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LETTER

Effect of historical land-use and climate change on tree-climate relationships in the upper Midwestern United States

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Abstract

Contemporary forest inventory data are widely used to understand environmental controls on tree species distributions and to construct models to project forest responses to climate change, but the stability and representativeness of contemporary tree-climate relationships are poorly understood. We show that tree-climate relationships for 15 tree genera in the upper Midwestern US have significantly altered over the last two centuries due to historical land-use and climate change. Realised niches have shifted towards higher minimum temperatures and higher rainfall. A new attribution method implicates both historical climate change and land-use in these shifts, with the relative importance varying among genera and climate variables. Most climate/land-use interactions are compounding, in which historical land-use reinforces shifts in species-climate relationships toward wetter distributions, or confounding, in which land-use complicates shifts towards warmer distributions. Compounding interactions imply that contemporary-based models of species distributions may underestimate species resilience to climate change.

Keywords

Anthropocene, climate change, climate disequilibrium, forest inventory and analysis (FIA), fundamental niche, historical ecology, land-use, niche shift, Public Land Survey System, realised niche.

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INTRODUCTION

Contemporary species occurrence databases and, increasingly, palaeohistorical data sets are used to map distributions of species and species traits within environmental space, study underlying processes and prepare for climate change (Pearman *et al.* 2008; Moritz & Agudo 2013; Lamanna *et al.* 2014; Maguire *et al.* 2015; Ivory *et al.* 2016). These distributions of species in geographical and environmental space, combined with future climate scenarios, are used to assess species exposure and sensitivity to climate change, identify species and habitats of concern, set conservation priorities and prepare for climate-driven shifts in habitat suitability (Iverson & Prasad 1998; Pellatt *et al.* 2012; Anderson 2013; Guisan *et al.* 2013; Iverson & McKenzie 2013). Forest inventories offer rich observational data sets that have been used to assess early signals of range shifts via the distributions of mature trees and seedlings (Zhu *et al.* 2012; Monleon & Lintz 2015) and to parameterise models of current and future tree distributions (Iverson & Prasad 1998; Iverson *et al.* 2008).

Increasingly, ecologists are turning to the palaeohistorical record to test the assumptions underlying ecological models and improve their predictive capacity (Moritz & Agudo 2013; Maguire *et al.* 2015). Projections relying only on contemporary observational data may overlook plasticity in species-climate responses (Maiorano *et al.* 2013), incompletely delimit species fundamental niches (Jackson & Overpeck 2000), miss responses to past no-analogue climates (Veloz *et al.* 2012), or fail to detect effects of anthropogenic land-use and other historical legacies (Svenning *et al.* 2015). Palaeoecological records show that forest responses lag abrupt climate change by a few years to centuries (Webb 1986; Svenning *et al.* 2015; Williams & Burke in press), suggesting that tree distributions have yet to fully respond to recent climate changes. In principle, mechanistic dynamic vegetation models (e.g. Leiblein-Wild *et al.* 2016) can represent the physiological, demographic and dispersal processes that cause tree populations to lag climate change. In practice, however, the parameterisation of these models is poorly constrained for slow ecological processes (Moorcroft 2006; Matthes *et al.* 2016).

Historical land-use has substantially affected species distributions and vegetation structure (e.g. Gehrig-Fasel *et al.* 2007) and may cause species distributions to incompletely fill available climates, or otherwise be at disequilibrium (Sarmento Cabral *et al.* 2013; Early & Sax 2014; Ivory *et al.* 2016). Anthropogenic land-use is structured and is often biased within climate space, hence, species distributions and protected natural areas often represent a biased selection from the available environmental space (Scott *et al.* 2001). Biasing can confound studies that use contemporary distributional data to understand the environmental controls on species distributions and predict species responses to future climate scenarios (Pyke 2004).

Interactions between climate and land-use change can be classified into three types: compounding, confounding and counteracting (modified from Pyke 2004). Compounding effects occur when climatic and land-use changes shift species distributions in the same direction along an environmental gradient. For example, warming has been compounded by land-use conversion at the lowest elevations in the Sierra Nevada Mountains of California, both causing upslope distributional shifts for butterfly species (Forister *et al.* 2010). Confounding effects may cause little overall change in species distributions, with land-use pressure occurring across the species' environmental gradient. For example, land-use conversion has excluded Garry oak (*Quercus garryana*) from the deep-soil sites it formerly occupied (Pellatt & Gedalof 2014), but land-use has not systematically shifted Garry oak distributions in climate space. Confounding effects may hinder detection of climatic forcing of historical species distributions. Counteracting effects occur when climate and land-use change act in opposite directions, narrowing the available geographical and climatic space available for species. For example bird species in the Sierra Nevadas are expected to move downslope due to increasing precipitation (Tingley *et al.* 2012), but this downslope migration is limited by land-use conversion in the lowlands.

Tree distributions and community composition in the upper Midwestern United States have been heavily influenced by land-use conversion associated with Euro-American Settlement in the 19th and 20th Centuries (Schulte *et al.* 2007; Rhemtulla *et al.* 2009a; Hanberry *et al.* 2012; Goring *et al.* 2016), outbreaks of exotic pathogens (Barnes 1979), climate changes accompanying the Little Ice Age (Hotchkiss *et al.* 2007) and current anthropogenic warming (WICCI 2011). Modern forests show greater homogeneity, weaker ecotones and significantly different species associations than forests surveyed as part of the Public Land Survey System (PLS) prior to widespread land-use conversion in the late 1800s (Schulte *et al.* 2007; Goring *et al.* 2016). *Pinus strobus* and *Tsuga canadensis* now occupy only 4% of their original coverage in Wisconsin (Rhemtulla *et al.* 2009a). Wildlands have been converted to agricultural and urban land-use (Rhemtulla *et al.* 2009a), particularly in historical prairie and savanna ecosystems (Fig. 1f), where almost 50% of deciduous savanna was converted to cropland (Rhemtulla *et al.* 2007). In northern forests, ranges of early successional species have expanded and abundances of late-successional species have been reduced due to widespread logging in the 19th and 20th centuries, and ongoing land management (Schulte *et al.* 2007; Goring *et al.* 2016). In addition, the formerly dominant *Ulmus americana* has experienced rangewide population collapses caused by the introduction of exotic pathogens (Barnes 1979), as did *Castanea dentata*, with other tree species currently threatened (*Tsuga canadensis*, *Fraxinus* spp.; Barnes 1979; Castello *et al.* 1995; Schlarbaum *et al.* 1998).

