Dear Dr. Thrall:

We submit for your consideration the revised manuscript “*Effect of historical land-use and climate change on tree-climate relationships in the upper Midwestern United States.*”

We have carefully revised the manuscript in response to reviewer comments and have paid particular attention to the potential limitations associated with 1) comparing the PLS and FIA data and 2) choice of climate normal. We completed several new analyses to test the sensitivity of our results to choice of climate normal and created a separate subsection within the Discussion assessing the robustness of our findings.

We have edited the manuscript for clarity and to respond to the other points raised by the reviewers. We include below a point-by-point response to all reviews. The revised version has XX words and 6 figures and tables. We have expanded the Supplementary Information to show several additional analyses.

We thank you and especially the reviewers for their thoughtful and constructive criticism – we believe that the manuscript has greatly improved as a result. Thank you too for extending the deadline as requested.

Sincerely,

Simon Goring

Jack Williams

# Response to Reviewers

## Editor

Editors Comments for the Author(s): The reviews highlight the importance and novelty of the main idea - that past land-use complicates our estimates of forest community responses to climate change. However, they express concern about the way that the results are presented. There are many suggestions for clarification that should be addressed in revision. In particular, it's important to address the limitations of comparing the two data types, as this was a concern expressed by each reviewer.

Thank you. Please see responses below.

## Reviewer 1:

The manuscript written by Goring and Williams (“Effect of historic land-use and climate change on tree-climate relationships in the northern United States”; ELE-00978-2016) addresses an important topic in global change research: what is the relative influence of climate vs. land-use change on contemporary species distributions. The question is relevant as the degree to which the two drivers are both important indicates potentially major errors in future projections previously published using species distribution models (SDMs). The authors present quite a clever method for addressing the issue: i.e., building SDMs with both historical and contemporary vegetation and climate data. This paper provides novel perspective concerning how our understanding of the role of climate change in vegetation change is still limited. The paper is exceedingly well written and the conclusions seem well-supported by the methods and results.

We thank the reviewer for the positive feedback and constructive criticisms. We address specific points below.

My primary critique (which I admit is relatively minor) is that I found the logic revolving around the “confounding effects” and how the results relate to that a bit difficult. In particular, there likely needs to be a bit of clarification around the concept and a justification for why treating two non-significant effects and a set of mixed effects (one significant and one not so) as equivalent within this framework.

To address this point, we’ve expanded Table 1 to indicate the individual terms (dV and dL) and their significance. This lets the reader see for her/himself what goes into ‘confounding.’ We also added to the Introduction (4th paragraph) the sentence “*These confounding effects may make it more difficult to detect climatic forcing of historical species distributions*.” As it turns out, in the primary analyses presented here, all instances of confounding involve a significant change in climate and no significant change in vegetation (Table 1)

Title: Here and throughout, replace “historic” with “historical” as the former refers to an exceptional event in the past while the latter refers to something in the past.

We have changed all occurrences of *historic* to *historical*.

Line 143-144: Shouldn’t miles be replaced with SI? I realize that the miles are in reference to the historical context of the PLS, but it might be good to keep things consistent throughout.

We have changed to *km*, retaining the reported miles in parentheses.

Lines 174-176: This is a key point, but expanding a bit would be helpful. For example, did the paper in review examine issues of detectability? I realize this is addressed in the discussion, but a bit more detail would be good here.

We have expanded on this point in both the Methods and the Discussion. To the Methods, we added the following paragraph:

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

To the discussion, we have added a new section called ‘Potential Limitations,’ to address this question and similar points raised by reviewers 2 & 3.

Line 179: Which PRISM data are the authors using, AN or LT. The LT data, for which one has to pay, uses only longer weather station records, which tends toward more reliable temporal trends. This seems like it would be important for the current study. Additionally, it would be good for the authors to at least acknowledge that increasingly sparse data early in the PRSIM record (i.e., late 19th and early 20th centuries) could contribute to greater uncertainties in historical vs. contemporary records. This might make historical climate relationships more difficult to identify.

We use the PRISM LT data. This has been clarified in the paper.

