2000 years. Gray crosses depict the entire data set and black circles depict the individual lake named above each panel. Samples adjacent in time are linked with a solid black line. Lake records are presented in order of their latitude from the upper right (northeast) across rows to the lower left (southwest).

greater CEC, and warmer temperatures due to a diminished lake influence.

The number of LIA fires also corresponds to the gradient in species composition shown by the first NMS axis in the ordination (Fig. 2). Sites with higher percentages of jack/red pine pollen had higher LIA fire frequency, whereas the sites with higher oak pollen percentages had lower LIA fire frequency (Table 3). Fire frequency was highest in the part of the landscape with very sandy, extremely well drained soils (Fig. 2). The frequency of fire also increased during the LIA at most sites, except for some sites in the more heterogeneous southwestern part of the landscape, Hellhole, Lily, Lone Star, and Little Round, and Sawdust in the extreme

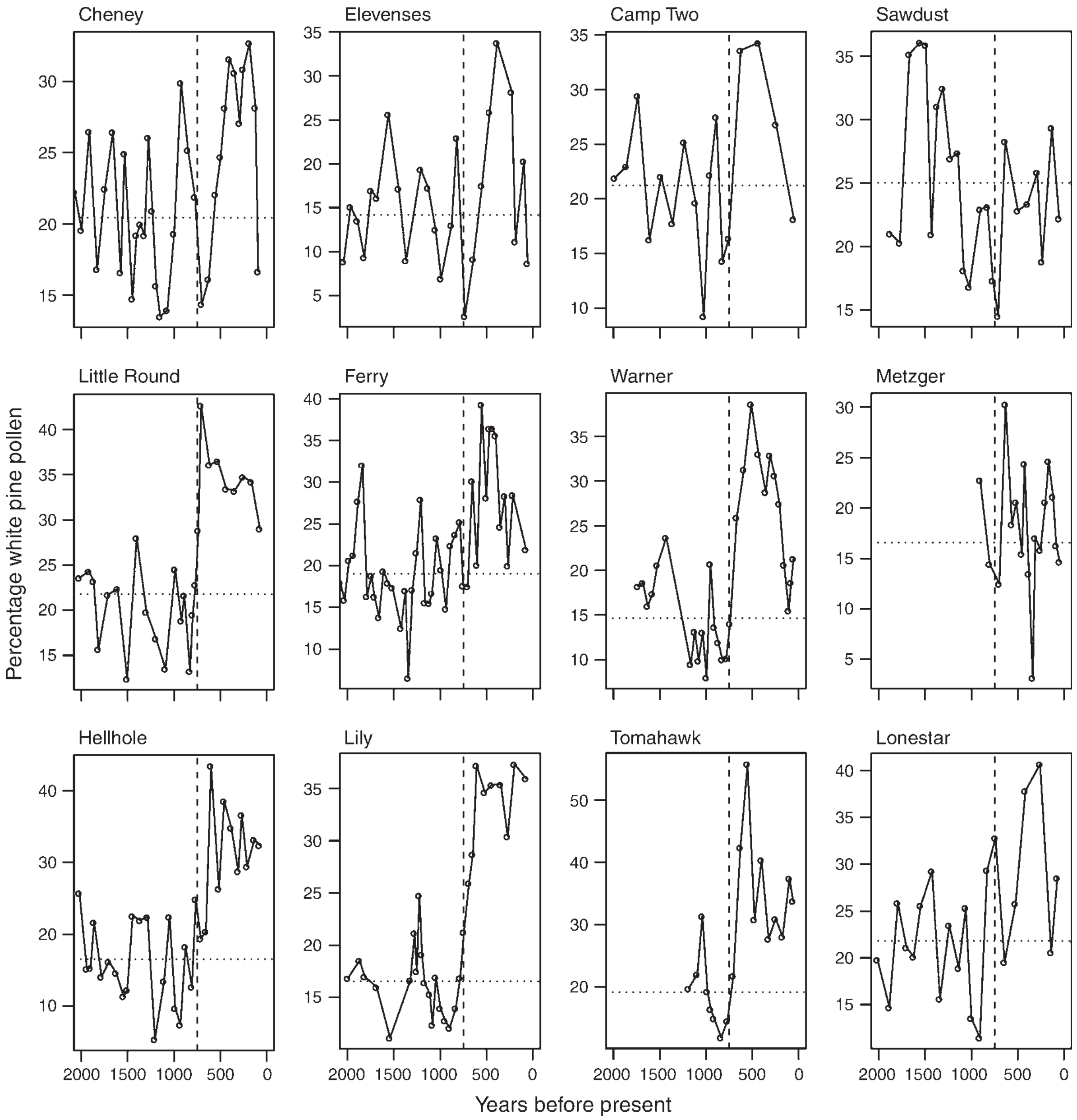

FIG. 4. Some lake sites show greater increases than others in the percentage of white pine pollen during the Little Ice Age (LIA; 700–75 yr BP). Vertical values depict the percentage of white pine pollen in the sample. Horizontal values represent sample age in calibrated years before the present (1950). Vertical dashed lines denote the beginning of the LIA at 700 yr BP. The horizontal dotted lines show the average white pine pollen percentage for all the site's samples preceding the LIA (2000–700 yr BP).

