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

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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
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>. 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

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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.

48 **Introduction**

49 Contemporary species occurrence databases, and, increasingly, paleohistorical datasets are
50 used to map distributions of species and species traits within environmental space, study
51 underlying processes, and prepare for climate change (Pearman et al. 2008, Moritz and
52 Agudo 2013, Lamanna et al. 2014, Maguire et al. 2015, Ivory et al. 2016). These
53 distributions of species in geographic and environmental space, combined with future
54 climate scenarios, can be used to assess species exposure and sensitivity to climate change,
55 identify species and habitats of concern, set conservation priorities, and prepare for
56 climate-driven shifts in habitat suitability (Iverson and Prasad 1998, Pellatt et al. 2012,
57 Anderson 2013, Guisan et al. 2013, Iverson and McKenzie 2013). Forest inventory datasets,
58 such as the US Forest Inventory Analysis (FIA), are particularly rich observational datasets
59 that have been used to assess early signals of range shifts via the distributions of mature
60 trees and seedlings (Zhu et al. 2012, Monleon and Lintz 2015) and to parameterize models
61 of current and future tree distributions (Iverson and Prasad 1998, Iverson et al. 2008).
62 Increasingly, the predictive capacity of ecological models is being improved by integrating
63 contemporary observational data with paleohistorical data, when available (Moritz and
64 Agudo 2013, Maguire et al. 2015). Projections relying only on contemporary observational
65 data may overlook plasticity in species-climate responses (Maiorano et al. 2013),
66 incompletely delimit species fundamental niches (Jackson and Overpeck 2000), miss
67 responses of species to past no-analog climates (Veloz et al. 2012), or fail to detect effects
68 of anthropogenic land use, and other historical legacies (Svenning et al. 2015).
69 Paleoecological records from the last deglaciation show that the time lag of forest

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3 70 responses to abrupt climate change varies from a few years to centuries (Webb 1986,
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5 71 Ordonez 2013, Svenning et al. 2015, Williams and Burke in press), suggesting that tree
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7 72 distributions have yet to fully respond to recent climate changes. In principle, mechanistic
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9 73 dynamic vegetation models (*e.g.*, Leiblein-Wild et al. 2016) can represent the physiological,
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11 74 demographic, and dispersal processes that cause tree populations to lag climate change. In
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13 75 practice, however, the parameterization of these models is poorly constrained for
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15 76 processes operating at large temporal and spatial scales (Moorcroft 2006, Matthes et al.
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17 77 2016).

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23 78 Historic land use has substantially affected species distributions and vegetation structure
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25 79 (*e.g.*, Gehrig-Fasel et al. 2007) and may cause species distributions to incompletely fill
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27 80 available climates, or otherwise be at disequilibrium (Sarmiento Cabral et al. 2013, Early
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29 81 and Sax 2014, Ivory et al. 2016). Anthropogenic land use is structured and is often biased
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31 82 within climate space, hence, species distributions and protected natural areas often
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33 83 represent a biased selection from the available environmental space (Scott et al. 2001).
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36 84 Biasing can confound studies that use contemporary distributional data to understand the
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38 85 environmental controls on species distributions and predict species responses to future
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40 86 climate scenarios (Pyke 2004).

