# Effect of historic land-use and climate change on tree-climate relationships in the northern United States

**Statement of Authorship**

Simon J Goring: Co-conceived, performed analysis, developed figures & co-wrote the paper

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**Data Accessibility**

All data for this manuscript, along with code and version-control are available at <http://github.com/SimonGoring/CompositionClimate>. The repository is currently listed as Private. An archived copy of the submitted version will be made available with DOI.

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**Keywords**

Anthropocene, climate change, climate disequillibrium, forest inventory and analysis (FIA), fundamental niche, historical ecology, land use, niche shift, Public Land Survey System, realized niche

**Running Title**

* Causes of recent climate shifts in trees

**Article Type**: Letters

**Number of Words**

* Abstract: 146
* Main Text: 4840
* Text boxes: 0

**Number of References**: 77

**Number of Figures, Tables & Text Boxes**: 6 (5 figures, 1 table)

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# Abstract

Contemporary forest inventory data are widely used to understand environmental controls on tree species distributions and to project forest responses to climate change, but the stability and representativeness of contemporary tree-climate distributions is poorly understood. Here we show that tree-climate relationships for 15 common tree genera in the northern US have significantly altered over the last two centuries due to historic land use, pathogen outbreaks, and climate change. Realized niches have shifted towards higher minimum temperatures, cooler maximum temperatures, and higher rainfall. A new attribution method implicates both historic 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 historic land-use reinforces climatic shifts in species distributions toward cooler or wetter distributions. The prevalence of compounding interactions imply that contemporary-based models of species distributions may underestimate species resilience to climate change.

# Introduction

Contemporary species occurrence databases, and, increasingly, paleohistorical datasets 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 and Agudo 2013, Lamanna et al. 2014, Maguire et al. 2015, Ivory et al. 2016). These distributions of species in geographic and environmental space, combined with future climate scenarios, can be 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 and Prasad 1998, Pellatt et al. 2012, Anderson 2013, Guisan et al. 2013, Iverson and McKenzie 2013). Forest inventory datasets, such as the US Forest Inventory Analysis (FIA), are particularly rich observational datasets that have been used to assess early signals of range shifts via the distributions of mature trees and seedlings (Zhu et al. 2012, Monleon and Lintz 2015) and to parameterize models of current and future tree distributions (Iverson and Prasad 1998, Iverson et al. 2008).

Increasingly, the predictive capacity of ecological models is being improved by integrating contemporary observational data with paleohistorical data, when available (Moritz and 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 and Overpeck 2000), miss responses of species to past no-analog climates (Veloz et al. 2012), or fail to detect effects of anthropogenic land use, and other historical legacies (Svenning et al. 2015). Paleoecological records from the last deglaciation show that the time lag of forest responses to abrupt climate change varies from a few years to centuries (Webb 1986, Ordonez 2013, Svenning et al. 2015, Williams and 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 parameterization of these models is poorly constrained for processes operating at large temporal and spatial scales (Moorcroft 2006, Matthes et al. 2016).

Historic 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 and 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 cause species distributions to shift in the same direction along an environmental gradient. For example, warming has been compounded by land-use conversion at the lowest elevations in the northern Sierra Nevada Mountains of California, both causing upslope distributional shifts for butterfly species (Forister et al. 2010). Confounding effects may cause little overall change on species distributions, with land-use pressure occurring across the species' environmental gradient. Predictive models for Garry oak (*Quercus garryana*) using only contemporary data (Pellatt et al. 2012) may be confounded by land-use conversion that excludes Garry oak from the deep-soil sites it formerly occupied (Macdougall et al. 2004, Pellatt and Gedalof 2014), but land use has not systematically shifted Garry oak distributions in climate space. Counteracting effects occur when climate and land use change act in opposite directions, narrowing the available geographic 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 US have been heavily influenced by land use conversion associated with EuroAmerican Settlement in the 19th and 20th Centuries (Schulte et al. 2007, Rhemtulla et al. 2009a, Hanberry et al. 2012, Goring et al. in review), outbreaks of exotic pathogens (Barnes 1979), climate changes accompanying the end of the Little Ice Age (Hotchkiss et al. 2007) and current anthropogenic warming (Wisconsin’s Changing Climate: Impacts and Adaptation 2011). Modern forests, as represented by FIA surveys (Woudenberg et al. 2010), 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. in review). Wildland ecosystems have been converted to agricultural and urban land use (Rhemtulla et al. 2009a), particularly in historical prairie and savanna ecosystems (Figure 1f). In northern forested regions, ranges of early successional species have expanded and abundances of late-successional species are reduced due to widespread logging in the 19th and 20th century, and ongoing land management (Schulte et al. 2007, Goring et al. in review). Additionally, 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.)