Here we demonstrate significant shifts in the climatic distributions of tree genera in the upper Midwestern United States over the last two centuries due to historical climate and vegetation change, and we diagnose the relative influence of historical climate change and, land-use changes and pathogen outbreaks (for *Ulmus*) on these shifts. We use gridded historical and contemporary climate observations (PRISM-LT) and estimates of pre-settlement and modern forest vegetation (Goring *et al.* 2016) to map the geographical and climatic distributions for 15 major tree taxa in the upper Midwest. We construct four observed and hypothetical sets of tree-climate relationships, using a 2 × 2 factorial of pre-settlement and modern vegetation and climates. We develop a new method, based on Hellinger distances among tree-climate distributions, to quantify the total change and attribute the relative importance of historical vegetation and climate change. We assess whether climate and vegetation changes are compounding, counteracting or confounding. We use this framework to discuss the potential impacts of historical land-use and climate change on inferences about species resilience to climate change, as predicted by species-distribution models based solely on modern distributional data.

MATERIALS AND METHODS

Historical and modern vegetation data

Estimates of settlement-era forest composition and tree distribution are based on survey data from the PLS (White 1983; Schulte & Mladenoff 2001; Goring *et al.* 2016), aggregated to a 64 km^2 grid across the upper Midwestern United States (Goring *et al.* 2016). PLS data originally were collected on a 1.61 × 1.61 km (1 × 1 mi) grid across the upper Midwest from 1830 to 1910 (White 1983; Schulte & Mladenoff 2001). At each survey point, surveyors noted the closest two to four trees and recorded their common name, distances from survey points, diameters at breast height and azimuth to trees. Goring *et al.* (2016) aggregated this data to an 8 × 8 km grid with an average of 61 survey points (122 trees) per cell. This process included data cleaning, taxonomic standardisation

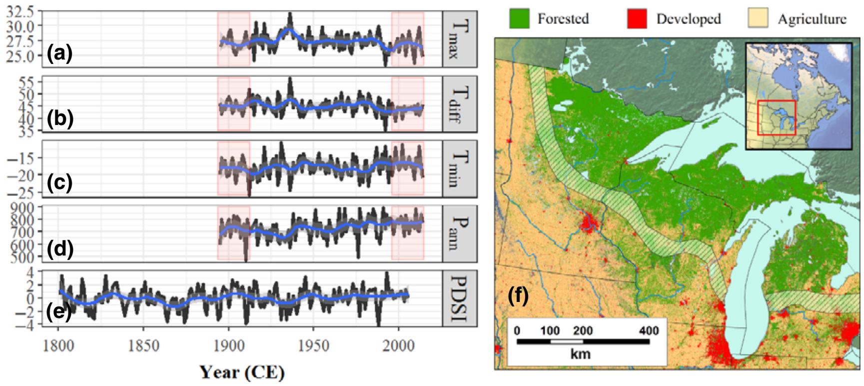

Figure 1 (a–e) Climate change in the upper Midwest over the last two centuries using PRISM data and North American Drought Atlas PDSI reconstructions with a LOESS smooth superimposed for illustration. Modern climate (normals indicated by rectangles). PDSI shows strong coherence with P_{ann} in this region. (f) Patterns of land-use change in the upper Midwestern United States, with the 'Tension Zone', differentiating sub-boreal from southern broadleafed forests superimposed. land-use data from the NLCD (Jin *et al.* 2013).

and the application of spatially varying correction factors (Goring *et al.* 2016). Using this data, we produce presence-absence distributions for each taxon, across the upper Midwest for 15 common tree genera. A few common names, such as 'Ironwood', cannot be clearly resolved to a single tree genus, and so we combine *Ostrya* and *Carpinus*, and *Thuja* and *Juniperus*. We define 'presence' as at least one recorded tree in any 8 × 8 km grid cell and use the term 'range' as the extent in geographical or climate space of all cells with recorded presence for a specific taxon.

Modern forest data are from the US Forest Inventory and Analysis (FIA) programme, which provides detailed inventories of contemporary tree distributions, for all regions with > 10% forest cover (Woudenberg *et al.* 2010). The FIA uses a nationally standardised sampling procedure; in the Phase 2/3 system, beginning in 1998, each plot consists of four, 7.32 m radius, circular sub-plots that are sampled intensively (Woudenberg *et al.* 2010).

Comparisons between historical and modern vegetation must address differences in sampling design between the PLS and FIA data sets (Kronenfeld *et al.* 2010; Kronenfeld 2014; Goring *et al.* 2016). Here, the primary solution for maximising comparability is via aggregation, both spatially, by aggregating records from both data sets to a common scale (8 × 8 km), and taxonomically, by aggregating taxa to the level of genera. Nonetheless, differences persist. The FIA contains fewer plots per 8 km cell, with more trees per plot than the PLS data. FIA plots are sited within forested or partially forested landscapes, while the PLS sampling is uniform. Scattered trees may be present in regions without permanent or temporary FIA plots, complicating the assignments of 'absence' within the FIA. However, the practice of using FIA data as a surrogate for tree distribution data is widespread (Iverson & Prasad 1998; Iverson & McKenzie 2013), so these complications are general. In prior comparative analyses of the PLS and FIA data, Goring *et al.* (2016) tested the effect of differential sampling design on the mapped patterns of novel and disappearing forests, and found little effect.

