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Continental-scale consequences of tree die-offs in North America: identifying where forest loss matters most

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Abstract

Regional-scale tree die-off events driven by drought and warming and associated pests and pathogens have occurred recently on all forested continents and are projected to increase in frequency and extent with future warming. Within areas where tree mortality has occurred, ecological, hydrological and meteorological consequences are increasingly being documented. However, the potential for tree die-off to impact vegetation processes and related carbon dynamics in areas remote to where die-off occurs has rarely been systematically evaluated, particularly for multiple distinct regions within a given continent. Such remote impacts can occur when climate effects of local vegetation change are propagated by atmospheric circulation—the phenomena of 'ecoclimate teleconnections'. We simulated tree die-off events in the 13 most densely forested US regions (selected from the 20 US National Ecological Observatory Network [NEON] domains) and found that tree die-off even for smaller regions has potential to affect climate and hence Gross Primary Productivity (GPP) in disparate regions (NEON domains), either positively or negatively. Some regions exhibited strong teleconnections to several others, and some regions were relatively sensitive to tree loss regardless of what other region the tree loss occurred in. For the US as a whole, loss of trees in the Pacific Southwest—an area undergoing rapid tree die-off—had the largest negative impact on remote US GPP whereas loss of trees in the Mid-Atlantic had the largest positive impact. This research lays a foundation for hypotheses that identify how the effects of tree die-off (or other types of tree loss such as deforestation) can ricochet across regions by revealing hot-spots of forcing and response. Such modes of connectivity have direct applicability for improving models of climate change impacts and for developing more informed and coordinated carbon accounting across regions.

Introduction

Broad-scale tree die-off events driven by drought and warming, sometimes associated with pests and pathogens, have occurred on every wooded continent in recent decades (Allen *et al* 2010, 2015, IPCC 2014), and even in the Amazon Basin (Phillips *et al* 2009). Particularly hard hit was Western North America

(Berner *et al* 2017). Broad-scale tree mortality initially impacted semiarid woodlands of the Southwestern US (Breshears *et al* 2005), while later Texas experienced extensive tree mortality (Moore *et al* 2016), and more recently more than 100 million trees have died throughout California (Asner *et al* 2016, Young *et al* 2017, USDA 2017), in addition to extensive lodgepole pine die-off in British Columbia (Raffa *et al* 2008).

These changes pose major challenges for managing forests into the future (Trumbore *et al* 2015, Cobb *et al* 2017). Projections based on observations, experiments and modeling all predict additional large increases in tree mortality as temperature continues to warm (Adams and Macalady 2010, Adams *et al* 2017, Allen *et al* 2015, Anderegg *et al* 2015, McDowell *et al* 2016, Williams *et al* 2013).

Plants profoundly influence local climate by controlling the exchange of energy and water with the atmosphere. Changes in and/or losses of plant type or plant functioning can alter the local climate, but also potentially large scale climate by modifying atmospheric circulation. It is well recognized that ocean-atmosphere interactions, such as the El Niño Southern Oscillation (i.e. Horel and Wallace 1981), are capable of altering global climate patterns through climate teleconnections. The concept of teleconnections is well accepted in the atmospheric science community, including the impacts of phenomena like the El Niño Southern Oscillation, but the potentially global impact of plant cover change on other ecosystems as communicated by the atmosphere has been under appreciated and is only beginning to be evaluated. Recent research has demonstrated that widespread tree loss associated with forest die-off or deforestation has the potential to affect large-scale climate (Avissar and Werth 2005, Chen *et al* 2012, Medvigy *et al* 2013, Badger and Dirmeyer 2015), and thus ecosystem productivity elsewhere via the process of 'ecoclimate teleconnections', where ecosystems in one location impact climate and ecosystems in another (Swann *et al* 2012, Garcia *et al* 2016, Stark *et al* 2016).

More specifically, plants influence the climate around them by modifying the exchange of energy, water, and momentum through changes in the absorption of shortwave radiation and fluxes of sensible and latent heat (Bonan 2008). Changes in plant type or loss of plant cover can affect surface albedo, and thus the amount of energy absorbed from shortwave radiation. Sensible heat fluxes rely on turbulent air and thus depend on the roughness of a surface which is strongly influenced by plant structure. Latent heat flux is determined by the combination of evaporation and transpiration, which are strongly plant dependent. The ability of a surface to shed energy through latent or sensible heat is key to determining that surface's temperature—shifts in the relative balance between the two can lead to increases in surface temperatures (where sensible heat is relatively higher) or decreases (where latent heat is relatively higher). Understanding how changes in plant cover alter surface properties (e.g. albedo, roughness) is therefore key to quantifying how plant cover changes will influence climate (Stark *et al* 2016).

