Composition-climate paper

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

# Abstract

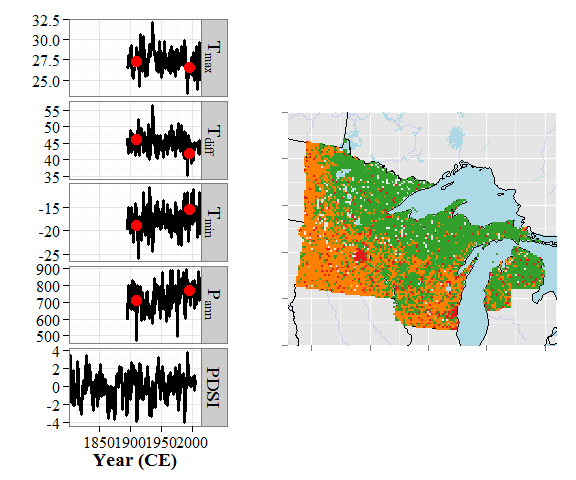
* Much of our understanding of species-climate relationships and functional-community relationships in forests is based on contemporary observations of tree distributions.
* Ecosystems are highly dynamic and contemporary forest have a heavy imprint of land use, while climate changes over decadal and centennial scales.
* Given long time-scale climate change and continued land use conversion, are species-climate relationships today representative of those in past.
* We assess the stability of species-climate relationships using historic PLS data and FIA data.
* We show that species-climate relationships have significantly shifted for many taxa.
* Contemporary trees have shifted to cooler maximum temperatures, warmer winter temperatures, reduced seasonal temperature range, and wetter conditions.
* Relative importance of land use and climate change varies by taxon and climate variable.
* Shifts in warmer temperature mainly due to land use change, etc.
* Implications sentence or two at the end.

*Historic land use and forest change over the centuries since Euroamerican settlement have significantly changed the structure and composition of forests in the upper Midwestern United States. The extent to which this change has affected the realized climate niche for key taxa is less well known.*

*Predictions for future species range shifts are largely predicated on correlative models that relate modern species distributions to climate parameters in the modern era. Given the extent of regional forest change, and recent losses to key forest taxa including Hemlock, Elm and Chestnut, it is possible that certain taxa have shifted their climatic distributions over the last century. The additional pressure of climatically biased land use conversion for agriculture along the western and southern margins of the upper Midwest means that the shift in climate space may be most pressing in a region of climate space that is critically important for understanding future species responses to climate change.*

# Introduction

Over the past 200 years centennial scale climate variability and land use change have interacted to transform the forests of the northeastern United States. There are clear indications that modern forests, as represented by the Forest and Inventory Analysis show greater homogeneity and significantly different species associations than pre-settlement forests (Schulte et al. 2007, Goring et al. in review). This shift has occured over a period during which climate has begun to show the effects of anthropogenic warming, and a period in which we have increasingly used the relationship between modern tree species distributions and climate to understand future responses of tree species and forest assemblages to climate change (Iverson and Prasad 1998, Iverson and McKenzie 2013). One of the most significant changes to forest tree distributions in the upper midwest is the loss of extensive cover through land use change (Rhemtulla et al. 2009), particularly along the historical prairie and savanna margins of the region (Figure 1f), where extensive land use conversion has left little natural land.



**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. Low temperatures in the 1970s result in lower Tmax during the modern era, but climate change has resulted in higher Tmin values than the early-century normals, along with increasing Pann. PDSI shows strong coherence with Pann in this region. (f) Patterns of land use change in the upper Midwestern United States. Data from the NLCD (Jin et al. 2013).*

The interaction of land use change and climatic change has been of interest to conservation managers and scientists (e.g., Pyke 2004) since managed natural areas often represent a biased selection from the available environmental space (Scott et al. 2001). Pyke (2004) lays out a useful framework for assessing the interaction of climate and land use change. By deliniating three types of interaction: (1) compounding, (2) confounding and (3) contradicting, it is possible to understand both the nature of the climate/land use interaction and the potential effect on apparent species resiliance and future response to broader regional change.