northeast (Table 1). Peak magnitude of fires generally decreased during the LIA, except at Hellhole, Ferry, and Camp Two, where it increased (Table 1).

Climate, fire, and soil variables are associated with the temporal vegetation dynamics of individual sites (Fig. 6). Greater increases of white pine during the LIA generally occurred on sites with less excessively drained soils ($R^2 = 0.41$, $P < 0.0256$). White pine also increased more at sites with warmer local temperatures ($R^2 = 0.55$, $P < 0.0056$). These sites occur in the southwest portion of the landscape and also had less snowfall and less total precipitation. Volatility in the rate of change between samples was positively associated with higher LIA fire frequency ($R^2 = 0.45$, $P < 0.0163$).

DISCUSSION

Patterns of variation in species composition

We found that vegetation response to past climatic shifts differed among sites with different landscape attributes. The most consistent difference was the extent

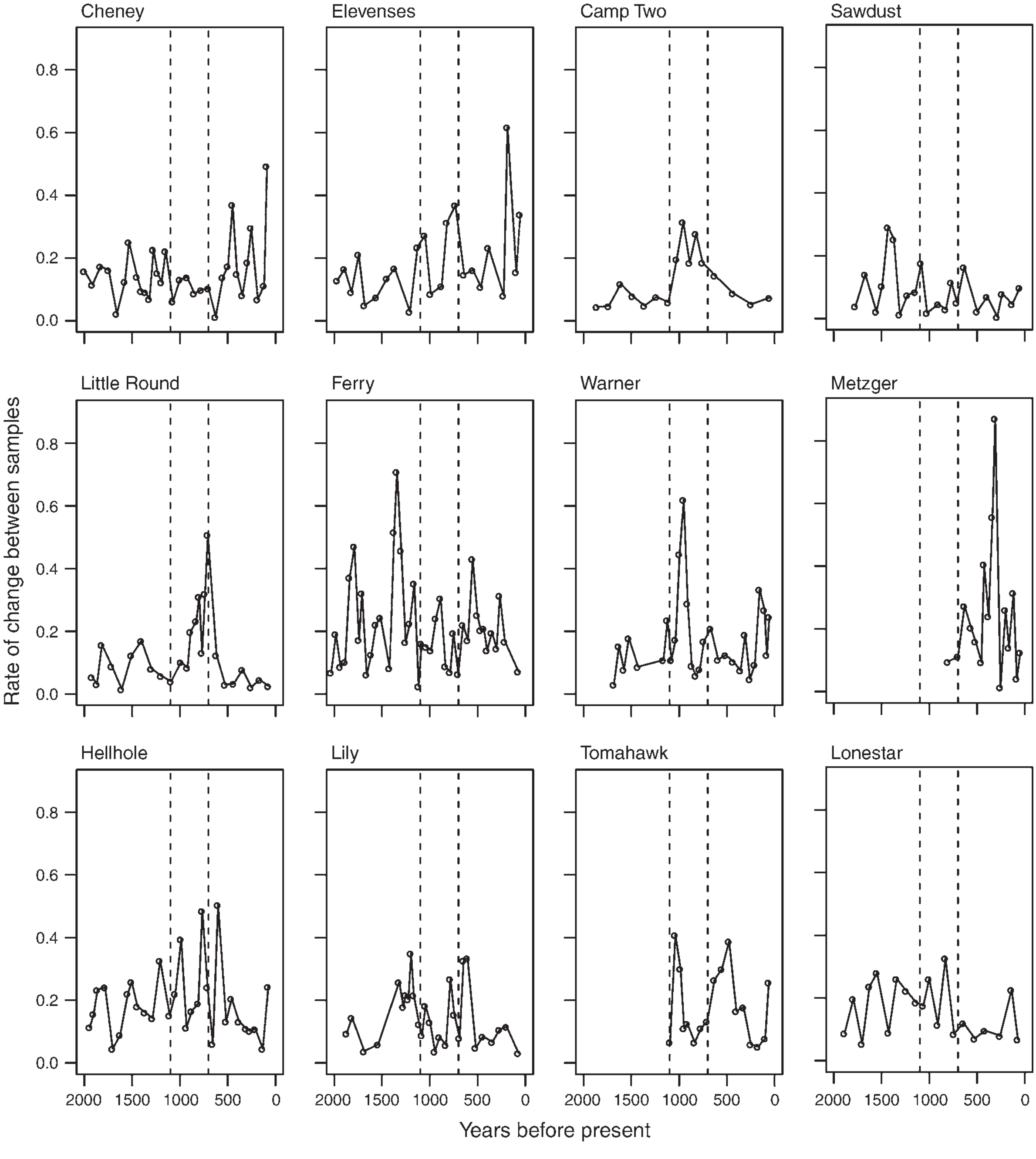

FIG. 5. Individual sites differ in the volatility of the rate of change in ordination space between samples. Vertical values show the distance traveled in the two-dimensional ordination from the previous sample divided by time between samples. Horizontal values represent sample age in calibrated years before the present. Vertical dashed lines denote the beginning of the Medieval Climatic Anomaly at 1100 yr BP and the beginning of the LIA at 700 yr BP.

to which white pine increased during the Little Ice Age (LIA). Taxa affiliated with mesic habitats increased at many western Great Lakes sites during the LIA climate period, suggesting cooler and/or wetter conditions (McAndrews 1968, Swain 1978, Grimm 1983, 1984, Gajewski et al. 1985, Hotchkiss et al. 2007, but see Shuman et al. 2009). On the northwest Wisconsin, USA, sand plain (NWSP), white pine increased most in the southwest where Lake Superior's (positive) effect on modern winter precipitation is least, suggesting that a moisture-related establishment threshold may have been crossed during the LIA at these drier-winter sites.

The positive relationship between LIA fire frequency and short-term vegetation change is another important pattern. Fires generally became less intense during the LIA as shown by lower peak magnitudes in the charcoal