Here we demonstrate significant shifts in the climatic distributions of tree genera in the upper Midwest over the last 100 years as a result of historic climate change, land use, and pathogen outbreaks, and we diagnose the relative influence of historic climate and land use changes on these shifts. We use gridded historic and contemporary climate observations (PRISM) and estimates of pre-settlement and modern forest vegetation (Goring et al. in review) to map the geographic and climatic distributions for 15 major tree taxa in the upper Midwestern United States. We construct four observed and hypothetical sets of tree-climate relationships, using a 2x2 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 historic vegetation and climate change. We assess whether climate and vegetation changes are compounding, counteracting or confounding based on the magnitude and direction of species-climate shifts. 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 soley 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 and Mladenoff 2001, Goring et al. in review), aggregated to a 64 km2grid across the upper Midwestern United States (Goring et al. in review). We briefly review the methods here. PLS data originally were collected on a 1 x 1 mi grid across the Upper Midwest from 1830 to 1910 (White 1983, Almendinger 1996, Schulte and 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 azimuths to each tree. Goring et al. (in review) aggregated this data to an 8x8 km grid, resulting in a gridded data product with an average of 61 survey points per cell, or approximately 120 trees per cell. This process included data cleaning, taxonomic standardization, and the application of spatially varying correction factors (Goring et al. in review). 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" can not be clearly resolved to a single tree genera and so we combine *Ostrya* and *Carpinus*, and *Thuja* and *Juniperus*. 'Presence' is defined as at least one recorded tree in any 8x8 km grid cell and 'range' is considered to be the extent in climate space of all cells with recorded presence for a specific taxon.

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

Comparisons between historical and modern vegetation must address differences in sampling design between the PLS and FIA datasets (Kronenfeld et al. 2010, Kronenfeld 2014, Goring et al. in review). Here, the primary solution for maximizing comparability is via aggregation, both spatially, by aggregating records from both datasets to a common scale (8x8 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 and FIA observations are collected only from forested or partially forested landscapes (Woudenberg et al. 2010), causing many tree taxa to have smaller spatial extents in the FIA than in the PLS datasets. Scattered trees may be present in regions without permanent or temporary FIA plots, complicating the ability to assign 'absence' within the FIA. However, the practice of using FIA data as a surrogate for tree distribution data is widespread (Iverson and Prasad 1998, Iverson and McKenzie 2013), so these complications are general. In prior comparative analyses of the PLS and FIA data, Goring et al. (in review) tested the effect of differential sampling design on the mapped patterns of novel and disappearing forests, and found little effect.

## Historical and Modern Climate Data

Historical and modern climate data are derived from monthly PRISM data for 1895 to 2014 CE (PRISM Climate Group, Oregon State University 2004). The PRISM climate variables are available at 800m resolution and have been interpolated from station locations using elevation, aspect and other data. Estimates for July temperature (), January temperature (), annual temperature range (), and annual precipitation () were resampled to the 8 x 8km grid used for PLS and FIA data. Two periods were selected for calculation of climate normals: 1895 to 1919 for the historical period and 1990 - 2014 for the modern period. There is an unavoidable temporal mismatch between the historical climate data and the PLS survey period, on the order of 50 to 70 years; few meteorological records exist in this region prior to 1895 CE, and no gridded dataset exists at high spatio-temporal resolution for this time period. The effects of temporal mismatch should be minor given that Northern Hemisphere temperature trends were generally small during the 19th century (Mann et al. 2009). To check whether an 1895 to 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) (Figure 1).