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45 87 Interactions between climate and land-use change can be classified into three types:
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47 88 compounding, confounding and counteracting (modified from Pyke 2004). Compounding
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49 89 effects occur when climatic and land-use changes cause species distributions to shift in the
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51 90 same direction along an environmental gradient. For example, warming has been
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54 91 compounded by land-use conversion at the lowest elevations in the northern Sierra Nevada
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3 92 Mountains of California, both causing upslope distributional shifts for butterfly species
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6 93 (Forister et al. 2010). Confounding effects may cause little overall change on species
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8 94 distributions, with land-use pressure occurring across the species' environmental gradient.
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10 95 Predictive models for Garry oak (*Quercus garryana*) using only contemporary data (Pellatt
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12 96 et al. 2012) may be confounded by land-use conversion that excludes Garry oak from the
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14 97 deep-soil sites it formerly occupied (Macdougall et al. 2004, Pellatt and Gedalof 2014), but
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16 98 land use has not systematically shifted Garry oak distributions in climate space.
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18 99 Counteracting effects occur when climate and land use change act in opposite directions,
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20 100 narrowing the available geographic and climatic space available for species. For example,
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22 101 bird species in the Sierra Nevadas are expected to move downslope due to increasing
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24 102 precipitation (Tingley et al. 2012), but this downslope migration is limited by land-use
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26 103 conversion in the lowlands.
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33 104 Tree distributions and community composition in the upper Midwestern US have been
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35 105 heavily influenced by land use conversion associated with EuroAmerican Settlement in the
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37 106 19th and 20th Centuries (Schulte et al. 2007, Rhemtulla et al. 2009a, Hanberry et al. 2012,
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39 107 Goring et al. in review), outbreaks of exotic pathogens (Barnes 1979), climate changes
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41 108 accompanying the end of the Little Ice Age (Hotchkiss et al. 2007) and current
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43 109 anthropogenic warming (Wisconsin's Changing Climate: Impacts and Adaptation 2011).
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45 110 Modern forests, as represented by FIA surveys (Woudenberg et al. 2010), show greater
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47 111 homogeneity, weaker ecotones, and significantly different species associations than forests
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49 112 surveyed as part of the Public Land Survey System (PLS) prior to widespread land-use
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51 113 conversion in the late 1800s (Schulte et al. 2007, Goring et al. in review). Wildland
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53 114 ecosystems have been converted to agricultural and urban land use (Rhemtulla et al.
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3 115 2009a), particularly in historical prairie and savanna ecosystems (Figure 1f). In northern
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6 116 forested regions, ranges of early successional species have expanded and abundances of
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8 117 late-successional species are reduced due to widespread logging in the 19th and 20th
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10 118 century, and ongoing land management (Schulte et al. 2007, Goring et al. in review).
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12 119 Additionally, the formerly dominant *Ulmus americana* has experienced rangewide
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14 120 population collapses caused by the introduction of exotic pathogens (Barnes 1979), as did
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16 121 *Castanea dentata*, with other tree species currently threatened (*Tsuga canadensis*, *Fraxinus*
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18 122 spp.)
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23 123 Here we demonstrate significant shifts in the climatic distributions of tree genera in the
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25 124 upper Midwest over the last 100 years as a result of historic climate change, land use, and
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27 125 pathogen outbreaks, and we diagnose the relative influence of historic climate and land use
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29 126 changes on these shifts. We use gridded historic and contemporary climate observations
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31 127 (PRISM) and estimates of pre-settlement and modern forest vegetation (Goring et al. in
32
33 128 review) to map the geographic and climatic distributions for 15 major tree taxa in the
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35 129 upper Midwestern United States. We construct four observed and hypothetical sets of tree-
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37 130 climate relationships, using a 2x2 factorial of pre-settlement and modern vegetation and
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39 131 climates. We develop a new method, based on Hellinger distances among tree-climate
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41 132 distributions, to quantify the total change and attribute the relative importance of historic
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43 133 vegetation and climate change. We assess whether climate and vegetation changes are
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45 134 compounding, counteracting or confounding based on the magnitude and direction of
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47 135 species-climate shifts. We use this framework to discuss the potential impacts of historical
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49 136 land-use and climate change on inferences about species resilience to climate change, as
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51 137 predicted by species-distribution models based solely on modern distributional data.
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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 km² grid 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