Compounding effects occur when both climatic change and land use change are biased in the same direction, *e.g.*, warming climate is compounded by land use change that is biased towards warmer environments. In the case of warming, a species may lose climatic suitability along the warmest margins of its range at the same time as land use pressure increases, hastening decline in response to warming. This pattern is seen for butterfly species in the northern Sierra Nevada mountains of California, where warming is compounded by land use conversion at the lowest elevations (Forister et al. 2010). Confounding effects may cause little overall effect on species distributions since land use pressure falls within the central distribution for the environmental gradient. Confounding effects may increase the variability of predictive models, but do little to the overall envelope. Garry oak (*Quercus garryana*) distributions in the Pacific Northwest may suffer from confounding effects. The spatial extent of the species has likely changed little, but it has been excluded from the deep soil sites it formerly occupied as a result of land use conversion for urban development and agriculture (Macdougall et al. 2004, Pellatt and Gedalof 2014), thus predictive models (Pellatt et al. 2012) may show greater uncertainty than if complete historical distributions had been used. Contradicting effects result in a narrower climate niche for taxa, where warming forces the distribution mean higher as populations in one tail of the climate distribution experience greater environmental pressure, and, secondarily environmentally biased land use pressure in the other end of the tail excludes the taxa from those regions. Here we might think of downward migrations of some bird species in the Sierra Nevadas in response to shifts in precipitation (Tingley et al. 2012), where downward migration may be limited by land use conversion in the lowlands.

In the midwestern United States we see a strong gradient of temperature and precipitation that results in two major ecotones, one from prairie/savanna to closed forest, in an approixmately west to east direction, and one from conifer dominated, sub-boreal forests to decidious forest in a north to south direction. Goring et al. (in review) have shown that land use change has significantly changed the strength and structure of this ecotone, and work across this regions has consistently shown a significant imprint of human land use change on this region (Radeloff et al. 2000, Schulte and Mladenoff 2001, Schulte et al. 2007, Rhemtulla et al. 2009). Given that much of the land use change within the region occurs in the south, where agricultural conversion has largely eliminated open forests (Rhemtulla et al. 2009) we might expect to see that species with more southerly distributions would show greater impacts of land use change on their distributions in climate space, assuming no shift in regional climate. Conversely, species in the north should show little change if we expect that pre-settlement trees show similar regeneration patterns (with respect to simple presence/absence) following widespread logging.

Interaction between environmental gradients, land use patterns and taxa are likely to vary by region and environmental variable of interest. Species in the north may experience a confounding land use effect with respect to temperature, northward shifts due to warming temperatures may not have significantly manifested themselves, and land use conversion is likely to be heterogenous with respect to temperature since there is little agriculture in northern Wisconsin and northeastern Minnesota. Thus, with respect to temperature we expect to see no shift in distribution along temperature gradients.

With respect to precipitation, particularly toward the forest-prairie margin, where land use conversion continues (Wright and Wimberly 2013) we would expect to see compounding effects of land use and climate change. Northern species should be shifting away from drier habitat while land use in the northern prairie-forest margin intensifies, shifting species further than expected along the precipitation gradient.

For southern tree species, land use conversion is primarily, and has primarily, occured along the southern margins of the region, parallel to temperature and precipitation gradients. This should result in compounding land use effects for all taxa with distributions in the region, resulting in narrower species distributions due to the loss of suitability and land use conversion along the southern margin of the species' range.

Critically, given the importance of modern distributional datasets for predicting species range shifts, contradicting and confounding land use effects may result in the impression of narrower climatic tolerances, or greater predictive uncertainty. Tree species are responding to climate change within forested landscapes, but the response is inconsistent. Differences in the distributions of mature trees and seedlings show responses in western North America (Monleon and Lintz 2015), but apar to indicate range contraction, rather than northward expansion in eastern temperate North America (“Failure to migrate” n.d.). Modern correlational analysis leaves out historical distributions that can further improve our ability to predict future distributions and management implications of species shifts, potentially clouding our interpretation of these patterns. For species that reach their northern or western range limits in the upper Midwestern United States (e.g., hemlock, beech, &tc.) this may be critical, since a narrowing of the apparent environmental envelope, dut to the twin action of land use change and changing climate, may result in underprediction of species resiliance to climate change.