## Shifts in Species Distributions in Climate Space

Distributions of tree genera within climate space are described as univariate density functions (PDFs) for the pre-settlement and modern eras. Differences among PDFs are quantified using Hellinger distances (Matthes et al. 2016) for the four combined states of vegetation and climate (, , , , where V represents vegetation, C represents climate, and M and H represent modern and historical conditions). The total shift () is calculated as the Hellinger distance between and (Figure 2a: top left to bottom right). The effect of historical climate change on shifting climate distributions of tree genera is , the difference between PLS and FIA tree distributions, overlaid on late 19th-century climates ( versus ; Figure 2a; left column). The effect of historical land use change on tree-climate distributions is , the difference between the PLSS tree distributions when overlaid on historical vs. modern climates ( versus ; Figure 2a; top row).

We develop an attribution index, (), such that negative values of indicate stronger influence of historical land use on shifting climate distributions, while positive values indicate a stronger influence of historical climate change on shifting tree distributions.

To assess whether the effects of historical land use and climatic changes are compounding, counteracting or confounding we perform a set of t-tests, using the conservative Bonferroni correction to account for multiple tests. For each taxon and climate variable pair we test whether and (attribution to climate change), and and (attribution to land-use change) distributions are significantly different. 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 or both changes are not significant, then the change is defined as confounding.

All analysis uses R (R Core Team 2014), RMarkdown (Allaire et al. 2016) and R packages colorspace, captioner, raster, ggplot2, mgcv, reshape2, plyr, gridExtra, rgdal, RColorBrewer, analogue, and maptools. 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.

# Results

Regionally, increased 3.3oC since the 1895-1924 normal (Figure 1), changed by -0.8oC, while changed by -4.1oC. Regionally, has increased by 55.3mm. The Palmer Drought Severity Index is closely coherent with trends from 1895 onward and indicates no major climatic trends between 1800 and 1900 (Figure 1e), suggesting that early 20th century climates are a reasonable proxy for mid-19th century climates.

For most tree genera, historic range losses dominate over range gains and are spatially structured (Figure 3). Range losses in the upper Midwest are concentrated in the south and west, along the prairie-savanna-forest ecotone (Figure 3). For *Ulmus* and *Larix*, however, losses occur throughout the range. Losses are highest for *Ostrya*/*Carpinus* and *Larix* when assessed as a proportion of total range (Supplemental Table 1), and range losses are high generally, with an average of 57% across all taxa, *Larix*, *Ulmus* and *Betula* have the largest absolute losses in range within the Upper Midwest. Gains, conversely, account for no more than 16.5% of any taxon's historical range, with the highest gains observed for *Populus* (Figure 3) and averages 6% across all taxa. Spatial patterns of range gains vary widely among tree genera, and often show less spatial bias than losses (Figure 3). Range gains for *Picea*, *Larix*, *Abies*, *Tsuga*, *Fagus*, *Ostrya*/*Carpinus*, *Tilia*, and *Fraxinus*, for example, all show a dispersed pattern of gains in a relatively few and widely scattered cells, suggesting that these apparent range gains are mainly caused by sampling uncertainty inherent in local-scale plots and stand heterogeneity, rather than systematic range gains. Conversely, gains for *Populus* and *Acer*, are concentrated in northern Minnesota, Wisconsin, and Michigan, suggesting range infilling, while *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 historic range, or beyond it.

The joint effects of historic climate change and land use on tree-climate distributions are illustrated for *Larix* (Figure 2). For *Larix* we see clear shifts in climate space when vegetation is held constant (from solid to dashed lines), regardless of whether modern or pre-settlement vegetation distributions are used, indicating that historical climate change plays a strong role in shifting the distribution of *Larix* in climate space across all climate variables. Historical land use contributes to shifting distributions, particularly for , where losses at the highest values are visible from pre-settlement to modern (Fig. 2d). However, for *Larix*, land use overall appears to exert a weaker influence than climate change.

Shifts in tree-climate distributions are significant for all genera and all climate variables (Figure 4), even accounting for multiple comparisons (all p < 0.0001). The directionality of shifts between historical and modern climate distributions is consistent across genera: *e.g.*, modern is lower for all genera, while is higher (Figure 4). Across all genera, modern is higher than in the past. *Ulmus* shows the largest increase in minimum temperature (Figure 4; = 4.2 oC), while the smallest increase occurs for *Larix*. Maximum annual temperature declines most for *Ostrya*/*Carpinus* ( = -1.3 oC) and declines least for *Ulmus* ( = -0.4 oC). *Ulmus* shows the largest increase in mean precipitation ( = 86mm), while the smallest change is for *Larix* ( = 42mm).