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3 181 elevation, aspect and other data. Estimates for July temperature (T_{max}), January
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5 182 temperature (T_{min}), annual temperature range (T_{diff}), and annual precipitation (P_{ann})
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8 183 were resampled to the 8 x 8km grid used for PLS and FIA data. Two periods were selected
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10 184 for calculation of climate normals: 1895 to 1919 for the historical period and 1990 - 2014
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12 185 for the modern period. There is an unavoidable temporal mismatch between the historical
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14 186 climate data and the PLS survey period, on the order of 50 to 70 years; few meteorological
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16 187 records exist in this region prior to 1895 CE, and no gridded dataset exists at high spatio-
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18 188 temporal resolution for this time period. The effects of temporal mismatch should be minor
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20 189 given that Northern Hemisphere temperature trends were generally small during the 19th
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22 190 century (Mann et al. 2009). To check whether an 1895 to 1919 CE climate normal is a
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24 191 reasonable surrogate for pre-settlement climates we compare the instrumental record
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26 192 against dendroclimatic reconstructions of the Palmer Drought Severity Index (Heim 2002)
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28 193 (Figure 1).
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36 194 **Shifts in Species Distributions in Climate Space**

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39 195 Distributions of tree genera within climate space are described as univariate density
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41 196 functions (PDFs) for the pre-settlement and modern eras. Differences among PDFs are
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43 197 quantified using Hellinger distances (Matthes et al. 2016) for the four combined states of
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45 198 vegetation and climate ($V_H C_H$, $V_H C_M$, $V_M C_H$, $V_M C_M$, where V represents vegetation, C
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47 199 represents climate, and M and H represent modern and historical conditions). The total
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49 200 shift (d_{tot}) is calculated as the Hellinger distance between $V_M C_M$ and $V_H C_H$ (Figure 2a: top
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51 201 left to bottom right). The effect of historical climate change on shifting climate distributions
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53 202 of tree genera is d_C , the difference between PLS and FIA tree distributions, overlaid on late
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19th-century climates ($V_H C_H$ versus $V_H C_M$; Figure 2a; left column). The effect of historical land use change on tree-climate distributions is d_l , the difference between the PLSS tree distributions when overlaid on historical vs. modern climates ($V_H C_H$ versus $V_M C_H$; Figure 2a; top row).

We develop an attribution index, ($\delta_d = d_c - d_l$), such that negative values of δ_d 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 $V_H C_H$ and $V_H C_M$ (attribution to climate change), and $V_H C_H$ and $V_M C_H$ (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, T_{min} increased 3.3°C since the 1895-1924 normal (Figure 1), T_{max} changed by -0.8°C, while T_{diff} changed by -4.1°C. Regionally, P_{ann} has increased by 55.3mm. The Palmer Drought Severity Index is closely coherent with P_{ann} 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 T_{max} , where losses at the highest T_{max} 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 T_{max} is lower for all genera, while T_{min} is higher (Figure 4). Across all genera, modern P_{ann} is higher than in the past. *Ulmus* shows the largest increase in minimum temperature (Figure 4; $\delta_{T_{min}} = 4.2$ °C), while the smallest increase occurs for *Larix*. Maximum annual temperature declines most for *Ostrya/Carpinus* ($\delta_{T_{max}} = -1.3$ °C) and declines least for *Ulmus* ($\delta_{T_{max}} = -0.4$ °C). *Ulmus* shows the largest increase in mean precipitation ($\delta_{P_{ann}} = 86$ mm), while the smallest change is for *Larix* ($\delta_{P_{ann}} = 42$ mm).