Previous research has simulated the impacts of very large-scale forest change on climate (e.g. global, Bala *et al* 2007; latitudinal bands, Devaraju *et al* 2015; mid-latitudes, Swann *et al* 2012; all of Western

North America and/or all of Amazonia, Garcia *et al* 2016, Stark *et al* 2016). The question remains: will forest loss at spatial scales smaller than those evaluated to date have climate impacts sufficient to affect ecosystem functioning elsewhere? If so, such cross-regional ecoclimate connections, which can be thought of as 'ricochets' of the impact of change in vegetation in one location to vegetation in remote locations, need to be known for cross-regional management of carbon or other ecological currencies. Such impacts likely depend on both the location and magnitude of tree loss. Without a robust predictive capability for ecoclimate teleconnections, land managers and policymakers will be ignorant of these processes and poorly equipped to deal with macrosystem-level impacts of global change, even as countries, states, and cities join globally-coordinated carbon management protocols.

Here we assess potential ecoclimate teleconnections across regions of the US triggered by tree die-off (or other analogous tree loss such as deforestation). We investigate tree loss from the most densely forested regions in the US and quantify the impacts across the country. We hypothesize that the effect of ecoclimate teleconnections caused by tree mortality depends on the location of the mortality event. To test this we implemented simulations of tree die-off in an earth system model for the 13 most densely forested bioclimatic regions in the US, identified as 'domains' by the US National Ecological Observatory Network (NEON) and evaluated Gross Primary Productivity (GPP) responses across North America. We evaluate both the potential of forest within a region to have a large impact elsewhere, and the sensitivity of a region to forest loss elsewhere. We find that location of forest loss matters, with some regions causing a much bigger impact on primary production across the US per unit of forest removed. Of particular interest, we find that the Pacific Southwest domain, which is a major hotspot of contemporary forest loss from climate related factors including pests and wildfire (Asner *et al* 2016, Berner *et al* 2017, USDA 2017), has a large and widespread detrimental effect on forest productivity in the midwestern and eastern United States.

Methods

Model setup and experimental design

For our simulations we used the National Center for Atmospheric Research (NCAR) Community Earth System Model version 1.3 (CESM) that couples the Community Atmosphere Model version 5 (CAM5) (Neale *et al* 2012) to the Community Land Model (CLM4.5) (Oleson *et al* 2013), the CICE4 sea ice model (Hunke *et al* 2010), and implements a slab ocean with prescribed heat transport derived from a fully-coupled ocean-atmosphere simulation (Neale *et al* 2012). Simulations were computed on

the Yellowstone supercomputing cluster (Computational and Information Systems Laboratory 2012). The slab ocean model is a computationally efficient scheme that allows sea surface temperatures to interact with the atmosphere, and it is necessary for propagating energy imbalances due to land cover change that lead to shifts in precipitation. There are several types of biogeophysical interactions between plants and the atmosphere. These include shortwave and longwave radiation interaction with a plant canopy, stomatal resistance, and wind turbulence. Stomatal resistance is calculated using a Ball-Berry formation (Collatz *et al* 1991, Oleson *et al* 2013) and is a function of leaf photosynthesis, relative humidity, atmospheric pressure, and parameters specific to plant functional type. Leaf area index (LAI) and biomass respond to climate such that albedo and transpiration can be changed. The land model has an interactive carbon cycle with the default nitrogen cycle modified to be constant, following Koven *et al* (2015). The geographical cover of plant functional types, once specified, however, remains constant. Model simulations are conducted at a resolution of 1.9° latitude by 2.5° longitude and are run for 100 years. Climate and terrestrial variables (LAI, temperature, precipitation) reach equilibrium after approximately 20 years of model spin up. The spin up period is discarded, and we then analyze time series for the remaining 80 years. This stable 80 year time series can be thought of as equivalent to two 40 year ensemble members, each starting from a different initial condition roughly in equilibrium with the forcing. All runs are conducted using present day (year 2000) land use conditions; orbital conditions are set for the year 2000. Because this study focused only on biogeophysical effects of forest disturbance, atmospheric CO_2 concentrations were held fixed at 367 ppm.