Line 195: Since the author’s use the abbreviation “PDF”, it would improve clarity to refer to “univariate probability density functions”.

Changed.

Line 207: Here and in a few other places, d\_l is used, but later d\_v is used. Please make symbology consistent throughout the paper.

We have all references from to . We changed this sentence in particular to read: "*The difference between the PLSS and modern tree distributions () when overlaid on historical climate ( versus ) is attributed largely to land use change, as described above, given the widespread post-settlement disturbance in the upper Midwest*"

Lines 217-218: I found the labeling of lack of significance in “either or both changes” as confounding to be hard to connect with the definition provided at Line 93. For example, Fagus shows a strong overall change in distribution relative to precipitation, but is classes as confounding. Presumably, this is a situation where climate was important, but history was not. I suppose a bit more clarification regarding what is meant by confounding and why grouping taxa where neither climate nor history has an effect with taxa where only one has an effect is necessary.

We've changed Table 1 – see response to prior comment.

Lines 231-232: Looking at the maps, it seems that this statement is limited by the fact that the current study does not incorporate the northern range limit for many species. Can the authors address this limitation at some point?

To address this point, we have added the following sentence to the end of the Methods section on the FIA: “*For all species, the range within the upper Midwest is an incomplete sample of the species range, however, the region contains several major ecotones and the southern and western range limit for many tree species (Curtis 1959), so this region represents an important boundary in geographic and climate space.”*

Lines 337-351: The authors discuss agriculture, but not timber harvesting and changes in fire regime in terms of the land-use drivers. It seems that the latter two are potentially important for some of the regional patterns. Additionally, I wonder if some of this could be discussed by looking at gains and losses relative to NLCD land-use layers. Perhaps that was in the supplement and I missed it.

We have added the sentence: *While fire and logging have altered tree distributions in the north, they have not widely excluded taxa from the northern regions and climate space, except for* Tsuga *(Fig. 3), a shade-tolerant and late-successional taxon.*

Figure 5: The x – axis needs more tick marks and numbers. At first, my mind assumed a linear scale, which would imply negative distances, but then I thought maybe this was some sort of log scale, which would make more sense with a distance metric. Some additional clarity is needed.

We have changed the x axis to a log10 scale and added more tick marks to the x-axis to make it clear that it is non-linear.

Table 1: Some of the taxa are listed with their scientific names and others by common names. Replace common names with scientific names

Table 1 is corrected so that only scientific names are displayed. Thanks for catching this error.

## Referee 2:

Comments for the Authors  
This paper compares tree/climate relationships between two time periods and concludes that modern forest data sets may not be adequate for quantifying the realized niches of tree species because tree populations may not be in equilibrium with environment under rapid land use and climate change and the data sets have limitations in estimating tree presence and absence.  This is a very important point and the paper will likely be of very high interest.  This comparison of pre-settlement times with modern times is unique in the species distribution modeling literature and nicely demonstrates the key points.  
  
The paper is well written and the graphics are generally very good.

We thank Reviewer 2 for the positive feedback and constructive criticism. We have performed several new analyses and revised existing analyses in response to Reviewer 2. We describe these further below.

I think the paper does not adequately point out the limitations of the data sets used for the analyses and that the authors overstate the likely differences in realized niches between the historic and current time periods.

The paper would be strengthened by stating more strongly the limitations of the methods and that the results may be over estimates and that data are not currently available to more accurately estimate the effect.

Moreover, other data sets should be called upon to try to corroborate the range shifts and changes in climate-tree relationships that emerge from the analyses. Also the ecological mechanisms that might underlay the effects of land use and climate on tree species distributions should be more fully discussed.

We thank the reviewer for these comments. We now more fully address the limitations through multiple solutions. 1) We have added references to long term weather records and used their early 19th century estimates as the basis for sensitivity analysis (see below). 2) We have experimented with two modern climate normals, representing time of sampling and time of establishment. 3) We strengthened the literature reiew section that indicates prior support for widespread land use change, and its impacts on tree species distributions in the region. 4) Lastly, in the **Discussion** we have reitterated what we believe are some of the limitations of the current study.