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

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3 269 climate variables (Figure 5). Shifts in realized climate distributions over the last 100 to 150
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6 270 years are largest for *Ulmus* (T_{min} , T_{max}), *Larix* (T_{max}), *Tsuga* (T_{max} and P_{ann}), and *Fagus*
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8 271 (P_{ann}). Attribution analyses based on d (Figure 5) reveal that while the imprint of historic
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10 272 land use on shifting climatic niches is important for many taxa, this shift is not uniform
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13 273 across taxa. The climatic signal is strongest for P_{ann} , with regional changes in P_{ann} being
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15 274 largely responsible for shifting climate niches, while only *Populus* and *Picea* have seen
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18 275 climate niche shifts due to land-use that are larger than climate shifts. The greatest land use
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20 276 signal across taxa is found in T_{max} (Figure 5), with effects particularly strong for *Larix*,
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23 277 *Ulmus*, and *Fagus* (all taxa lie below the equality line for $d_c - d_v$). The large shift in the
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25 278 distribution of *Tsuga* relative to T_{max} , conversely, appears to be mainly attributable to
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28 279 historic climate change. For T_{min} (Figure 5), shifting distributions of *Ulmus* and
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30 280 *Thuja/Juniperus* can be mainly attributed to land use change, while *Larix* and *Betula* have
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32 281 large shifts that are equally attributable to historic climate change and land use, and the
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35 282 niche shifts for *Quercus*, *Fraxinus*, *Picea*, *Acer*, and *Tilia* are attributable to changing climate.
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38 283 The majority of climate - land-use interactions are compounding ($n = 30$) or confounding (n
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40 284 $= 28$), while few ($n = 2$) show counteracting effects (Table 1). Compounding interactions,
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43 285 where both climate and land use shifts push species distributions in the same direction
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45 286 along the climate gradient, are particularly strong for T_{max} (Table 1), and are consistent
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48 287 with the observed trend of cooling T_{max} (Figure 1, Figure 4) and losses concentrated in the
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50 288 southern portions of most species ranges (Figure 3); both tend to shift tree-climate
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52 289 distributions to cooler portions of climate space. Compounding interactions are also strong
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55 290 for P_{ann} and are caused by both land use and climate change shifting species to a wetter
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57 291 portion of climate space than they occupied historically. These analyses are insensitive to
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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 P_{ann} and T_{diff} are significantly correlated ($\chi^2_4 = 15.22$), 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* (T_{max}) and *Larix* (T_{min}). 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 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 (Figure 3), with few gains in those regions. *Fraxinus*, *Tsuga* and *Tilia* all show confounding interactions with P_{ann} , T_{diff} and T_{min} , with compounding interactions with 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 importance of historical datasets for examining relationships between species and climate, and their importance for forecasting future species

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3 312 distributions (Moritz and Agudo 2013, Maguire et al. 2015). Modern surveys sample only a
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6 313 subset of historical distributions, both spatially and within multidimensional climate space.
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8 314 Our analyses demonstrate that species-climate relationships are changing as a result of
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10 315 land use and climate change over the past few centuries, and adds to our understanding of
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12 316 the interacting effects of climate change and land-use (Pyke 2004). Land use change
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14 317 reduces the correlational structure between species and climate (Devineau 2011) and is
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16 318 likely to have one of the strongest effects on changes in global biodiversity over the next
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18 319 century (Sala et al. 2000). While rates of land-use change may be declining in North
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20 320 America and in the upper Midwest (Dale 1997, Rhemtulla et al. 2009b) the legacies of land-
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22 321 use are likely to persist, both in terms of forest composition (Kujawa et al. accepted, Goring
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24 322 et al. in review), and the correlational structure between species and climate.
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30 323 Previous studies have shown that the realized climate niches of tree species shifted during
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32 324 the climate changes accompanying the last deglaciation. To a first order, many species
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34 325 accommodated past climate changes by shifting their ranges; *i.e.* they maintained a
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36 326 relatively stable distribution in environmental space by shifting their distributions within
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38 327 geographic space. Range shifts are well documented by paleodata and generally well
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40 328 simulated by species distribution and community-level models driven by paleoclimatic
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42 329 simulations (Prentice et al. 1991, Martínez-Meyer and Peterson 2006, Maguire et al. 2015).
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45 330 However, species tracking of past climatic change was imperfect and other studies
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47 331 indicates shifts in species realized niches over time (Pearman et al. 2008, Maiorano et al.
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49 332 2013). Mechanisms for these realized niche shifts include species lagging rapid climate
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51 333 change (Ordóñez 2013), occupying non-analogue climates (Veloz et al. 2012), or shifts in
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53 334 competition resulting from changing patterns of co-occurrence through time (Maiorano et
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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*