We conducted 13 experiments and one control simulation. In each of the 13 experiments we simulated forest die-off for an ecoregion that corresponds to one of the domains of the US National Ecological Observatory Network (NEON) (table S1 available at stacks.iop.org/ERL/13/055014/mmedia). We simulated forest die-off by removing the forested area within the domain and replacing the forested area and bare ground with C3 grass (areas reported in table S1). Our experiments simulate forest loss in the 13 domains with the highest density of forest cover. We additionally excluded domains that have very small total area (e.g. Hawaii, Puerto Rico and South Florida) from both experiments and analysis. This resulted in experiments that represented forest loss in all domains except for the predominantly prairie domains and the two small tropical domains. The NEON domains themselves were defined statistically based on climate data and soil properties (Hargrove and Hoffman 2005) and are intended to sample across the covariance of climate, soils, ecology, and land-management practices (Schimel *et al* 2007).

Analysis methods

Our analysis focuses on the anomalous difference between each experiment and the control simulation, in which no forest die-off was implemented. In particular, we analyze changes in near-surface air temperature, gross primary production (GPP), precipitation, low cloud fraction, and the height of the 500 mb pressure surface in the atmosphere (a metric of column heating or cooling in the lower atmosphere, which indicates changes in atmospheric circulation patterns). We also look at changes in evapotranspiration and surface albedo. Grid cells are uniquely assigned to a single domain, and not shared between domains. Area weighted averages are reported for each domain, as well as for the entire US for all domains outside of the one in which forest was removed.

We tested the statistical significance of the impact of forest loss on a given variable by testing the difference between experiment and control run samples using a student's *t*-test; a *p* value less than or equal to 0.05 indicated significant difference from zero with 95% confidence. The degrees of freedom for the t-test were determined by assuming a lagged auto-correlation of 2 years or less for all variables, with 40 degrees of freedom for the 80 years of computed results (the first 20 simulation years are discarded as spin-up). We use best fit least-squares linear regression lines to show how some variables change relative to one another. We perform an Empirical Orthogonal Function (EOF) analysis (Bretherton *et al* 1992) on spatial fields from the 13 experiments to identify the common shared spatial patterns of atmospheric response. EOFs are essentially spatial principal components analysis that identify orthogonal geographical patterns (Modes) that explain the most variance across all 13 experiments simultaneously. The corresponding weighting coefficient (principal component) for each experiment describes how much variability each individual experiment shares with (i.e. projects onto) the common response modes. In this way we can identify the atmospheric and primary production patterns which are common across experiments.