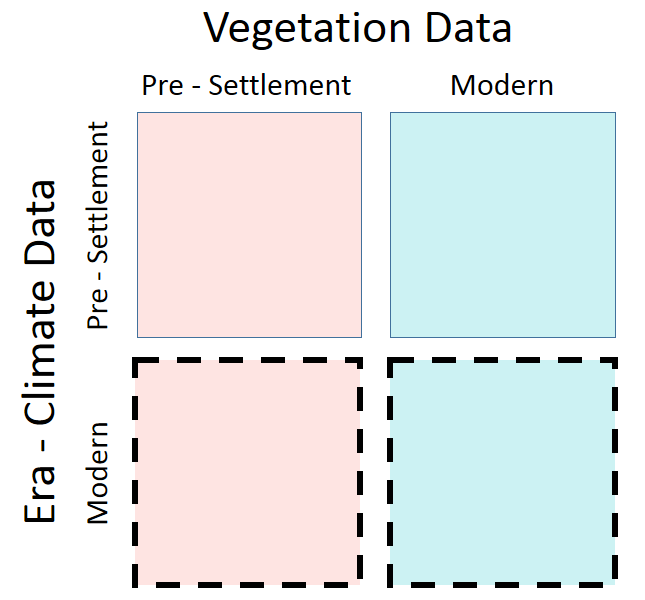
We use gridded climate data products (PRISM) and estimates of pre-settlement and modern forest vegetation (Goring et al. in review) to develop climate-vegetation relationships for 15 major tree taxa in the upper Midwestern United States. By examining the interactions between climate, species distributions and land use change since EuroAmerican settlement we examine the possible implications of range shifts for future estimates of species resillience to climate change across the region.

# Methods

We pair pre-settlement vegetation data from the Public Land Survey System (PLSS) aggregated to a 64 grid (Goring et al. in review) with annually resolved climate data for the region. The PLSS era data is aggregated from survey data collected on a 1 x 1 mi grid across the Upper Midwest during the PLS, from 1830 - 1904, in a time transgressive manner, from the south east to the north west. At each survey point surveyors noted the closest two to four trees, recorded their distances to the plot center point, diameters and the azimuth to the tree. Goring et al. (in review) aggregated this data to an 8 x 8 km grid to reduce local-scale variability, resulting in a gridded data product with an average of 61 plots per cell, or approximately 120 trees per cell. When examining relationships between FIA and PLS data, Goring et al. (in review) report significant relationships within the FIA relating dissimilarity from PLSS era forests and the number of FIA plots within an 8x8km cell, however this relationship accounts for only 3% of the total change in dissimilarity, indicating statistical significance, but little ecological significance on this regional scale.

Another complication is the structure of the FIA dataset. While the PLS data was collected across the western US on a uniform grid the FIA data is only collected from forested or partially forested landscapes (Woudenberg et al. 2010). As such trees may be present in regions without permanant or temporary FIA plots, but no record of them exists within the FIA. This complicates our ability to assign 'absence' within the FIA, however the practice of using FIA data as a surrogate for presence/absence data is widespread (Iverson and Prasad 1998, Iverson and McKenzie 2013), and, at a broad scale, the presence of individual and isolated trees in unforested agricultural landscapes may be significant for adaptation, but it may also be the case that these trees remain on the landscape through anthropogenic agency, for example, as a result of irrigation or landscaping care within urban or rural locations, agency that ultimately leads urban ecosystems in deserts to closely resemble those in the northeastern United States (Groffman et al. 2014).