Both the total shift in realized tree-climate distributions and the attribution of these changes to historic land use or climate change varies strongly among taxa and among climate variables (Figure 5). Shifts in realized climate distributions over the last 100 to 150 years are largest for *Ulmus* (, ), *Larix* (), *Tsuga* ( and ), and *Fagus* (). Attribution analyses based on (Figure 5) reveal that while the imprint of historic land use on shifting climatic niches is important for many taxa, this shift is not uniform across taxa. The climatic signal is strongest for , with regional changes in being largely responsible for shifting climate niches, while only *Populus* and *Picea* have seen climate niche shifts due to land-use that are larger than climate shifts. The greatest land use signal across taxa is found in (Figure 5), with effects particularly strong for *Larix*, *Ulmus*, and *Fagus* (all taxa lie below the equality line for ). The large shift in the distribution of *Tsuga* relative to , conversely, appears to be mainly attributable to historic climate change. For (Figure 5), shifting distributions of *Ulmus* and *Thuja*/*Juniperus* can be mainly attributed to land use change, while *Larix* and *Betula* have large shifts that are equally attributable to historic climate change and land use, and the niche shifts for *Quercus*, *Fraxinus*, *Picea*, *Acer*, and *Tilia* are attributable to changing climate.

The majority of climate - land-use interactions are compounding (n = 30) or confounding (n = 28), while few (n = 2) show counteracting effects (Table 1). Compounding interactions, where both climate and land use shifts push species distributions in the same direction along the climate gradient, are particularly strong for (Table 1), and are consistent with the observed trend of cooling (Figure 1, Figure 4) and losses concentrated in the southern portions of most species ranges (Figure 3); both tend to shift tree-climate distributions to cooler portions of climate space. Compounding interactions are also strong for and are caused by both land use and climate change shifting species to a wetter portion of climate space than they occupied historically. These analyses are insensitive to the type of correction applied to the *p*-value, although running the analysis without a correction factor reduces the counts of insignificant (confounding) relationships and increases the number of counteracting and compounding interactions. Patterns of interaction, by species, for and are significantly correlated ( = 15.22), but are not significantly correlated for other climate variables.

Counteracting interactions, where climate shifts and land use shifts show opposite signs relative to baseline climate, effectively narrowing the realized climatic niche from both directions, exist only for *Ulmus* () and *Larix* ()

Several genera show common patterns in their relationships to climate/land-use interactions. *Populus*, *Picea*, *Quercus*, *Acer* and *Betula* all show compounding relationships for both and , either compounding or confounding interactions for . and confounding interactions for (Table 1). These taxa all show significant losses in range along the southern and western margins of their distribution (Figure 3), with few gains in those regions.

*Fraxinus*, *Tsuga* and *Tilia* all show confounding interactions with , and , with compounding interactions with (Table 1). Each of these taxa experiences range losses, but patterns of gain and loss differ among taxa.

# Discussion

This work reinforces the importance of historical datasets for examining relationships between species and climate, and their importance for forecasting future species distributions (Moritz and Agudo 2013, Maguire et al. 2015). Modern surveys sample only 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 few centuries, and adds 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 is likely to have one of the strongest effects on changes in global biodiversity over the next century (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. accepted, Goring et al. in review), and the correlational structure between species and climate.