Given the differences in sampling design, FIA data should be better at detecting species presence at the level of individual plots, whereas detectability at the level of 8 km grid cell (the analysis unit of this study) should be similar between FIA and PLS data or higher in the latter. Within grid cells, there is a trade-off between the intensive sampling within FIA plots vs. more PLS points per grid cell and more uniform sampling of landscape heterogeneity. The PLS data may be better at detecting tree presence in low-density regions, due to the variable radius of PLS plots. Both the FIA and PLS data sets both have good coverage in the upper Midwest, with 5172 8 km grid cells with at least one FIA plot and 7376 grid cells with at least one PLS point.

In mapping tree distributions in the upper Midwest we consider three classes: 'gain,' where a tree species was present within a grid cell in the FIA, but absent in the PLS; 'loss,' where a tree was present in a grid cell during the PLS but absent in the FIA; and 'presence,' where a tree was present within a grid cell in both FIA and PLS eras. We present gain and loss estimates for all grid cells (Table S1) and for the subset of grid cells with both PLS and FIA observations (Table S2). For all species, the range within the upper Midwest incompletely samples species ranges, however, the region contains several major ecotones and the southern and western range limit for many tree species (Curtis 1959) so this region represents an important boundary in geographical and climate space.

Historical and modern climate data

We use monthly PRISM LT data for 1895–2014 CE (PRISM Climate Group, Oregon State University 2004) for the historical and modern climate data. The PRISM climate variables are available at 800 m resolution and are interpolated from station locations using elevation, aspect and other data. We resample estimates for mean daily July temperature ($T_{\max}$), mean daily January temperature ($T_{\min}$), annual temperature range (T_{diff}: $T_{\max} - T_{\min}$), and annually summed daily precipitation (P_{ann}) to the 8 × 8 km grid used for PLS and FIA data. These climate variables represent three major climatic controls on plant distributions: summer warmth, winter minimum temperatures and moisture availability; these or similar bioclimatic variables are widely used in plant distributional modelling (Woodward 1987; Iverson & Prasad 1998; Maiorano *et al.* 2013).

Three periods were selected for calculation of climate normals: 1895–1919 for the historical period and two alternatives for the modern period; 1950–1979 representing the average period of establishment for stand in the upper Midwest and 1985–2014 covering the period of sampling for the FIA data. We report results for the 1985–2014 normals, with the 1950–1980 results shown in Supporting Information. There is an unavoidable temporal mismatch between the historical climate data and the PLS survey period, on the order of 50–70 years. Few meteorological records exist in this region prior to 1895 CE, and no gridded data set exists at high spatiotemporal resolution for this time period for all climate variables. To check whether an 1895–1919 CE climate normal is a reasonable surrogate for pre-settlement climates we compare the instrumental record against dendroclimatic reconstructions of the Palmer Drought Severity Index (Heim 2002) (Fig. 1) and to early temperature observations from US military forts and observer stations, which extend to the 1830s (Baker *et al.* 1985; Burnette *et al.* 2010).

The alternative modern climate normals correspond to time of sampling vs. time of tree establishment. The 1990–2014 normal encompasses the period of sampling (2000–2015) for the FIA data used here. The 1950–1979 normal encompasses the time of establishment of FIA trees, which have an average age of 50 years in this region (USDA Forest Service, 2016). We report results for the 1990–2014 normals, with the 1950–1979 results shown in Supporting Information.

Shifts in species distributions in climate space

Distributions of tree genera within climate space are shown using box plots and described as univariate probability density functions (PDFs) of tree species presence in vegetation (V) along a climate (C) gradient, estimated using an unweighted Gaussian kernel density estimator, using R's density function.

Differences among univariate PDFs are quantified for each climate variable using Hellinger distances (Matthes *et al.* 2016) among the univariate PDFs representing the four combined states of vegetation and climate (V_HC_H, V_HC_M, V_MC_H, V_MC_M, where M and H represent modern and historical conditions). The Hellinger distance for two discrete probability distributions is:

$$H(P,Q) = \frac{1}{\sqrt{2}}\sqrt{\sum_{i=1}^{k}\left(\sqrt{p_i}-\sqrt{q_i}\right)^2}$$

where P and Q are the distributions, with a common index i.

The total observed shift (d_{tot}) between a historical and modern PDF is the Hellinger distance between V_MC_M and V_HC_H (Fig. 2a: top left to bottom right). The conditions V_MC_H and V_HC_M are synthetic, generated by superimposing historical climate patterns on modern vegetation distributions and *vice versa*. The effect of climate change on shifting PDFs (d_c) is the difference between PDFs using the early climate normals (C_H) and modern climate normals (C_M) overlaid on PLS vegetation (e.g. V_HC_H vs. V_HC_M; Fig. 2a; left column). The effect of vegetation change on shifting PDFs is d_v, the Hellinger distance between V_HC_H and V_MC_H (top row of Fig. 2a). Because Euro-American land-use is the dominant driver of vegetation change in the upper Midwest over the past two centuries (Introduction), we often attribute shifts recorded by d_v to the land-use change associated with Euro-American settlement.

We develop an attribution index, ($\Delta_d = d_c - d_v$), such that $\Delta_d < 0$ indicates stronger influence of historical land-use on shifting climate distributions, whereas $\Delta_d > 0$ indicates a stronger influence of historical climate change.