The analysis presented here follows a blocked sampling method (Figure 2). We generate probability density functions along climate gradients for actual PLSS presence, by taxon, at the settlement era and for the same PLS taxa (and point locations) in the modern era. We do the same for FIA presence, and for anthropogenic land use classes. Climate data is derived from monthly PRISM data from 1895 - 2014. A 30-year climate was generated for modern July temperature, January temperature, the continentality (difference between T\_jul\_ and T\_jan\_), and annual precipitation.



**Figure 2**. *Blocked method for analysis. Data presented represent 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). A diagonal shift from the top left to bottom right represents the true change in forest-climate relationships.*

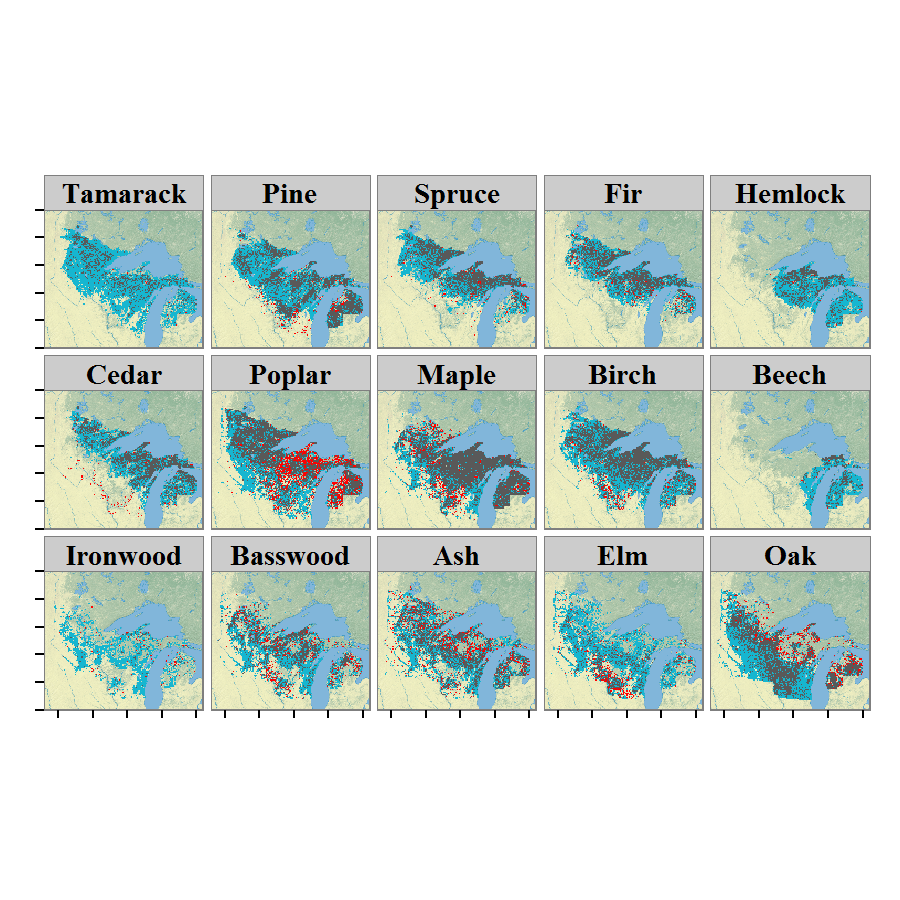
The choice of a thirty year normal for the PLS data is potentially problematic. The time transgressive nature of the PLS Survey means that some of the PLS data was sampled in the early 1800s, while other come from the early 1900s (White 1983, Goring et al. in review), and for much of this time period no climatological records exist. Regardless, throughout this period climate variability exists (Figure 1d), and trees that were on the landscape from the 1830s to the 1880s are not expected to have been completely extirpated by annual scale climate variability in that same time period. As such the use of a 'pre-settlement' climate normal from 1895-1925 is likely a reasonable choice. Regional-scale reconstructions from tree-rings and from pollen-based climate reconstructions tell us that there has been a trend of increasing temperatures (approximately 0.3oC in the Northern Hemisphere) since the 1800s, with pollen-based reconstructions showing even higher rates of change in the Midwestern United States (Viau et al. 2006), with tree rings showing cooling at the 1800s to warming from the 1900s (Ahmed et al. 2013).