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3 357 spp. are now experiencing rapid mortality due to exotic pests. These pathogen-induced
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6 358 changes in tree distributions do not align neatly with the land use/climate attribution index
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8 359 described here, but they do fall under a broader set of vegetation changes caused by
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10 360 anthropogenic changes factors, both inadvertent and intentional.
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14 361 Some of these apparent shifts in climate niches may be due to differences in sampling
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16 362 design rather than to actual shifts in species distributions. In particular, the FIA dataset
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18 363 may be underrepresenting tree distributions in unforested or semi-forested regions. If so,
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20 364 estimates of forest loss (Figure 3) and niche shifts (Figures 4 & 5) may be overestimated.
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23 365 Regardless of cause, the differences between the PLS and FIA tree distributions are
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25 366 important for distributional modeling because FIA data provides the most detailed and
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27 367 most widely used source of tree distributional data over the entire contiguous United
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29 368 States (Bell et al. 2014, Nieto-Lugilde et al. 2015, Wang et al. 2016). Hence, any
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31 369 incompleteness in the representation of realized climate niches based on FIA data that are
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33 370 affecting this study should also affect ecological assessments that are based on FIA data.
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38 371 Anthropogenic agency may also be extending the range of some tree species, for example,
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40 372 as a result of irrigation or landscaping care within urban or rural locations that might
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42 373 otherwise not support forest cover (Brazel et al. 2000, Groffman et al. 2014). Human
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44 374 agency may also support the extension of forest ecosystems at historical range margins, or
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46 375 preserve historical range margins from land use conversion to agriculture as windrows, or
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48 376 isolated woodlots. Detailed sampling of tree species, particularly in urban and agricultural
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50 377 environments beyond the current expected range limits of species, may provide better
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52 378 representation of species' fundamental climate niches or tolerance niches (Sax et al. 2013).
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3 379 However, usage of species distributional data from highly managed ecosystems must
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6 380 account for the intensive management that may be required to maintain species beyond
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8 381 their realized niche.
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11 382 Compounding and confounding interactions between historic climate change and land use,
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13 383 and the consequent shifts in realized climate space have important implications for the
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15 384 management and genetics of forest communities. On the one hand, the observation that
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17 385 historical realized niches are broader than modern niches suggests that some tree genera
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19 386 may have more resilience to climate change than expected based on contemporary
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21 387 observations alone. Regionally, annual temperature is expected to increase in Wisconsin by
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23 388 3.6°C in 2055 from a 1980s baseline (Wisconsin's Changing Climate: Impacts and
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25 389 Adaptation 2011) and P_{ann} projections range from -17 to 110mm by 2055 relative to 1980s
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27 390 baselines, based on fourteen global climate models from the Climate Model
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29 391 Intercomparison Project (Wisconsin's Changing Climate: Impacts and Adaptation 2011).
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31 392 Every tree genera examined in this study had historical T_{max} values from 0.4 to 1.3°C
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33 393 higher than modern estimates, and P_{ann} from 42 to 86mm lower than modern estimates.
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35 394 These higher temperatures and lower precipitation across taxa distributions during the
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37 395 pre-settlement period indicate the potential for greater resilience to climate change than
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39 396 might be assessed using modern data only. This evidence for historical resilience to
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41 397 warmer and dryer climates may be particularly critical for species that reach their
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43 398 northern or western range limits in the upper Midwest (e.g., *Tsuga*, *Fagus*).
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50 399 However, projected temperature rises by 2100 far exceed the shifts due to historical land
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52 400 use and climate change. In addition, coupled migration and adaptation in response to
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3 401 future climate change is likely to be impeded by the extirpation of adapted populations due
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6 402 to land use change and loss of genetic diversity. Local adaptation is an important
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8 403 component of tree responses to climate change (Aitken et al. 2008). Hence, the loss of
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10 404 genotypes adapted to warmer and drier conditions (the trailing edge of distributions for
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12 405 many taxa in the Upper Midwest) caused by land use may mean more rapid losses at the
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14 406 trailing edges of the species range. Long distance gene flow of adaptive traits to central and
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17 407 leading populations from the trailing edge (Hu and He 2006) is lost when land use
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19 408 conversion to agricultural production results in the extirpation of locally adapted
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22 409 populations. Thus net gene flow in populations along the remaining trailing edge will be
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24 410 from the central and leading populations, individuals maladapted to warmer conditions.
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27 411 This maladaptive gene flow could potentially amplify the effects of climate change on
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29 412 populations along the forest-prairie boundary leading to increasing risk of local extinction
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32 413 among natural populations (Kremer et al. 2012).
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35 414 Species distribution models fall along a continuum from more correlative to more process-
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37 415 based (Dormann et al. 2012), and correlational species-distribution models are likely to be
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39 416 the most affected by the use of contemporary observational datasets that are biased by
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42 417 historical climate and land-use change and climatic disequilibrium. However, even process
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44 418 based models are partially parameterized from contemporary distributions, particularly
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46 419 with respect to the environmental tolerances of plant functional types (*e.g.* Wullschleger et
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48 420 al. 2014). In this case, both correlative and process based models might be affected by the
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51 421 shifting climatic niches demonstrated here, and the underlying processes of spatially
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54 422 biased land-use conversion, changing climates, and climatic disequilibrium.
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In summary, historical datasets and multitemporal studies such as this one add 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.