To assess whether the effects of historical land-use and climatic changes are compounding, counteracting, or confounding we perform *t*-tests, using the conservative Bonferroni correction to account for multiple tests and adjustments for spatial autocorrelation (Supporting Information). For each taxon and climate variable pair we test whether V_HC_H and V_HC_M (attribution to climate change), and V_HC_H and V_MC_H (attribution to vegetation change) distributions are significantly different (Fig. 2). If both changes are significant and of the same sign, then the shift is compounding. If both are significant and in opposite directions, then the shift is counteracting. If either climate change or land-use is significant, but the other is not, then the change is confounding, since in both cases, the climate signal is weak or obscured by local, non-directional vegetation change.

Analysis

All analyses use R (R Core Team 2014), RMarkdown (Allaire *et al.* 2016) and R packages colorspace, captioner, raster, ggplot2, mgcv, reshape2, plyr, gridExtra, rgdal, RColorBrewer, analogue, maptools, dplyr and purrr. All code is hosted on GitHub (http://github.com/PalEON-Project/Composition_Climate). Maps use the public domain Natural Earth Data (http://naturalearthdata.com) products for political and landscape features.

In the Supporting Information, we present sensitivity analyses that employ alternate choices for climate normal and choice of PLS and FIA grid cells for gain/presence/loss estimates. We further discuss (in the main text and Supporting Information) the degree to which FIA and PLS differences in sampling design affect this study and show that the main findings of this study are robust.

RESULTS

Regionally, T_{min} increased 3.3 °C between 1895–1924 and 1985–2014 (Fig. 1), T_{max} changed by −0.8 °C, whereas T_{diff} changed by −4.1 °C (see Supporting Information for estimates based on the 1950–1979 normals). P_{ann} increased by 55.3 mm. The Palmer Drought Severity Index is correlated with P_{ann} trends from 1895 onward (r = 0.43) and, with LOESS (Local

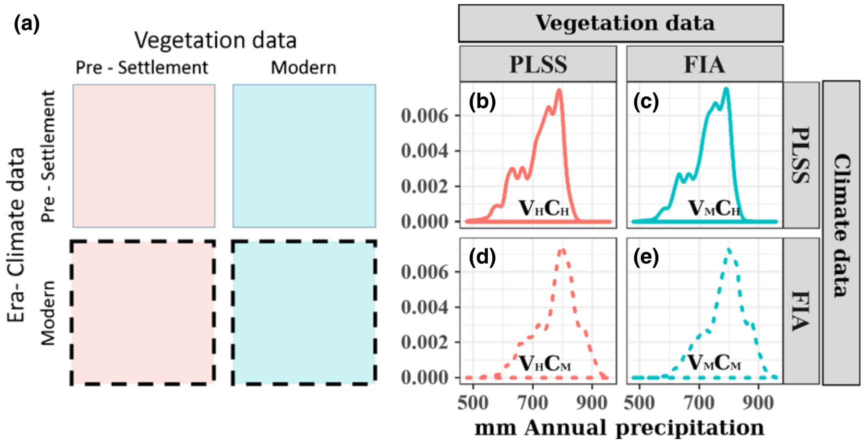

Figure 2 (a) The 2 × 2 factorial design used to diagnose the effects of historical climate and vegetation change on observed shifts in tree-climate relationships. Observed and hypothetical tree-climate relationships for one of four combinations of pre-settlement vegetation (pink fill, left column) or modern vegetation (blue fill, right column) and pre-settlement climate (solid border, top row) or modern climate (dashed border, lower row). (b–e) Representative normalised probability densities for *Quercus* for each of the four combinations of climate and vegetation states, plotted relative to T_{max} (b), T_{diff} (c), T_{min} (d) and P_{ann} (e).

regression), indicates no major climatic trends between 1800 and 1900 (Fig. 1e), suggesting that early 20th-century precipitation is a reasonable surrogate for mid-19th-century precipitation. Early temperature observations from US military forts indicate warming between the middle 19th and early 20th centuries at Fort Snelling, Minnesota (Baker *et al.* 1985) and Fort Leavenworth, Kansas (Burnette *et al.* 2010). The latter shows faster increases during winter (0.10 °C decade^{-1}) than summer (0.07 °C decade^{-1}). Hence, our estimates of historic climate change may be too conservative for $T_{\min}$ and T_{diff} and too large for $T_{\max}$ (Supporting Information).

All tree genera show higher losses than gains (Table S1, Fig. 3). Range losses are high generally, with an average of 57% across all taxa and are heavily concentrated in the south and west (Fig. 3). For *Ulmus* and *Larix*, however, losses occur throughout the range. *Larix*, *Ulmus* and *Betula* have the largest absolute losses in range within the upper Midwest. Gains average 6% across all taxa, with the highest gains (16.5%) observed for *Populus* (Fig. 3). Spatial patterns of gains vary widely among tree genera, and often show less spatial bias than losses (Fig. 3). *Picea*, *Larix*, *Abies*, *Tsuga*, *Fagus*, *Ostrya/Carpinus*, *Tilia* and *Fraxinus*, all show a dispersed pattern of gains in few and widely scattered cells, suggesting that these apparent range gains are mainly caused by sampling uncertainty inherent in local-scale plot and stand heterogeneity, rather than systematic range gains. Gains for *Populus* and *Acer* are concentrated in northern Minnesota, Wisconsin and Michigan, suggesting range infilling, whereas *Quercus* gains are consistent with some range extension northwards. *Pinus*, *Juniperus/Thuja* and *Ulmus* range gains are limited but primarily in the southern portion of their historical range, or beyond it.