By generating kernel density estimates of taxon presence along climate gradients drawn from each of the four states of climate and vegetation (Figure 2) we can use Hellinger distance to estimate the effects of changing climate (d\_H\_ between kernel densities in the same column of Figure 2), or the effect of changing land use (d\_H\_ between kernel densities in the same row of Figure 2). In particular, the effect of changing land use and climate (d\_H\_ between the top left and bottom right in Figure 2) can be parsed as the sum of differences in the left hand column (testing climate change) and the top row (testing land use only). The relative magnitudes of these differences gives us an indication of the influence of either land use or climate in driving shifts in species distributions along the climate gradients in the Upper Midwest.

## Results

Mean temperatures in the region show an average increase of -4.11oC since the 1895-1925 normal. Annual precipitation has increased slightly (55mm), and maximum annual temeprature has declined slightly (-0.79oC). The most significant change has been in annual minimum temperatures, which have increased by 3.3oC since the 1895-1925 normal. This broad scale increase in winter temperatures is widely accepted, and results in an overall shift in the winter 'climate space' for the region.

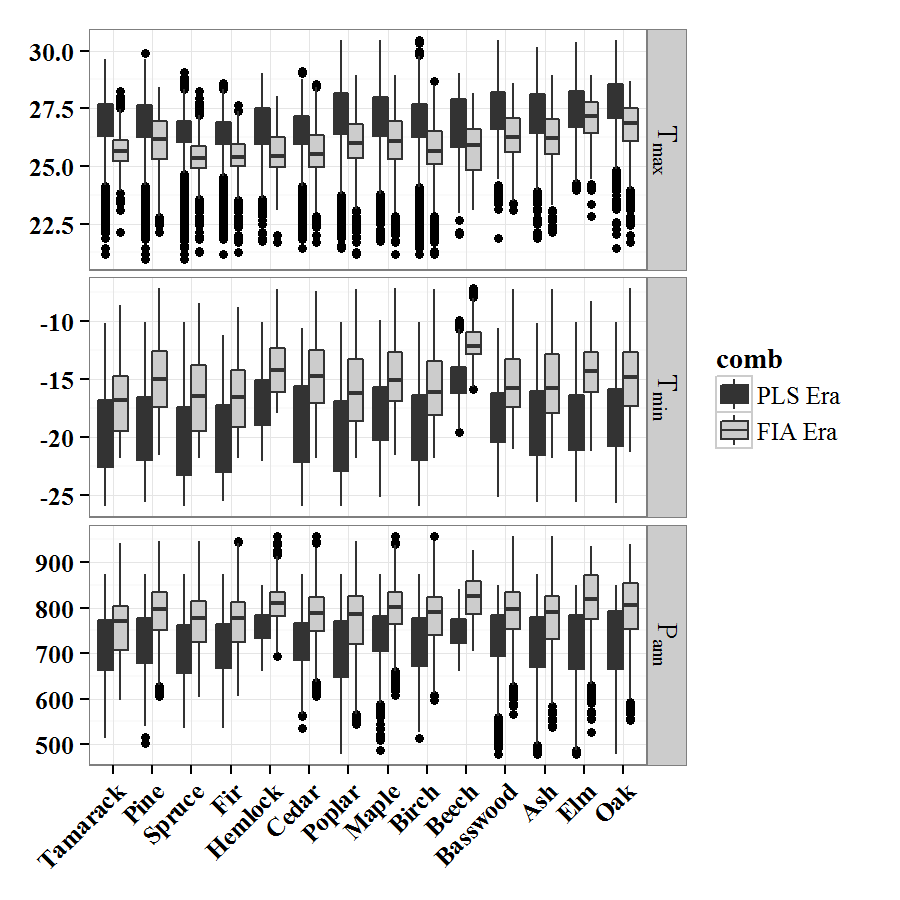
The Public Lands data is spatially extensive, sampling occured across the region in a regular pattern, while the FIA is limited to regions with forest cover. As such, the extent of points is not overlapping. Given the extensive use of FIA data in generating and estimating climate responses of tree taxa and forest types to changing climate, the use of the FIA data as an estimate for tree species distributions is acceptable fo estimating shifts in climate space, and attributing the loss or gain of climate niche space due to land use and climate variability and change during the 20th century.