Results

We identified ecoclimate teleconnections in our simulations of forest die-off that link the effect of forest loss from one domain to others. To illustrate this, we highlight the results from one of our 13 experiments where we implemented tree loss from mortality at the domain scale—in this case for the Pacific Southwest (PS, figure 1(*a*)), which has recently experienced the loss of more than 100 million trees (Asner *et al* 2016, Berner *et al* 2017, USDA 2017). Domain-scale tree loss led to changes in local (within same domain) surface properties and fluxes including albedo and evapotranspiration (figure 1(*b*)). These changes in surface properties modified local surface climate (e.g.
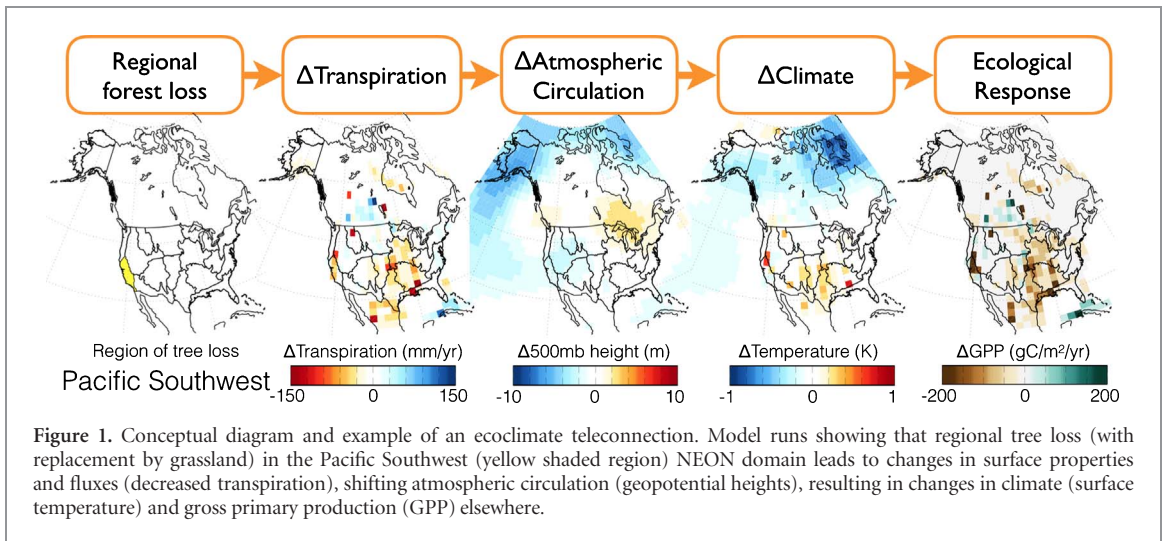
Figure 1. Conceptual diagram and example of an ecoclimate teleconnection. Model runs showing that regional tree loss (with replacement by grassland) in the Pacific Southwest (yellow shaded region) NEON domain leads to changes in surface properties and fluxes (decreased transpiration), shifting atmospheric circulation (geopotential heights), resulting in changes in climate (surface temperature) and gross primary production (GPP) elsewhere.
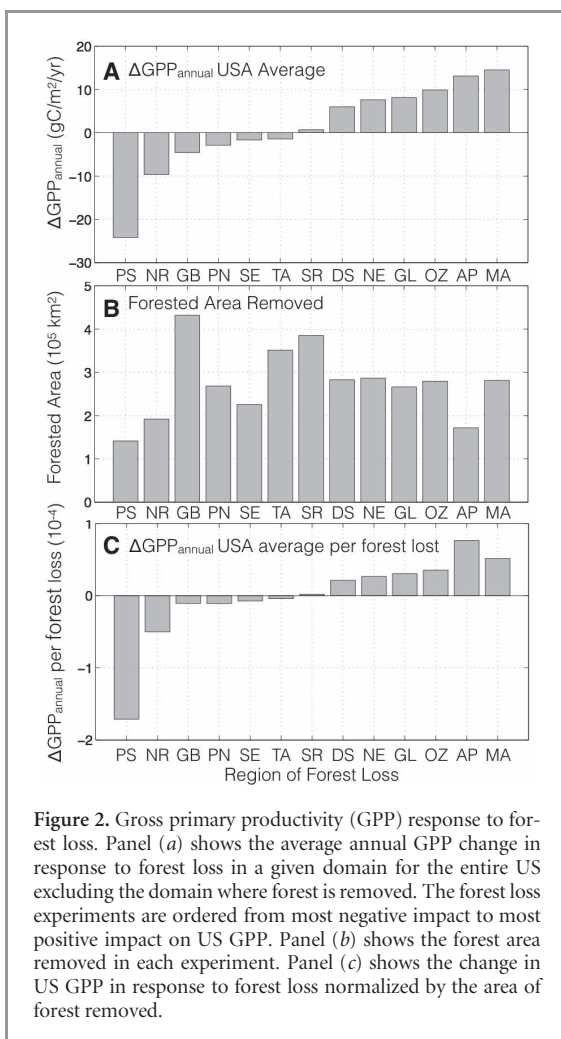