### More specific comments

2 "north-central" US would be more accurate? Also change this throughout the ms.

Here and elsewhere, we have adopted ‘upper Midwestern US’ throughout ms. as the most spatially precise geographic place name.

175-176 While that study found little effect of the differences between the PLS and FIA data sets, be sure to cover fully the potential effect of these differences on results of this study. One has to presume that the differences in realized niches between historic and present would be substantially smaller if FIA was sampling low density and widespread occurrence of species as did the PLS.

Please see our response above to Reviewer 1 and the expanded treatment of this question in the Methods and Discussion.

181-182 Provide evidence that these climate variables have been shown to be strong correlates of tree species presence in previous species distribution modeling studies. It is important to do your analysis on climate variables that are known to be ecologically relevant to tree niche dimensions.

We have added this sentence: *These climate variables represent three major climatic controls on plant distributions: summer warmth, winter minimum temperatures, and moisture availability; these or similar bioclimatic variables are widely used in plant distributional modeling (Woodward 1987, Iverson and Prasad 1998, Maiorano et al. 2013).*

183-185 First, it is a serious stretch to use 1895-1919 climate to represent tree/climate relationships during 1830-1910. The verbal statement (without statistical analysis) that the dendro-based PDSI did not change over that period is not very convincing. Moreover, the analysis specifically should be done on the climate predictors used in the niche modeling. Also, evaluate to what extent does this PDSI index represent trends in Tmin and the other predictors used?

We respectfully disagree that it is a serious stretch to use 1895-1915 climates to represent 1830-1910 climates. The PDSI data shows no evidence of long-term trend between 1800 and 1910, based on a LOESS line fitted to the time series shown in Fig. 1 (see other responses below). PDSI correlates well to precipitation (r=X), suggesting that PDSI is a good proxy for precipitation.

To further address this point, we have added a review of early meteorological records from US military forts. These records do indicate some warming in the region (Baker et al, 1985, Burnett et al. 2010). We have added the following text to the first paragraph of the results.

*Early temperature observations from US military forts suggest some warming between the middle 19th and early 20th Centuries, with increases in mean annual temperature at Fort Snelling, Minnesota (Baker et al. 1985) and Fort Leavenworth, Kansas (Burnette et al. 2010). The latter shows increasing temperatures in all seasons, with faster increases during winter (0.10oC decade-1) than during summer (0.07oC decade-1). Hence, our estimates of historic climate change may be too conservative for Tmin and Tdiff and too large for Tmax (Supplementary Information).*

We have used these findings as the basis of a simple sensitivity analysis to the Supplementary Information (Supplementary Figure 3) in which adjust the historic climate data and historic-modern differences based on 19th-century trends observed in the US fort data. This analysis is summarized by the following new sentences in the results:

*These patterns are unchanged by a simple sensitivity analysis in which the historical temperature changes are further augmented by the 1850 to 1900 temperature trends (Supplementary Figure 3).*

*The patterns of confounding and compounding interactions are insensitive to the incorporation of estimates of 19th century temperature changes from US forts (Burnette et al., 2010) (Supplementary Table 3).*

Another issue is lack of discussion about the time period when the forests sampled by FIA got established. It is typical in SDM studies to test the strength of models from different time periods in tree SDM work and select the time period that is most strongly associated with species presence. In the western US, we found 1950-1980 to produce stronger models than 1980-2010.

We have addressed this point by adding an analysis in which we use climate normals for 1950-1980 for the modern climate instead of 1990-2014. We report the results from the latter in the main paper, and have added several new figures to the supplementary information. We’ve also analyzed tree age in the FIA data, which shows a mean age of 52, 56, and 49 years in WI, MN, and MI. Based on this, the 1950-1980 is a good alternative time window for the time of tree establishment.

We also note that this paper is not intended as an exercise in creating SDMs, a point we will return to later, but take the point of the association between vegetation and climate varies between establishment and long term survival of forest stocks.