**Figure 3.**. *Gain loss and continuous presence for PLSS and FIA tree taxa. Loss is assessed where previously PLSS data indicated presence of a taxon but FIA data do not record presence (light blue). Continuous presence is indicated by dark gray, for where both FIA and PLSS cells indicate presence. For most taxa it is the central parts of their distribution that show continuous presence. Few taxa show novel presence (red), although taxa such as poplar, ash and basswood show gains of over 10%.*

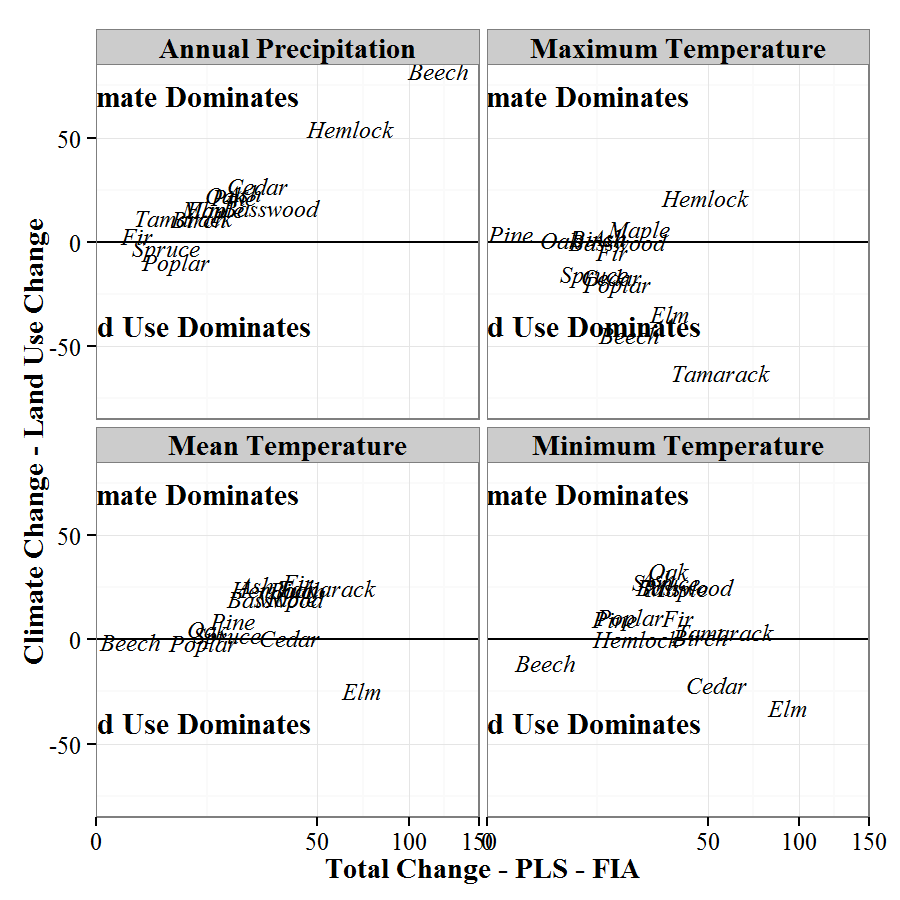
**Table 1.** *Gain and loss of the various forest tree types of interest since the pre-settlement era. Gain since the pre-settlement era is the number of new cells as a proportion of historical cover for the tree taxon, thus positive values are not indicative of higher overall spatial coverage. Loss and Presence columns sum to 100% and represent the proprtion of the historical range that has been lost, or shown continuous presence.*