Figure 2. Gross primary productivity (GPP) response to forest loss. Panel (*a*) shows the average annual GPP change in response to forest loss in a given domain for the entire US excluding the domain where forest is removed. The forest loss experiments are ordered from most negative impact to most positive impact on US GPP. Panel (*b*) shows the forest area removed in each experiment. Panel (*c*) shows the change in US GPP in response to forest loss normalized by the area of forest removed.
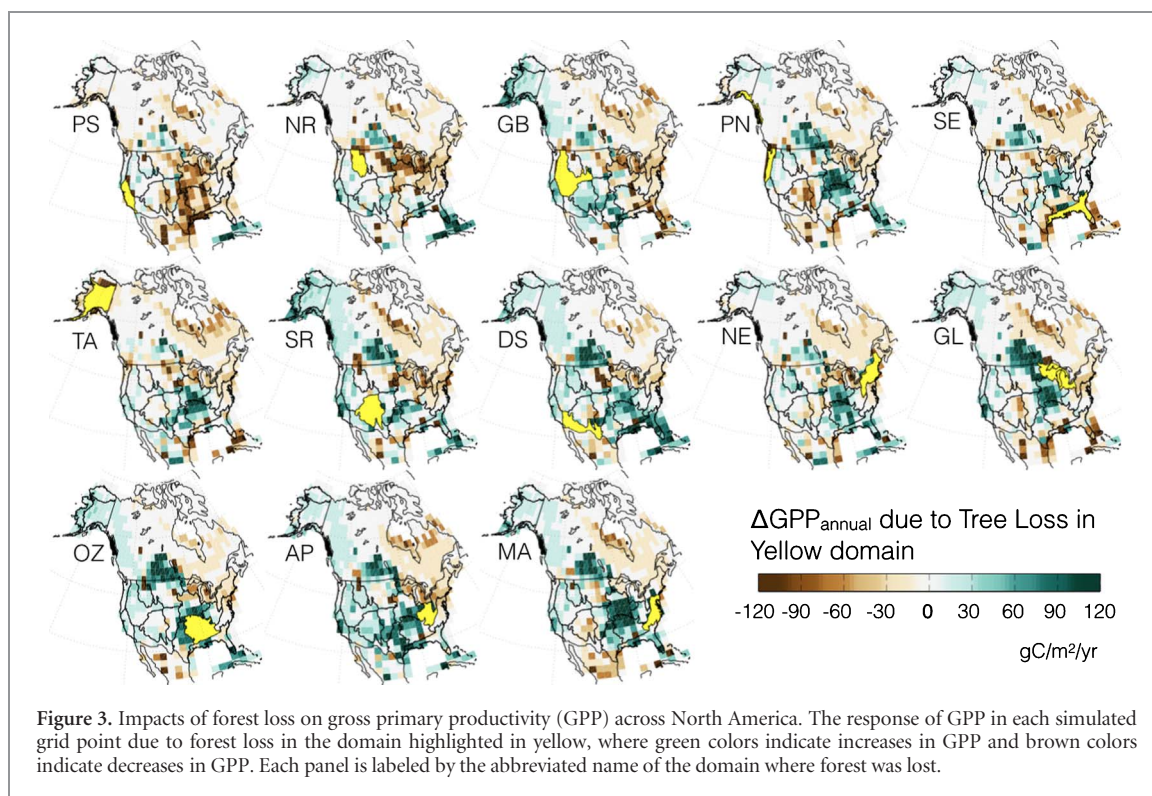
precipitation and temperature), as well as impacted atmospheric circulation (e.g. 500 mb height, figure 1(*c*)). The atmospheric circulation response connects the direct forcing of tree loss on the local atmosphere to other regions, impacting climate (figure 1(*d*)) and thus resulting in altered Gross Primary Productivity (GPP) across North America (figure 1(*e*)). We have shown the example for a single experiment (Pacific Southwest).

These patterns vary depending on where tree die-off is implemented as we discuss further below.

Response of GPP to forest loss
More generally we found that tree die-off in one domain affects GPP aggregated across the other domains of the US (figure 2(*a*)), with forest loss in some domains leading to large average declines (e.g. Pacific Southwest, PS), and some leading to moderately large average increases (e.g. Mid-Atlantic, MA). We would expect that the forcing of forest loss on the atmosphere, and thus the climate and large-scale GPP impact of forest loss from a given domain, would scale with the area of forest removed (figure 2(*b*)); however, this is not the case (figure 2(*c*)). In fact, the continental-scale GPP change per area of forest loss is far larger for some domains than others (figure 2(*c*))—suggesting that the location of these domains likely has a correspondingly large influence either through atmospheric feedbacks or changes in circulation.