Shifts in tree-climate distributions are significant for all genera and climate variables (Fig. 4), even accounting for multiple comparisons and spatial autocorrelation (all $P < 0.0001$). The directionality of shifts is consistent across genera: for example modern $T_{\max}$ is lower for all genera, whereas $T_{\min}$ and P_{ann} are higher (Fig. 4). *Ulmus* shows the largest increase in minimum temperature (Fig. 4; $\Delta_{T_{\min}} = 4.2$ °C), whereas *Larix* has the smallest. Maximum annual temperature declines most for *Ostrya/Carpinus* ($\Delta_{T_{\max}} = -1.3$ °C) and least for *Ulmus* ($\Delta_{T_{\max}} = -0.4$ °C). *Ulmus* shows the largest increase in mean precipitation ($\Delta_{P_{\text{ann}}} = 86$ mm) and *Larix* the smallest ($\Delta_{P_{\text{ann}}} = 42$ mm). These patterns are unchanged by a

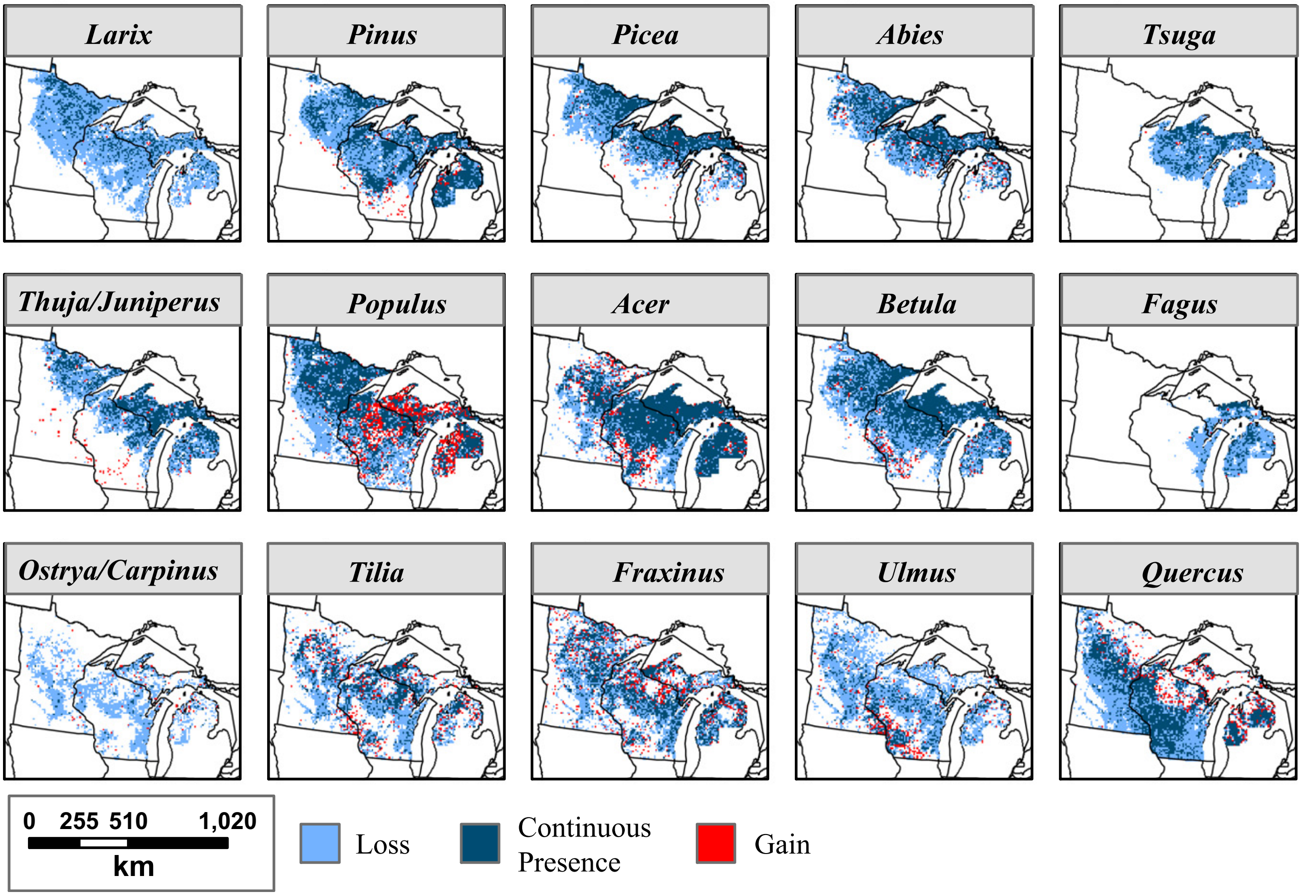

Figure 3 Maps showing areas of gain, loss and continuous presence of tree genera. 'Loss' indicates 8 × 8 km grid cells where PLS data indicated presence of a genus but FIA data do not record presence (light blue). 'Gain' indicates areas where a genus is absent in the PLS data but present in the FIA data (red). 'Continuous presence' represents locations where both FIA and PLS data indicate presence (dark grey). Losses are more common than gains, particularly in the southwestern portion of tree ranges. Few taxa show gains, although *Populus*, Fraxinus and Tilia show gains of over 10% (Supporting Information).