Previous studies have shown that the realized climate niches of tree species shifted during the climate changes accompanying the last deglaciation. To a first order, 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 geographic space. Range shifts are well documented by paleodata and generally well simulated by species distribution and community-level models driven by paleoclimatic simulations (Prentice et al. 1991, Martínez-Meyer and Peterson 2006, Maguire et al. 2015). However, species tracking of past climatic change was imperfect and other studies indicates shifts in species realized niches over time (Pearman et al. 2008, Maiorano et al. 2013). Mechanisms for these realized niche shifts include species lagging rapid climate change (Ordonez 2013), occupying non-analogue climates (Veloz et al. 2012), or shifts in competition resulting from changing patterns of co-occurrence through time (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 realized climate niches and the underlying interactions between climate change and land use emerge from three basic processes. First, climates have changed over the 20th and early 21st centuries, with rising winter minimum temperatures, declining summer temperatures, and higher precipitation. These climate changes are produced by a combination of natural variability and anthropogenic change; the latter signal is strongest in the second half of the 20th century and early 21st century (Estrada et al. 2013). Second, tree species distributions have not yet fully adjusted to these climate changes, causing tree distributions to be in partial disequilibrium with climate (Svenning and Sandel 2013, Williams and Burke in press). Third, anthropogenic land use has selectively eliminated portions of geographic and environmental space from species' potential ranges. Agricultural conversion has largely eliminated open forests in warm and dry regions, while summer temperatures have declined and precipitation increased, resulting in a compounding effect; species occupy cooler habitats with higher precipitation than during historical times. Intensification of land-use in the northern prairie-forest margin shifts species further than expected along the precipitation gradient.

In addition to land use changes, the near total regional collapse of *Ulmus* distributions provides another case in which human agency (in this case, accidentally introduced Dutch elm disease) has affected distributions through near extirpation (Barnes 1979), although reintroduction efforts are underway. *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. These pathogen-induced changes in tree distributions do not align neatly with the land use/climate attribution index described here, but they do fall under a broader set of vegetation changes caused by anthropogenic changesfactors, both inadvertent and intentional.

Some of these apparent shifts in climate niches may be due to differences in sampling design rather than to actual shifts in species distributions. In particular, the FIA dataset may be underrepresenting tree distributions in unforested or semi-forested regions. If so, estimates of forest loss (Figure 3) and niche shifts (Figures 4 & 5) may be overestimated. Regardless of cause, the differences between the PLS and FIA tree distributions are important for distributional modeling because FIA data provides the most detailed and most widely used source of tree distributional data over the entire contiguous United States (Bell et al. 2014, Nieto-Lugilde et al. 2015, Wang et al. 2016). Hence, any incompleteness in the representation of realized climate niches based on FIA data that are affecting this study should also affect ecological assessments that are based on FIA data.

Anthropogenic agency may also be extending the range of some tree species, for example, as a result of irrigation or landscaping care within urban or rural locations that might otherwise not support forest cover (Brazel et al. 2000, Groffman et al. 2014). Human agency may also support the extension of forest ecosystems at historical range margins, or preserve historical range margins from land use conversion to agriculture as windrows, or isolated woodlots. Detailed sampling of tree species, particularly in urban and agricultural environments beyond the current expected range limits of species, may provide better representation of species' fundamental climate niches or tolerance niches (Sax et al. 2013). However, usage of species distributional data from highly managed ecosystems must account for the intensive management that may be required to maintain species beyond their realized niche.

Compounding and confounding interactions between historic climate change and land use, and the consequent shifts in realized climate space have important implications for the management and genetics of forest communities. On the one hand, the observation that historical realized niches are broader than modern niches suggests that 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 3.6oC in 2055 from a 1980s baseline (Wisconsin’s Changing Climate: Impacts and Adaptation 2011) and projections range from -17 to 110mm by 2055 relative to 1980s baselines, based on fourteen global climate models from the Climate Model Intercomparison Project (Wisconsin’s Changing Climate: Impacts and Adaptation 2011). Every tree genera examined in this study had historical values from 0.4 to 1.3oC higher than modern estimates, and from 42 to 86mm lower than modern estimates. These higher temperatures and lower precipitation across taxa distributions during the pre-settlement period indicate the potential for greater resilience to climate change than might be assessed using modern data only. This evidence for historical resilience to warmer and dryer climates may be particularly critical for species that reach their northern or western range limits in the upper Midwest (e.g., *Tsuga*, *Fagus*).

However, projected temperature rises by 2100 far exceed the shifts due to historical land use and climate change. In addition, coupled migration and adaptation in response to future climate change is likely to be impeded by the extirpation of adapted populations due to land use change and loss of genetic diversity. Local adaptation is an important component of tree responses to climate change (Aitken et al. 2008). Hence, the loss of genotypes adapted to warmer and drier conditions (the trailing edge of distributions for many taxa in the Upper Midwest) caused by land use may mean more rapid losses at the trailing edges of the species range. Long distance gene flow of adaptive traits to central and leading populations from the trailing edge (Hu and He 2006) is lost when land use conversion to agricultural production results in the extirpation of locally adapted populations. Thus net gene flow in populations along the remaining trailing edge will be from the central and leading populations, individuals maladapted to warmer conditions. This maladaptive gene flow could potentially amplify the effects of climate change on populations along the forest-prairie boundary leading to increasing risk of local extinction among natural populations (Kremer et al. 2012).