&nbsp; Gain Loss Presence   
 -------------- ------ ------ ----------  
 \*\*Tamarack\*\* 0.4 80.9 19.1   
 \*\*Pine\*\* 4.1 54 46   
 \*\*Spruce\*\* 3.8 54.2 45.8   
 \*\*Fir\*\* 4.6 52.4 47.6   
 \*\*Hemlock\*\* 0.6 67.8 32.2   
 \*\*Cedar\*\* 4.2 55.1 44.9   
 \*\*Poplar\*\* 19.7 43.7 56.3   
 \*\*Maple\*\* 8.7 33.4 66.6   
 \*\*Birch\*\* 3.4 47.4 52.6   
 \*\*Beech\*\* 0.8 73.8 26.2   
 \*\*Ironwood\*\* 3.8 94 6   
 \*\*Basswood\*\* 12.9 62.2 37.8   
 \*\*Ash\*\* 14.6 56 44   
 \*\*Elm\*\* 7.4 78.5 21.5   
 \*\*Oak\*\* 9.9 50.6 49.4



**Figure 4.** *Changes in the realized climate space for genera in the upper Midwestern United States. For forest taxa maximum temperatures decline across the region from the PLS era to the modern era. At the same time minimum temperatures and annual precipitation have both increased.*

While these changes in climate are visible across the whole range, we would expect that species with significant shifts in distribution as a result of land use change in the post-settlement era should show changes that superceed the changes resulting from climate alone. In particular, if the land use pressure is biased spatially or climatically then these changes should be even more dramatic. Hellinger distance is used to understand the difference in the shape of kernel densities. Using the distributions in climate space for each of the key taxa we can shift climate, or vegetation to understand the relative effects of land use change and climatic change across the region.



**Figure 5**. *For each of the four variables examined we see differences in the relative contributions of land use and climate in driving patterns of change over the settlement era. Taxa with negative y values have changes in distributions along the climate gradient that are driven largely by land use, while positive y axis values can be largely attributed to regional climate change.*

The Hellinger distances reveal that while taxa may show the imprint of land use change on shifting climatic niches, this shift is not uniform across taxa not climatic variables. Maximum temperature shows the greatest change attributed to land use change. Tamarack, elm, poplar, spruce beech, cedar, and fir all show a greater influence for land use change than regional climate change.

The precipitation panel (Figure 5) indicates that precipitation across the region has driven change in the species climate niche for this variable. Only spruce and poplar show a marginally greater effect of land use change than climate change, wheras taxa such as beech and hemlock show a strong climate signal.

Since the pre-settlement era maximum temperatures have declined, while minimum temperatures have increased strongly.

## Discussion

This work adds to our understanding of the relationships between shifts in realized climate niches and the interacting effects of climate change and land use.

Land use is likely to have one of the strongest effects on changes in global biodiversity over the next century (**???**). Land use change reduces the correlational structure between species and climate (“To what extent does land-use affect relationships between the distribution of woody species and climatic change? A case study along an aridity gradient in western burkina faso” n.d.). While rates of land use change may be declining in North America and in the upper Midwest (Rhemtulla et al. 2009, “The relationship between land-use change and climate” n.d.) the legacies of land use are likely to persist, both in reorganizing forested landscapes (**???**), and in the correlational structure between species and climate. Paleoclimatic modeling indicates shifts in realized niches for species over time, potentially resulting from non-analogue climates or shifts in competition resulting from changing patterns of co-occurence through time (**???**).

From a modern perspective, the US Forest Service's Forest Inventory and Analysis data set is an important resource for researchers, providing detailed data at fine grain over the entire contiguous United States. However, the FIA is also an incomplete record of tree species distributions in the United States since it limits plot surveys to plots with > 10% tree cover (Woudenberg et al. 2010). In much the same way, climatic data plays an important role in building correlative models, but we are limited to the modern era (Iverson and Prasad 1998, Pellatt et al. 2012), while evidence strongly suggests historical datasets add considerably to our understanding of the breadth of species' climatic niches (**???**, **???**).

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