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(<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 T_{max} , but higher T_{min} relative to early-19th Century normals, along with increasing P_{ann} . 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 broadleaved 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 T_{max} (b), T_{diff} (c), T_{min} (d), and P_{ann} (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 gray). 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 (d_{tot}) plotted against the amount of shift caused by historic climate change vs. changes in tree distributions ($d_C - d_V$), 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 $d_C - d_V$ (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.

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683 **Tables**

For Review Only

Table 1: Compounding (\square), confounding (-) and counteracting (\circ) relationships between land-use and climate change. 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}
<i>Ulmus</i>	\square	\circ	\square	\square
<i>Thuja/Juniperus</i>	-	-	\square	\square
<i>Pinus</i>	\square	-	\square	\square
<i>Larix</i>	-	\square	-	\circ
<i>Abies</i>	-	-	-	-
<i>Fraxinus</i>	-	\square	-	-
<i>Tsuga</i>	-	\square	-	-
<i>Tilia</i>	-	\square	-	-
<i>Fagus</i>	-	\square	\square	-
<i>Ostrya/Carpinus</i>	-	\square	\square	\square
<i>Populus</i>	\square	\square	\square	-
<i>Picea</i>	\square	\square	\square	-
Oak	\square	\square	\square	-
Maple	\square	\square	-	-
Birch	\square	\square	-	-