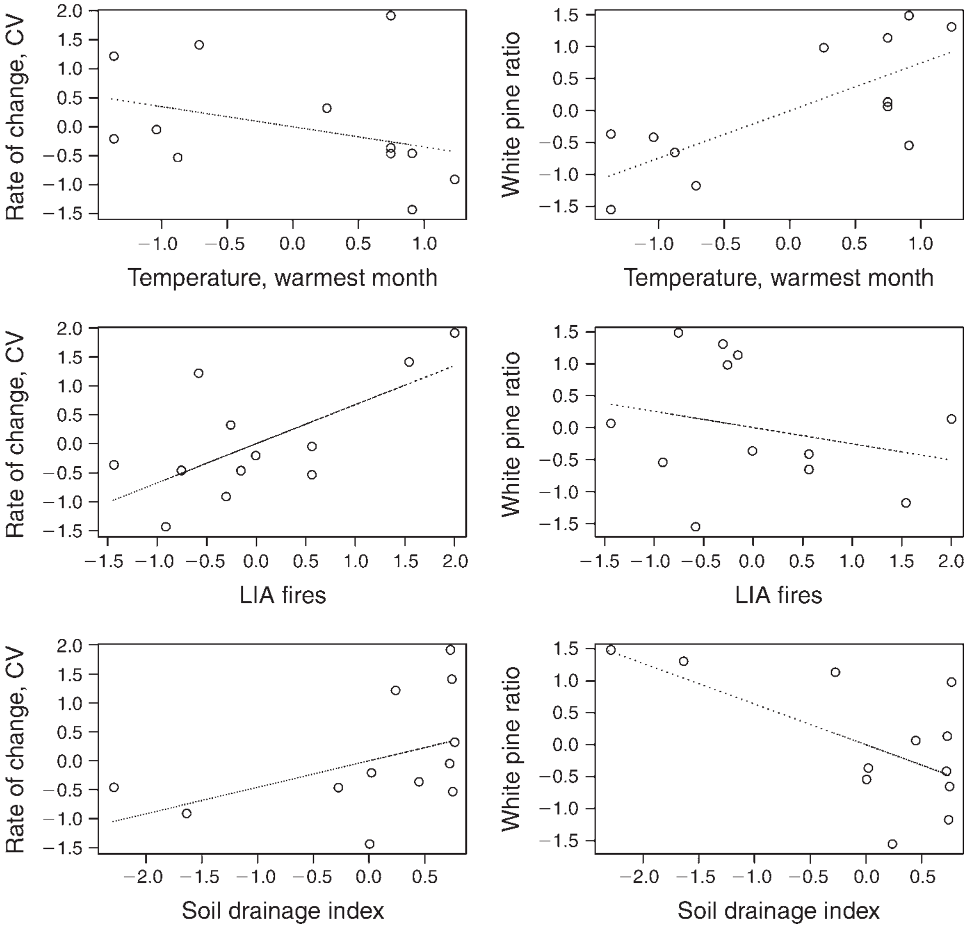

Fig. 6. The two temporal-variability metrics differ in their relationships to soils, climate, and disturbance factors. The coefficient of variation (CV) of the rate of change (left column) was not related to temperature ($R^2 = 0.12$, $P < 0.26$) or soil drainage index ($R^2 = 0.21$, $P < 0.13$), but was associated with higher LIA fire frequency (number of fires/500 yr; $R^2 = 0.45$, $P < 0.0163$). White pine ratio (right column) was associated with temperature in the warmest month ($R^2 = 0.55$, $P < 0.0056$) and soil drainage index ($R^2 = 0.41$, $P < 0.0256$), but had no relationship with LIA fire frequencies ($R^2 = 0.06$, $P < 0.42$). All data were standardized to 0 ± 1 (mean ± SD) before plotting.

data (Table 1). However, sites with sandier, excessively drained soils showed a slight increase in fire frequencies and were associated with rapid pollen assemblage shifts over a few decades and compositional volatility. Disturbance and vegetation feedbacks on fire can either facilitate shifts in species composition (Davis and Botkin 1985, Overpeck et al. 1990, Bradshaw and Hannon 1992, Clark et al. 1996, Clark et al. 2001, Scheller and Mladenoff 2005, Booth et al. 2012) or maintain stability of vegetation types during climate changes (Heinselman 1973, Cleland et al. 2004, Lytle 2005, Umbanhowar et al. 2006). Overall, change in vegetation composition on the NWSP during the LIA was driven by variation in soils and local climate more than by changing fire frequencies. However, vegetation on sites with excessively well drained soils and low-nutrient availability was not affected as much by climate. Disturbance by fire at these sites introduced sudden compositional shifts and volatility in forest composition.

Implications for forest management

Changes in forest composition on this glacial outwash landscape over the past 2000 years were driven primarily by white pine interactions with both soils and local climate, and by shifts in fire frequency. In the 21st century, however, neither fire nor white pine will play the same role as they did in the past. Projections of higher temperatures and lower summer precipitation on the NWSP (WICCI 2009) suggest that wildfire frequency and intensity may increase with climate change (Flannigan et al. 2009), but future fire regimes will also be strongly influenced (dampened) by habitat fragmentation and modern fire-containment capability (Swanston et al. 2011). In a similar vein, white pine is unlikely to become more abundant in northwestern Wisconsin with projected 21st century climate change (Swanston et al. 2011). However, other species will likely proliferate due to changing climate conditions, so principles derived from the history of white pine can inform management expectations for other species.