We’ve added the following text to the manuscript:

*The use of two climate normals for the modern period reflects two reasonable alternative arguments about what to use for describing and modeling tree-climate relationships. The 1990 to 2014 climate normal encompasses the period of observation (2000 to 2015) for the FIA data used in this study. The 1950 to 1980 normal is closer to the time of establishment of FIA trees, which have an average age of 50 years in this region (REF). Results in the main text are based on the 1990-2014 normals, with the 1950-1980 results shown in Supplementary Information.*

A third issue is the role of climate variability over the 1895 to 2014 time period. Decadal oscillations are common in this period in many parts of the US. Trees are likely integrating over 2 or more of these climate cycles. SDMs should be done to best represent the climate and variability that selected for tree presence when the trees were measured. Your analysis would be strengthened with statistical analysis of climate patters from 1895 to present for your predictor variables and an analysis of which time period produces the best SDMs.

We believe that this point is now addressed in responses to other comments. We have added a LOESS curve to Figure 1 (in response to a later comment), we have selected an alternate modern climate normal that reflects the period of establishment, and have provided additional support to the choice of the modern normal. Note too that we specifically chose 30-year climatologies in order to smooth out the effects of interannual and interdecadal-scale variability on our results.

195 It is important to discuss why univariate climate tree presence functions are relevant to the climate factors that strongly influence tree species presence or absence. SDM modeling typically shows that a particular combination of climate and habitat factors is much more strongly associate with tree presence and any random climate variable. Your analysis would be stronger to do model selection for best multivariate SDM functions and then compare these functions between historic and present.

We apreciate this point and thank the reviewer for bringing it up. Please note that this analysis is not intended to focus on the construction of SDMs, but rather to show the joint effects of historical land use and climate change on tree-climate relationships. We respectfully believe that a multivariate SDM would obscure these shifting relationships by blending together the climate variables. Further, a multi-model SDM approach might weight climate variables differently across models, through time. We believe that there is value and insight in focusing on individual climate variables and the distribution of trees along individual axes.

Shifts in the strength of SDMs between time scales and potential utility of climate variables in SDM construction is worthwhile, but a separate analysis and paper.

211-218 The analyses should control for spatial autocorrelation, simple t-tests would seem to have an inflated sample size due not including spatial autocorrelation in the model.

We have now included spatial autocorrelation in this analysis, and describe the methods in the Supplementary Information.

226-230 and Figure 1. Statistical analysis should be done of the climate trends, showing a least a trend line and a 95% confidence interval. A moving window regression might better show breakpoints in the trend line. This is needed because the data show high interannual variability and it is not obvious by eyeing these graphics for which variables trends exist or not. Also, say in the legend what the red dots are.

We have added a LOESS curve onto Figure 1, representing a span of 20 years, along with the SE fit. We have added light shading over boxes corresponding to the chosen climate normals. As indicated above, we have provided a more detailed analysis of the choice of normal periods and described the effect of the choice on outcomes.

231-239 I find the maps of range loss in Fig 3 to be stunningly large. I am not sure anything in the literature would document such large losses in tree species presence from land use or 100 yrs of climate change. It would seem important to use other data sets to validate these estimates of range loss. Are the patterns in these maps real or mostly due to the differences among the PLS and FIA data sets? If real, what are the mechanisms of local extinction?

I have added an explicit statement to quantify losses in the paragraph beginning at **l**104. There is strong support for extensive loss of coverage since the PLSS for certain species, and expansion for others, all referenced in this paragraph. These patterns are well supported in the literature. Rhemtulla et al (2007) cite estimates of land use conversion up to 79% for southern deciduous savanna, and Rhemtulla et al (2009) show that losses in oak-hickory forest complexes surpass 5,000,000 ha. As noted in the new sentences: "*Rhemtulla et al. (2009) estimate that* Pinus strobus\* and *Tsuga canadensis* now occupy only 4% of their original coverage in Wisconsin. Wildland ecosystems have been converted to agricultural and urban land use (Rhemtulla et al. 2009), particularly in historical prairie and savanna ecosystems (Figure Xf), where 79% of deciduous savanna was converted to cropland (Rhemtulla et al. 2007).\*"

Given the extensive support for broad scale land use change, and the associated impacts of fire & logging, we believe that these patterns are real.