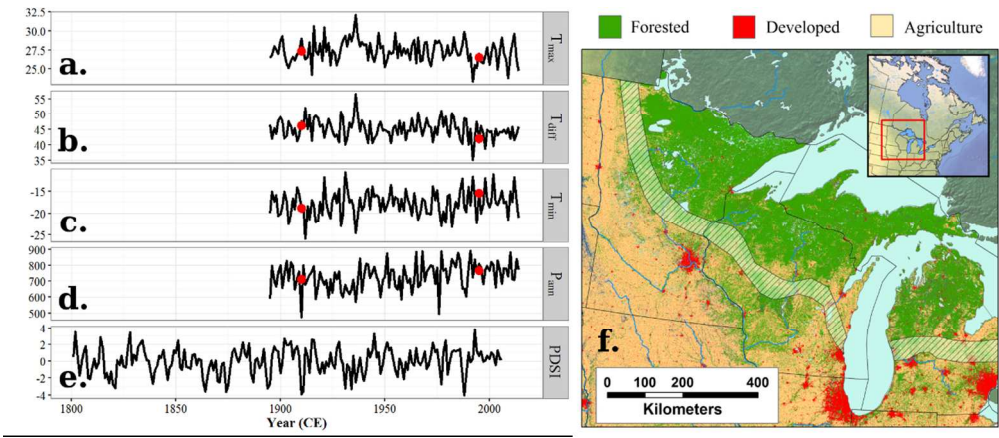


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Climate change in the Upper Mi
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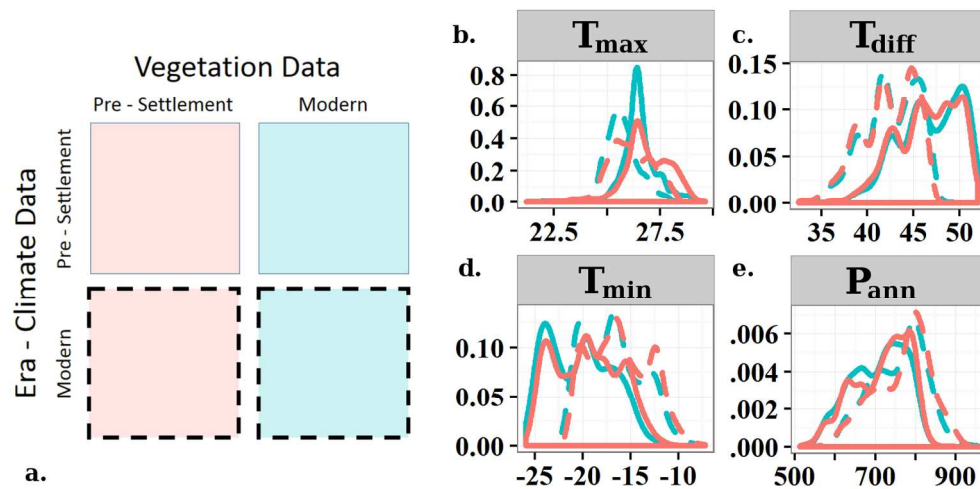
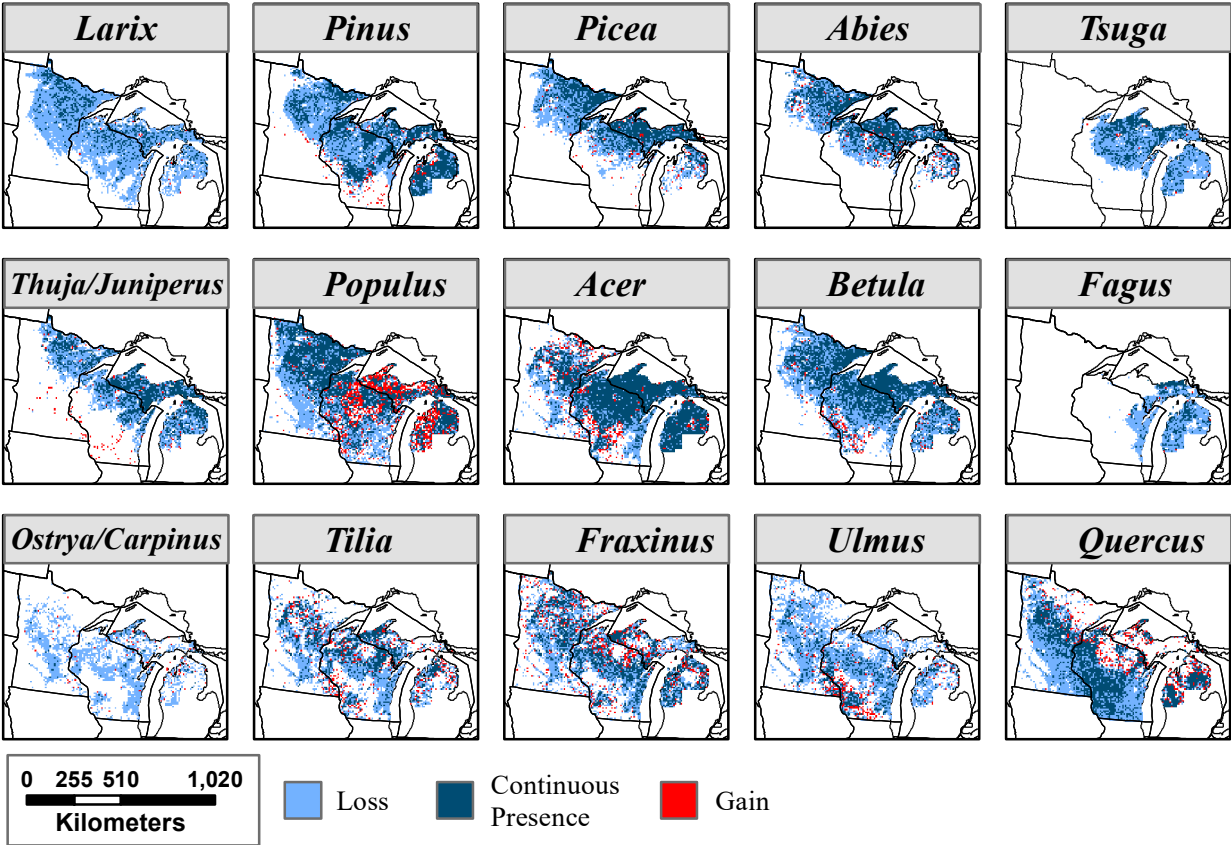
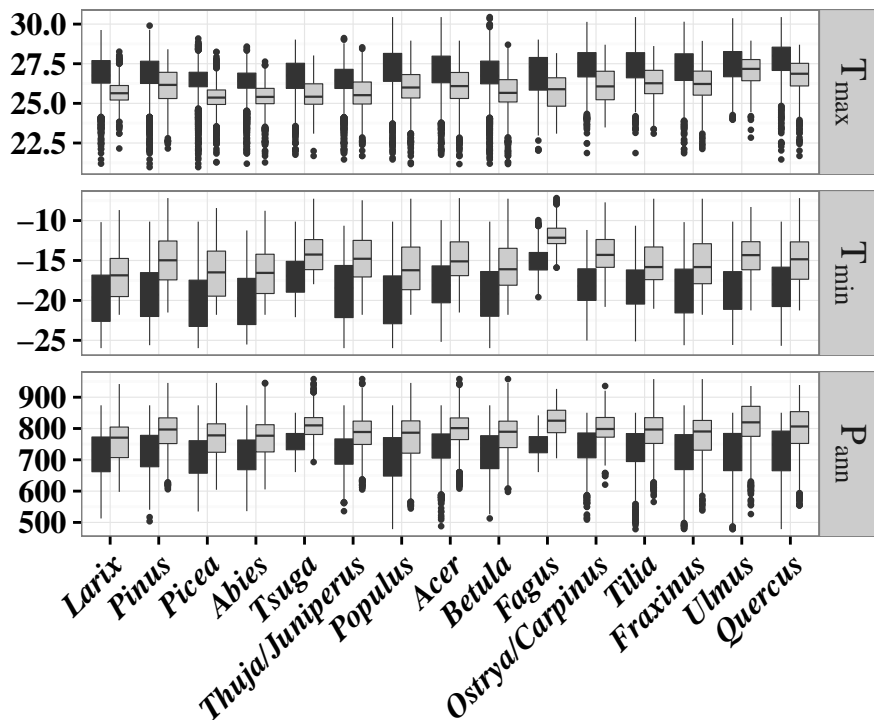


Figure 2: (a) The 2x2 factorial design used to diagnose the effects of historic climate and vegetation change on observed shifts in tree-climate relationships. Observed and hypothetical tree-climate relationships for one of four combinations of pre-settlement vegetation (pink fill, left column) or modern 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 T_{max} (b), T_{diff} (c), T_{min} (d), and P_{ann} (e).

The 2x2 factorial design used
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