In addition to differences in the average continental response, the response of GPP across North America to forest loss in our 13 experiments has spatial structure, often showing positive responses in some locations and negative responses in others (figure 3, table S2). Although the spatial pattern varies across experiments, there are common aspects. We used Empirical Orthogonal Function (EOF) analysis to assess commonalities in spatial patterns and found two dominant modes for the spatial pattern of GPP response across our 13 experiments. The first spatial mode had a positive GPP response along a relatively North-South axis following the Mississippi River and into central Canada and explained 34% of the variance in GPP across experiments (figure S1A). All 13 experiments correlate positively with this pattern, although some have higher weighting coefficients than others indicating a stronger correspondence. The second mode showed a more localized change in GPP centered over the Ozarks (OZ) domain and explained ~17% of the variance overall. Forest loss experiments which lead to an

Figure 3. Impacts of forest loss on gross primary productivity (GPP) across North America. The response of GPP in each simulated grid point due to forest loss in the domain highlighted in yellow, where green colors indicate increases in GPP and brown colors indicate decreases in GPP. Each panel is labeled by the abbreviated name of the domain where forest was lost.

overall positive response of GPP across the USA tend to have a positive correspondence to this mode (left columns in figure S1B), while experiments that lead to overall negative responses in continental-scale GPP tend to have a negative correspondence with this mode (right columns in figure S1B).

In addition to the impact of regional forest loss on climate and thus GPP across the continent, we found that some regions are more sensitive to remote tree loss regardless of where it occurred (figure 4, table S2). For example, the Great Lakes (GL) experienced a decrease in productivity in response to forest loss almost anywhere in the USA, while the Pacific Southwest (PS) experienced an increase in GPP in response to every experiment (figure 4). These consistent responses are likely due to similarities in the large-scale atmospheric response to forest loss in the US, revealed in part by EOF analysis. By contrast, the Ozarks (OZ) show increasing GPP in response to forest loss in some domains and decreasing GPP in response to forest loss in other domains suggesting that atmospheric responses are less uniform over this region (figure 4). Our set of experiments collectively provides information on how each domain could be impacted by forest loss in any of the forested domains (figure 5, tables S2–S4).
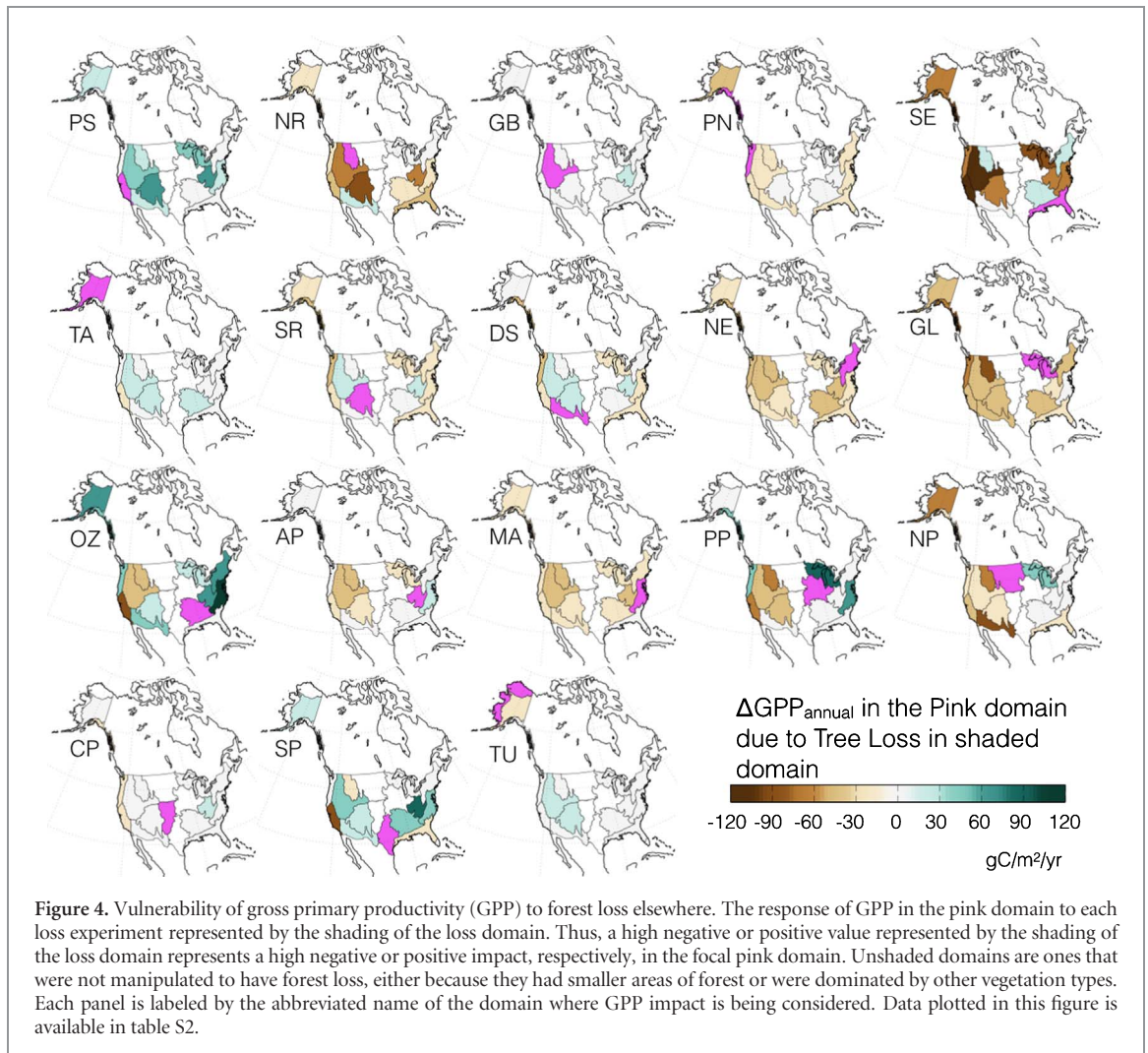
Photosynthesis is sensitive to environmental factors, and thus the proximate cause for changes in GPP is changes to local climate. Temperature at the surface, precipitation amount, and incoming sunlight are altered locally by forest cover change, and non-locally by changes communicated through the atmosphere due to forest change elsewhere. Thus, we can explain