347-350 Is it accurate to infer that ag has “largely eliminated open forests” which does not sample low density forests? It seems likely that most of these tree species are present in at least low densities in the areas where your maps show they are not present.

As above, we believe that these patterns are real. We extend this point however beginning at **l**371, where we discuss the potential use of isolated trees or trees unsampled in the FIA data.

Figure 2 b-e, The axes should be labeled and units indicated. Consider reformatting these figures. The current versions make visual separation of the lines hard to detect.

Done.

Lines 361-364. The topic of this sentence should be elaborated upon to more fully point out the limitations of the study and appropriate inference. Say how much the estimates of forest loss and niche shifts may be overestimated.

Please see the response to the next comment.

365-370 These sentences are a bit of bait and switch. Yes, readers will agree that SDM based on FIA may not fully represent the realized niche of tree species. However, some of your argument hinges on the magnitude of the error that is made by using FIA. I think your paper way over states that error. The paper would have more impact if you were careful to emphasize the limitations of the data sets for this analysis and say that the degree to which FIA leads to SDM error is not knowable with available data sets.

We have created a standalone section in the Discussion (and the various sensitivity analyses described above) that more fully works through these points. Our takeaway message here is that the limitations are real and need considering, but do not detract from the main finding that historic land use and climate changes in this region have been large and have interacted to alter tree-climate relationships.

## Referee 3:

Goring and Williams investigated the overall distribution changes and relative influence of historic land use and climate change on these changes in the upper Midwestern United States. This is an interesting topic because climate change has been changing tree species distribution, meanwhile land use change may be interacting with climate change to compound, confound, or contract these changes. However, the manuscript is not very compelling for several reasons:

We thank the reviewer for these comments and hope that the revised manuscript addresses these concerns.

Firstly, its rigor and clarity do not meet the standards for Ecology Letters. For example,

Title: The authors used the upper Midwestern United States throughout the manuscript. But why the authors used the northern United States in the title?

See response to Reviewer 2. e have changed the title to ‘upper Midwestern United States’.

This study equally emphasized the distribution changes for 15 common tree genera over the last two centuries and the effects of climate change and land use change on these changes. Was it better to say “the effects of historical land use and climate change on species distribution changes” in the tittle?

We respectfully believe the title should stand as is. This paper does indeed present evidence for both changes in geographic distributions and tree-climate relationships. However, we believe the latter is of more interest to the Ecology Letters readership and have focused the paper’s attention on it.

Abstract: P2-L34-37, forest inventory data cannot be used to project forest responses to climate change. Rather, forest inventory data were used in models to make projections. It was distribution-climate relationships. In my opinion, this study was not about the stability and representativeness of distribution-climate. This study was to build up or extend the distribution-climate relationships.

We appreciate the clarification of the reviewer regarding the first point and have addressed it by changing the introductory sentence to:

*Contemporary forest inventory data are widely used to understand environmental controls on tree species distributions and to construct models to project forest responses to climate change, but the stability and representativeness of contemporary tree-climate distributions is poorly understood*

We respectfully disagree with the reviewer regarding the second point. We believe that the central aspect of this paper is its analysis of the stability of tree-climate relationships over the past two centuries. The paper shows that, for many taxa, land use following EuroAmerican settlement in the north-central US limits the representitiveness of modern inventory-based distribution models. We do not attempt here to use historical and contemporary data to build better predictions for the future, but have inserted a pointer to other papers where that has been done:

*One solution is to use both historical and contemporary data when calibrating species distribution models (Nogues-Bravo et al. 2016 Maiorano et al. 2013)*

1. One of the objectives in this manuscript was to investigate the effects of climate change, land use change, and pathogen outbreaks on distribution changes (L125-126). However, the pathogen outbreaks were nearly ignored in the title and methods, results, and discussion sections.