Species distribution models fall along a continuum from more correlative to more process-based (Dormann et al. 2012), and correlational species-distribution models are likely to be the most affected by the use of contemporary observational datasets that are biased by historical climate and land-use change and climatic disequilibrium. However, even process based models are partially parameterized from contemporary distributions, particularly with respect to the environmental tolerances of plant functional types (*e.g.* Wullschleger et al. 2014). In this case, both correlative and process based models might be affected by the shifting climatic niches demonstrated here, and the underlying processes of spatially biased land-use conversion, changing climates, and climatic disequilibrium.

In summary, historical datasets and multitemporal studies such as this oneadd to our ability to understand the stability and dynamic of species-climate distributions and their adaptive potential in the face of climate change. The strong changes in climate and land use over the past two centuries, combined with the likelihood that tree distributions are lagging recent climate changes (Svenning and Sandel 2013), create the strong likelihood that tree-climate distributions have shifted and that current tree-climate distributions are not representative of pre-settlement conditions. Given the importance of modern distributional datasets 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.

## Acknowledgements

The authors would like to thanks the large number of individuals who have worked to first, undertake the Public Lands System Survey, to bring the original survey data together, to digitize and standardize much of the survey results, and finally, to assist in interpreting and compiling the data in its present form. In particular, we thank David Mladenoff, Charlie Cogbill, Ed Schools, and the PalEON Settlement Vegetation working group. The authors than Andria Dawson and PalEON participants for helpful comments in the drafting of this manuscript. This material is based upon work carried out by the PalEON Project (<http://paleonproject.org>), under NSF Award Numbers 1241868 and 1065656. Maps were made using data from Natural Earth (<http://naturalearth.com>).

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# Figures

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. Modern climate shows lower , but higher relative to early-19th Century normals, along with increasing . PDSI shows strong coherence with 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).

Figure 2: (a) The 2x2 factorial design used to diagnose the effects of historic 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 normalized probability densities for *Larix* for each of the four combinations of climate and vegetation states, plotted relative to (b), (c), (d), and (e).

Figure 3: Maps showing areas of gain, loss, and continuous presence of tree genera. 'Loss' indicates 8x8km 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 blue). 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% (Supplemental Material).

Figure 4: Changes in the realized climate distributions for tree genera in the upper Midwestern United States. In the box-and-whisker plots, 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. These shifts in realized climate distributions are produced by the joint effects of historical climate change, pathogen-induced tree mortality, and land-use change.

Figure 5: The total shift in climatic distribution over the last 100 to 150 years for each tree genus () plotted against the amount of shift caused by historic climate change vs. changes in tree distributions (), the latter mainly due to historic land-use and pathogen outbreaks. 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 (Y-axis), negative values indicate a stronger influence of historic land-use on shifting climate distributions, while positive values indicate a stronger influence of historic climate change on shifting distributions.

# Tables

Table 1: Compounding (), confounding (-) and counteracting () relationships between land-use and climate change. When the land-use/climate interaction was regressed against spatial vaariables (latitude, longitude) no significant relationship was found.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Taxon | Pann | Tmax | Tdiff | Tmin |
| *Ulmus* |  |  |  |  |
| *Thuja/Juniperus* | - | - |  |  |
| *Pinus* |  | - |  |  |
| *Larix* | - |  | - |  |
| *Abies* | - | - | - | - |
| *Fraxinus* | - |  | - | - |
| *Tsuga* | - |  | - | - |
| *Tilia* | - |  | - | - |
| *Fagus* | - |  |  | - |
| *Ostrya/Carpinus* | - |  |  |  |
| *Populus* |  |  |  | - |
| *Picea* |  |  |  | - |
| Oak |  |  |  | - |
| Maple |  |  | - | - |
| Birch |  |  | - | - |