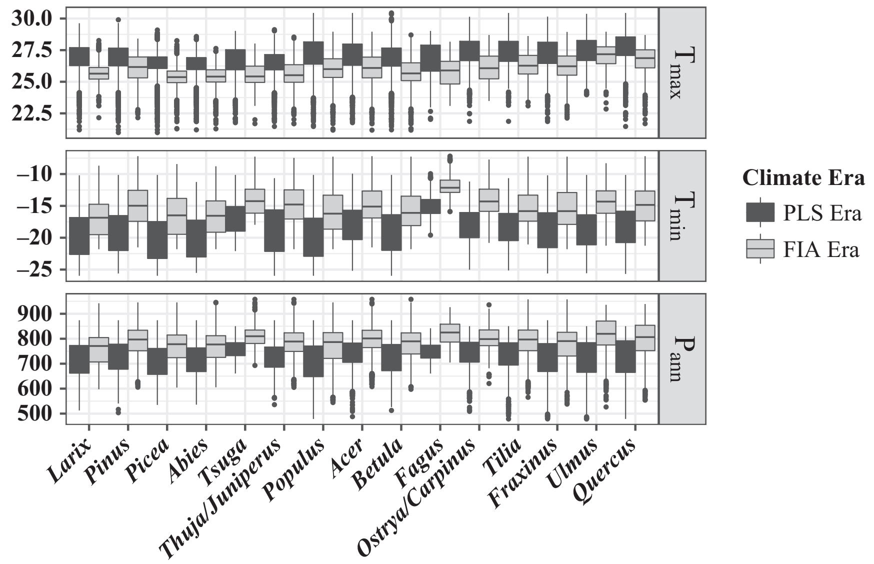

Figure 4 Changes in the realised climate distributions for tree genera in the upper Midwestern United States produced by the joint effects of historical climate change and land-use change. The central line indicates the median, box margins indicate 25th and 75th percentiles, whisker tips indicate 5th and 95th percentiles and dots indicate outliers beyond the 95th percentile.

sensitivity analysis in which the historical temperature changes are augmented by estimated temperature trends reported from the historical records, but the $T_{\max}$ changes are sensitive to choice of modern climate normal (Supporting Information).

Both the total shift in realised tree-climate distributions and the attribution of these changes to historical vegetation or climate change vary among taxa and among climate variables (Fig. 5). The joint effects of historical climate and vegetation change on tree-climate distributions are illustrated for *Quercus* (Fig. 2). For *Quercus* we see changes due to both climate (Fig. 2b and d) and vegetation change (Fig. 2b and c), but a stronger effect of historical climate change, reflected in the attribution index Δ_d (Fig. 5).

Shifts in realised climate distributions over the last 100–150 years are largest for *Ulmus* ($T_{\min}$, $T_{\max}$), *Larix* ($T_{\max}$), *Tsuga* ($T_{\max}$ and P_{ann}) and *Fagus* (P_{ann}). Attribution analyses based on Δ_d (Fig. 5) reveal that while the imprint of historical vegetation change on shifting climatic niches is important for many taxa, the effect varies across taxa. The climatic signal is strongest for P_{ann}, with regional changes in P_{ann} being largely responsible for shifting climate niches, whereas only *Populus* and *Picea* have seen precipitation niche shifts that are slightly more attributable to land-use than climate shifts (Fig. 5). The greatest land-use signal across taxa is found in $T_{\max}$ (Fig. 5), with effects particularly strong for *Larix*, *Ulmus* and *Fagus* (all taxa lie below the equality line for $d_c - d_v$). Conversely, the large shift in the distribution of *Tsuga* relative to $T_{\max}$ appears to be mainly attributable to historical climate change. For $T_{\min}$ (Fig. 5), shifting distributions of *Ulmus* and *Thuja*/*Juniperus* are mainly attributed to land-use change, whereas *Larix* and *Betula* have large shifts that are equally attributable to historical climate change and land-use. The $T_{\min}$ shifts for *Quercus*, *Fraxinus*, *Picea*, *Acer* and *Tilia* are attributed to changing climate.

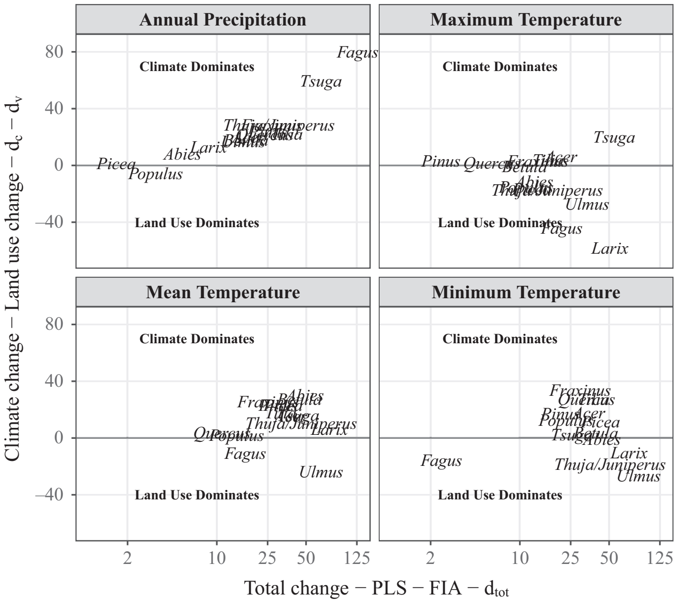

Figure 5 The total shift in climatic distribution over the last 100 to 150 years for each tree genus (d_{tot}) plotted against the amount of shift caused by historical climate change vs. changes in tree distributions ($d_c - d_v$), the latter mainly due to historical land-use. Results are plotted separately for each of the four climate variables considered here. Shifts in distributions are calculated as the Hellinger distance between tree-climate distributions for different combinations of pre-settlement and modern vegetation and climate (Fig. 2). For $d_c - d_v$ (*Y*-axis), negative values indicate a stronger influence of historical land-use on shifting climate distributions, whereas positive values indicate a stronger influence of historical climate change on shifting distributions.