We agree. Pathogen outbreaks cannot be ignored, because their impacts are significant for *Ulmus*, and (outside the current range) for *Castanea*, but they are not central to this paper. We have reduced their importance in the manuscript, but continue to acknowledge them as a factor in changing distributions in the Discussion and in the Introduction. We’ve also added several references about the past effects of pathogens on tree mortality and forest composition.

Most importantly, the way that the authors included the effects of land use change in data analyses (let’s forget pathogen outbreaks for now) was not justified. Thus, I was not convinced the data analyses were robust to answer the question about the effects of climate change, land use change, and pathogen outbreaks on distribution changes. Although the authors argued the land use effects were represented as the difference between VHCH, VMCH. Why?

The reviewer is pointing out an important distinction: what we can observe is historical climate change and vegetation change. Yet we often make inferences about land use because, in this region, forest composition has been so heavily altered by past and current land use. Previous authors have clearly indicated that EuroAmerican settlement in the north-central United States can be almost entirely attributed to human agency. Euro-American Settlement is associated with a suite of land use changes, including logging, associated slash fires, and large scale conversion of forested landscape to agriculture. Shulte et al (2007) and Rhemtulla et al (2009) have used similar language to explain the set of changes associated with EuroAmerican settlement. Initial clearance for agricultural and urban development was contemporaneous with massive logging operations, and, in the late 1800s, widespread fire originiating from human sources. Given this, and the fact that very little "old growth" forest remains, modern forests are indelibly imprinted with the signal of human land use, whether agricultural conversion or timbering. The IPCC considers forestry to be a component of land use. The Peshtigo firestorm, the Michigan fires of 1871 and 1881 were driven by slash buildup following logging. While sucession processes occurred since clearance and settlement, these were directly affected by the initial land clearance. For example, Rhemtulla et al. (2009) indicate that the loss of hemlock was caused both by logging, and recruitment failure as the result of the loss of seed source because of the extensive logging, thus both cause & effect are rooted in EuroAmerican settlement.

Thus, VH, from the PLSS forest survey (ignoring climate data for now), mostly represents forest structure and distribution in the absence of settlement impacts. VM represents a modern landscape, sampled over the last decade as part of the FIA program. Differences between VH and VM is almost entirely attributable to anthropogenic agency, either loss of forested land (oak-hickory forest lost 5x106 ha of coverage since settlement due to agricultural conversion, as pointed out in the response to Reviewer 2) or logging, tree plantations, or other forms of forestry use. Hence we are confident in ascribing most changes from VC to VM to land use.

To further clarify, we have modified the explanation of Figure 2 in the Methods as follows:

*The effect of vegetation change on shifting PDFs is similarly described as , the Hellinger distance between and (top row of Figure 2a). Because Euro-American land use is the dominant driver of vegetation change in the upper Midwest over the past two centuries (Introduction), we often attribute shifts recorded by to the land use change associated with EuroAmerican settlement.* Firstly, it is not possible to get the distribution data under VMCH. Secondly, the distribution changes over the last two centuries were caused by many factors including land use change, disturbances (e.g., pathogen outbreaks, fire, harvest), and endogenous succession processes. Why the difference VH and VM could represent the land use change effects? This was too arbitrary. A stronger rationale is needed.

See response to prior comment.

The authors should use present tense not past tense in the methods and results sections.

In our experience, either present or past tense is acceptable, as long as verb tense is used consistently. We have not changed tense, but are happy to comply with any request by Ecology Letters.

The results section was not well organized. Subtitles should be used to describe the overall distribution changes, shifts along climate change, the relative importance, and interactions. The four paragraphs of interaction subsection in the results section were not concise and like bullets.

We have ensured that each paragraph in the results has a clear and informative topic sentence.

Secondly, the materials and method section was vague and not logically articulated. 1) July temperature (Tmax) was the minimum, maximum, or mean temperature in July? January temperature (Tmin) was the minimum, maximum, or mean temperature in January? Annual temperature range (Tdiff) was the difference between the minimum and maximum temperature over the year? Annual precipitation (Pann) was the minimum, maximum, or mean precipitation across over the year?