A principle emerging from the NWSP paleoecological record is that soil attributes and the landscape context constraining fire behavior shape forest response to climate changes and disturbance even at very local scales (Lynch et al. 2014). Soils with higher water-holding capacity supported a proliferation of white pine during the LIA, whereas more excessively drained soils tended to have a fluctuating but consistently jack pine-dominated community. These specific relationships may not hold under the unique conditions of future climate; changing conditions could just as well favor species that proliferate on low CEC, sandy soils, and thereby show a pattern opposite the one observed with white pine during the LIA. What these observations of past changes show, however, is that soil differences are important influences on vegetation response to climate change. Our results support the call to consider the full range of biophysical features when planning for climate adaptation across regions, i.e., "conserving the stage" (Anderson and Ferree 2010), and suggest that managers tailor monitoring and management to the full range of soil and geophysical features at the landscape or management-unit level. A manager or management partnership, for example, could encourage stratification of forest research and monitoring across soil types to develop consistent baseline and trend data. This understanding is important because the effect of alternative management regimes and climate adaptation efforts on different soil types may be the most significant predictor of future forest composition changes (Swanston et al. 2011).

Conclusions

Changes in forest composition over the past 2000 years differed among sites on a fairly homogeneous glacial outwash landscape. Vegetation at some sites was more volatile in the past, and some sites demonstrated a greater increase in white pine abundance during the climate changes of the Little Ice Age period. These differences in temporal dynamics corresponded to differences in local climate and soil characteristics as well as fire history.

The historical record shows that climate change will likely affect vegetation differently on different soil types. Resource managers must account for spatial variability in soil properties and local climate in monitoring and in planning responses to future climate change.

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