All climate-vegetation interactions are compounding (□; $n = 30$) or confounding (–; $n = 30$), with no counteracting effects found (Table 1). Compounding interactions are strongest for $T_{\max}$ (Table 1), and are consistent with the observed trend of cooling $T_{\max}$ (Fig. 1, Fig. 4) and losses concentrated in the southern portions of most species ranges (Fig. 3); both

Table 1 Compounding ($\square$), confounding ($-$) and counteracting ($\bigcirc$) relationships between land-use and climate change. No counteracting relationships were found. The signs within parentheses indicate whether a given historical shift in climate (c) or vegetation (v) has pushed a tree-climate distribution towards warmer/wetter conditions (+) or colder/drier conditions ($-$), or is non-significant (.). When the land-use/climate interaction was regressed against spatial variables (latitude, longitude) no significant relationship was found.

Taxon	P_{ann}	T_{max}	T_{diff}	T_{min}
Larix	$-\ (+_c,\cdot_v)$	$\square\ (-_c,-_v)$	$-\ (-_c,\cdot_v)$	$\square\ (+_c,+_v)$
Pinus	$\square\ (+_c,+_v)$	$-\ (-_c,\cdot_v)$	$\square\ (-_c,-_v)$	$\square\ (+_c,+_v)$
Picea	$\square\ (+_c,+_v)$	$\square\ (-_c,-_v)$	$\square\ (-_c,-_v)$	$-\ (+_c,\cdot_v)$
Abies	$-\ (+_c,\cdot_v)$	$-\ (-_c,\cdot_v)$	$-\ (-_c,\cdot_v)$	$-\ (+_c,\cdot_v)$
Tsuga	$-\ (+_c,\cdot_v)$	$\square\ (-_c,-_v)$	$-\ (-_c,\cdot_v)$	$-\ (+_c,\cdot_v)$
Thuja/Juniperus	$-\ (+_c,\cdot_v)$	$-\ (-_c,\cdot_v)$	$\square\ (-_c,-_v)$	$-\ (+_c,\cdot_v)$
Populus	$\square\ (+_c,+_v)$	$\square\ (-_c,-_v)$	$\square\ (-_c,-_v)$	$-\ (+_c,\cdot_v)$
Acer	$\square\ (+_c,+_v)$	$\square\ (-_c,-_v)$	$-\ (-_c,\cdot_v)$	$-\ (+_c,\cdot_v)$
Betula	$\square\ (+_c,+_v)$	$\square\ (-_c,-_v)$	$-\ (-_c,\cdot_v)$	$-\ (+_c,\cdot_v)$
Fagus	$-\ (+_c,\cdot_v)$	$\square\ (-_c,-_v)$	$\square\ (-_c,-_v)$	$-\ (+_c,\cdot_v)$
Ostrya/Carpinus	$-\ (+_c,\cdot_v)$	$\square\ (-_c,-_v)$	$\square\ (-_c,-_v)$	$\square\ (+_c,+_v)$
Tilia	$-\ (+_c,\cdot_v)$	$\square\ (-_c,-_v)$	$-\ (-_c,\cdot_v)$	$-\ (+_c,\cdot_v)$
Fraxinus	$-\ (+_c,\cdot_v)$	$\square\ (-_c,-_v)$	$-\ (-_c,\cdot_v)$	$-\ (+_c,\cdot_v)$
Ulmus	$\square\ (+_c,+_v)$	$\square\ (-_c,-_v)$	$(-_c,-_v)$	$\square\ (+_c,+_v)$
Quercus	$\square\ (+_c,+_v)$	$\square\ (-_c,-_v)$	$-\ (-_c,\cdot_v)$	$-\ (+_c,\cdot_v)$

tend to shift tree-climate distributions to cooler portions of climate space ($-_c$). Compounding interactions are also strong for P_{ann} and are caused by both land-use and climate change shifting species to a wetter portion of climate space ($+_c$) than they occupied historically. The patterns of confounding and compounding interactions are insensitive to alternative estimates of 19th century temperature changes (Table S3). However, the 1950–1980 climate normal results in non-significant T_{max} changes, resulting in a loss of all compounding interactions for T_{max} (Table S4). All T_{max} interactions are then confounding, with significant shifts for vegetation changes (all negative), except for *Pinus* and *Abies*, where changes of vegetation in climate space are non-significant.

Several genera show common patterns in their relationships to climate/land-use interactions. *Populus*, *Picea*, *Quercus*, *Acer* and *Betula* all show compounding relationships for P_{ann} and T_{max}, either compounding or confounding interactions for T_{diff}, and confounding interactions for T_{min} (Table 1). These taxa all show significant losses in range along the southern and western margins of their distribution (Fig. 3), with few gains. *Fraxinus*, *Tsuga* and *Tilia* all show confounding interactions for P_{ann}, T_{diff}, and T_{min}, and compounding interactions for T_{max} (Table 1). Each of these taxa experiences range losses, but patterns of gain and loss differ among taxa.

DISCUSSION

This work reinforces the utility of historical data sets for examining relationships between species and climate, and their importance for forecasting future species distributions (Moritz & Agudo 2013; Maguire *et al.* 2015). Modern surveys sample a subset of historical distributions, both spatially and within multidimensional climate space. Our analyses demonstrate that species-climate relationships are changing as a result of land-use and climate change over the past two centuries, and add to our understanding of the interacting effects of climate change and land-use (Pyke 2004). Land-use change reduces the correlational structure between species and climate (Devineau 2011) and has been one of the strongest drivers of changes in global biodiversity over the 20th and 21st centuries (Sala *et al.* 2000). While rates of land-use change may be declining in North America and in the upper Midwest (Dale 1997; Rhemtulla *et al.* 2009b), the legacies of land-use are likely to persist, both in terms of forest composition (Kujawa *et al.* 2016; Goring *et al.* 2016), and the correlational structure between species and climate.