We have clarified the description of these variables in the Methods: "*Estimates for mean daily July temperature (), mean daily January temperature (), annual temperature range (: - ), and annually summed daily precipitation () . . .*"

1. More detailed information in the materials and method section was needed to show how the authors analyzed the overall distribution changes, climate change effects, and the relative importance of land use and climate change. It should not be only in the figure titles. For example:

The authors used gain, loss, and continuous persistence to demonstrate the distribution changes over the last two centuries in Figure 3. However, this approach was not described in the materials and method section but was only in the title of Figure 3.

We have added the following sentence to the Methods:

*In mapping tree distributions in the Upper Midwest we consider three classes: "gain", where a tree species was present within a grid cell in the FIA, but absent in the PLS; "loss", where a tree was present in a grid cell during the PLS but absent in the FIA; and "continuous presence", where a tree was present within a grid cell in both FIA and PLS eras.*

The authors used the box-and-whisker plots to demonstrate the distribution changes along Tmax, Tmin, and Pann. Likewise, this approach was not described in the materials and method section but was only in the title of Figure 4.

We’ve amended a sentence in Methods to read *“Distributions of tree genera within climate space are shown using box plots and described as univariate probability density functions (PDFs) of tree species presence”*

The approach used in Figure 5 was not described in the materials and method section but was only in the title of Figure 5. More detailed information should be given to better analyze the relative importance of land use change and climate change effects.

The approach shown in Fig. 5 is described in the section of Methods ‘Shifts of Species Distributions in Climate Space.’ We have edited it for clarity.

More detailed information about the univariate density functions (PDFs) and Hellinger distances was needed to better describe the approach.

We have modified the sentence discussing the density functions to read:

*Distributions of tree genera within climate space are described as univariate probability density functions (PDFs) for the pre-settlement and modern eras, estimated using an unweighted Gaussian kernel density estimator, using R's density function.*

We have added the equation for the Hellinger distance:

*Hellinger distance for two discrete probability distributions is defined as:*

H(P, Q) = ;

*where and are the distributions, with a common discrete index .*

1. Again, how the effects land use and exotic pathogens were included in the analyses?

See responses to prior comments.

1. The 2×2 factorial design with pre-settlement and modern vegetation and climates (VHCH, VHCM,VMCH,VMCM) was very confusing (Figure 2a). The historical distribution data for VHCH scenario were derived from PLS and the contemporary distribution data for VMCM were derived from US FIA data. Then, what were the data for VHCM and VMCH scenarios. It was impossible to get the data for VHCM and VMCH scenarios, right? If my understanding was wrong, then the more detailed information was needed to better describe the factorial design and data used for each scenario.

We revised this section of the methods for clarity, in part by re-writing this paragraph:

*The total shift () is calculated as the Hellinger distance between and (fig\_nums("fourPanel", display = "cite")a: top left to bottom right). These conditions are observed or recorded in data. The conditions and are synthetic, generated by superimposing historical climate patterns on modern vegetation distributions and by superimposing modern climate on historical distributions. The effect of climate change on shifting species PDFs is described as , the difference between PDFs using the early climate normals () and modern climate normals () overlaid on PLS vegetation (e.g., versus ; fig\_nums("fourPanel", display = "cite")a; left column). We interpret PDF changes estimated from vegetation change ( to {) superimposed on historical climate (*e.g.*, versus ; modeled by a shift along the top row of Figure 2a) to indicate change in vegetation attributed to land use change, or, more precicely, the land use change associated with EuroAmerican settlement. We describe the Hellinger distance between and as .*

1. About the t-tests to assess the interaction effects between land use and climate change (e.g., compounding, confounding, counteracting), what the responsible variables were used for the comparisons between the VHCH and VHCM, VHCH and VMCH. More detailed information was needed to better describe these tests.

Thirdly, the discussion section was not well written. Many contents in the discussion section ventured beyond the domain of the results. I suggest that the authors should set the results in a broader context and logically discuss the implications for distribution-climate relationships, distribution modeling, historical database, and management. 1) L316-L322 were not the findings of this study. How were these points related to the findings? They read like introduction and should not be in discussion section.