Previous studies have shown that the realised climate niches of tree species shifted during the climate changes accompanying the last deglaciation (Pearman *et al.* 2008; Veloz *et al.* 2012; Maiorano *et al.* 2013). Many species accommodated past climate changes by shifting their ranges; i.e. they maintained a relatively stable distribution in environmental space by shifting their distributions within geographical space. Range shifts are well documented by palaeodata and generally well simulated by species distribution and community-level models driven by palaeoclimatic simulations (Prentice *et al.* 1991; Martínez-Meyer & Peterson 2006; Maguire *et al.* 2015). Mechanisms for realised niche shifts include species lagging rapid climate change (Ordonez 2013), non-analogue climates (Veloz *et al.* 2012), or shifts in competition resulting from changing species associations (Maiorano *et al.* 2013). This study adds to prior work by showing that the land-use changes of the last several centuries can also significantly modify species-climate relationships.

In this study, shifts in realised climate niches and the underlying interactions between climate change and land-use emerge from three processes. First, climates have changed over the 20th and early 21st centuries, with rising winter minimum temperatures, higher precipitation and variable summer temperatures. These trends are produced by a combination of natural variability and anthropogenic change; the latter signal strengthens beginning in the second half of the 20th century (Estrada *et al.* 2013). Second, tree species distributions presumably have not yet fully adjusted to these climate changes, causing tree distributions to be in partial disequilibrium with climate (Svenning & Sandel 2013; Williams & Burke in press). Third, anthropogenic land-use has selectively eliminated portions of geographical and environmental space from species' potential ranges (Fig. 1f). Agricultural conversion has greatly reduced the extent of savanna and open forests in southern Wisconsin and Minnesota, causing tree species to occupy cooler habitats with higher precipitation than historically. While logging and altered fire regimes have altered community composition in the north, they have not widely excluded taxa from the northern regions and associated climates, except for *Tsuga* (Fig. 3), a shade-tolerant and late-successional taxon.

In addition to land-use, the regional collapse of *Ulmus* points to the importance of forest pathogens as mechanism by which human agency (introduced Dutch elm disease) has affected tree-climate relationships (Barnes 1979). *Castanea dentata* was also effectively wiped out by chestnut blight, with reintroduction efforts underway, and *Tsuga canadensis* and *Fraxinus* spp. are now experiencing rapid mortality due to exotic pests (Castello *et al.* 1995; Schlarbaum *et al.* 1998).

Hence, land-use is not the sole driver of vegetation changes reported here, although it is the dominant one.

Compounding and confounding interactions between historical climate change and land-use have important implications for the management and genetics of forest communities. Some tree genera may have more resilience to climate change than expected based on contemporary observations alone. Regionally, annual temperature is expected to increase in Wisconsin by 3.6 °C in 2055, with P_{ann} projections ranging from -17 to 110 mm, relative to a 1980s baseline (WICCI 2011). Every tree genera examined in this study had historical T_{max} values from 0.4 to 1.3 °C higher than modern estimates (primarily attributable to land-use change, Fig. 5), and P_{ann} from 42 to 86 mm lower than modern estimates (primarily attributable to climate change, Fig. 5). The higher temperatures and lower precipitation associated with pre-settlement tree distributions may suggest greater resilience to climate change than might be assessed using modern data only. This evidence for historical resilience to warmer and dryer climates is particularly critical for species that reach their range limits in the upper Midwest (e.g. *Tsuga*, *Fagus*).

Conversely, adaptation to future climate change may be impeded by the historical reduction in locally adapted populations due to past land-use change. Local adaptation is an important component of tree responses to climate change (Aitken *et al.* 2008), so the historical loss of genotypes adapted to warmer and drier conditions may mean more rapid losses at the trailing edges of the species range. Similarly, long-distance gene flow of adaptive traits to central and leading populations from the trailing edge (Hu & He 2006) may be lost when land-use conversion to agricultural production results in the extirpation of locally adapted populations. Net gene flow in populations along the remaining populations may be weighted towards individuals maladapted to warmer conditions, which could amplify the effects of climate change at the trailing edge (Kremer *et al.* 2012).

Correlational species-distribution models are likely to be the most affected by the use of contemporary observational data sets that are biased by historical climate and land-use change and climatic disequilibrium. However, even mechanistic models are partially parameterised from contemporary distributions, particularly with respect to the environmental tolerances of plant functional types (e.g. Wullschleger *et al.* 2014). Hence, the predictive ability of both correlative- and process-based models should be sensitive to the shifting climatic niches demonstrated here, and the underlying processes of spatially biased land-use conversion, changing climates and climatic disequilibrium. One solution is to combine historical and contemporary data when building species distribution models (Maiorano *et al.* 2013).

Historical data sets and multitemporal studies such as this one add to our understanding of the stability and dynamic of species-climate distributions and their adaptive potential in the face of climate change. Land-use over the past two centuries and its legacies, combined with the likelihood that tree distributions are lagging recent climate changes, create the strong likelihood that tree-climate distributions in the upper Midwest have shifted and that current tree-climate distributions are not representative of pre-settlement conditions. The main conclusions of this study are robust to changes in vegetation sampling design over time and choice of historical and modern climatic normals, although both concerns are important and deserve further study. Given the importance of modern distributional data sets for predicting species range shifts, compounding interactions between historical climate and land-use change may result in the impression of narrower climatic tolerances than actually exist, leading to underestimates of species resilience. Both empirical and process-based vegetation models need to combine, whenever possible, both contemporary and historical information on tree distributions, tree-climate relationships and their respective shifts through time.

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AUTHORSHIP

Simon J Goring: Co-conceived paper, performed analyses, developed figures and co-wrote the paper. John W Williams: Co-conceived paper and co-wrote the paper.

DATA ACCESSIBILITY

All data for this manuscript, along with code and version-control are available at http://github.com/SimonGoring/CompositionClimate. In addition, an archived copy of the submitted version is available with the following doi: 10.6084/m9.figshare.4600162.

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