We have heavily revised the discussion in response to all reviewers’ comments. Note that we were unsure about how to best address this comment, because it seems to ask that the discussion be both broadened and narrowed. We hope that the revised discussion addresses these concerns.

1. Likewise, L323-l336 how were these points related to your findings? It stood alone now.

This paragraph is intended to review mechanisms by which species-climate relationships may change over time. We have not changed this text.

1. L337-l351 should be better related to your findings. The first and second points stood alone now.

We have added two pointers back to figure 1, to better link this discussion to that figure.

1. L352-L360 here, the authors finally mentioned the pathogen outbreaks effects. However, the pathogen outbreaks effect were not included in the data analyses. This seems just speculation.

See prior response to prior comments.

## Specific comments:

1. P2-L36, change “is poorly understood” to “are poorly understood”.

Fixed.

1. P2-L41, change “implicates” to “implicated”.

This edit goes back to prior stylistic disagreements about choice of present vs. past tense. We have kept the abstract in the present tense.

1. P2-L43, change “are compounding” and “reinforces” to “were compounding” and “reinforced”.

See response to prior comment.

1. The figures were not well made. The axis titles in Figure 1 were two small. The four lines in the Figure 2 b-e were difficult to read. The genera names in Figure 5 were too crowd and hard to tell. It may be better to use shorter names instead.

We have edited figures…

1. All figure titles were too long. Many of these contents were approach and should be put in methods section.

We have added more information to the Methods section, while also retaining much of this information in the Figure legends.

Bell, D. M., J. B. Bradford, and W. K. Lauenroth. 2014. Early indicators of change: Divergent climate envelopes between tree life stages imply range shifts in the western United States. Global Ecology and Biogeography 23:168–180.

Burnette, D. J., D. W. Stahle, and C. J. Mock. 2010. Daily-mean temperature reconstructed for kansas from early instrumental and modern observations. Journal of Climate 23:1308–1333.

Goring, S. J., D. J. Mladenoff, S. Cogbill Charles V Record, C. J. Paciorek, S. T. Jackson, M. C. Dietze, A. Dawson, J. H. Matthes, and J. S. McLachlan. in review. Changes in forest composition, stem density, and biomass from the settlement era (1800s) to present in the upper Midwestern United States. PLoS One.

Iverson, L. R., and A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68:465–485.

Jacques, J.-M. S., B. F. Cumming, and J. P. Smol. 2008. A pre-European settlement pollen–climate calibration set for Minnesota, USA: Developing tools for palaeoclimatic reconstructions. Journal of Biogeography 35:306–324.

Maiorano, L., R. Cheddadi, N. Zimmermann, L. Pellissier, B. Petitpierre, J. Pottier, H. Laborde, B. Hurdu, P. Pearman, A. Psomas, and others. 2013. Building the niche through time: Using 13,000 years of data to predict the effects of climate change on three tree species in Europe. Global Ecology and Biogeography 22:302–317.

Nieto-Lugilde, D., K. C. Maguire, J. L. Blois, J. W. Williams, and M. C. Fitzpatrick. 2015. Close agreement between pollen-based and forest inventory-based models of vegetation turnover. Global Ecology and Biogeography 24:905–916.

Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2007. Regional land-cover conversion in the us upper midwest: Magnitude of change and limited recovery (1850–1935–1993). Landscape Ecology 22:57–75.

Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2009. Historical forest baselines reveal potential for continued carbon sequestration. Proceedings of the National Academy of Sciences 106:6082–6087.

Tipton, J., M. Hooten, and S. Goring. accepted. Reconstruction of spatio-temporal temperature from sparse historical records using robust probabilistic principal component regression. Advances in Statistical Climatology, Meteorology and Oceanography.

Wang, W. J., H. S. He, F. R. Thompson III, J. S. Fraser, and W. D. Dijak. 2016. Landscape-and regional-scale shifts in forest composition under climate change in the central hardwood region of the United States. Landscape Ecology 31:149–163.