the patterns of GPP change by the patterns of changes in photosynthetically relevant environmental variables triggered by forest loss. Forest loss leads to changes in summertime surface temperatures, precipitation, and low cloud cover across North America (figure 5, figures S2–S5, tables S2–S4). The dominant spatial mode patterns of all three variables shows similarity to the spatial pattern of GPP change (figure 5, figure S1). Cooler summertime temperatures lead to higher GPP, with the exception of Alaska where higher GPP is correlated with warmer summers (figure 5(*e*)). Higher amounts of summertime precipitation also leads to higher GPP in nearly every domain, suggesting that GPP is water limited across the USA (figure 5(*f*)). Furthermore, the 500 mb pressure surface EOF mode corresponded with a low pressure anomaly over the Western US that projects strongly onto all but two of the 13 experiments and explains 50% of the total variance across experiments (figure S1E).

Discussion

Atmospheric response to forest loss
Although the climate influence of very large-scale forest loss has been previously investigated (e.g. Garcia *et al* 2016), little has been known about the potential of forest loss at sub-continental scales to create significant impacts outside of their local climate. Our results thus provide strong model-based evidence that forest loss at regional scales—encompassing the scales of actual major forest losses—can create significant ecoclimate teleconnections to other regions.

Figure 4. Vulnerability of gross primary productivity (GPP) to forest loss elsewhere. The response of GPP in the pink domain to each loss experiment represented by the shading of the loss domain. Thus, a high negative or positive value represented by the shading of the loss domain represents a high negative or positive impact, respectively, in the focal pink domain. Unshaded domains are ones that were not manipulated to have forest loss, either because they had smaller areas of forest or were dominated by other vegetation types. Each panel is labeled by the abbreviated name of the domain where GPP impact is being considered. Data plotted in this figure is available in table S2.

The continental-scale GPP response to regional forest loss in different places in the US shows common patterns (figure 3, S1A, S1B). Given that the atmosphere must be responsible for communicating the forcing from forest loss in one location to the impacts in another, this commonality in pattern suggests that forest loss in many domains is forcing a similar atmospheric response. The atmosphere has preferred modes of variability, and so it would not be unexpected for there to be a similar pattern of response to forcing occurring in the same general region. For example, the spatial pattern of the first mode of 500 mb variability, which indicates changes to lower atmospheric heating and alterations in circulation explained half of the total variance across all 13 experiments (figure S1E). Thus, the atmosphere is responding to forcing from forest loss in North America with a very similar spatial pattern no matter where the forcing occurs, like a bell which rings with the same tone no matter where it is struck. The EOF analysis allowed us to go further in showing that not only are the climate responses at the surface similar, but the atmospheric circulation responses are also similar across experiments.

Forest loss impacts the atmosphere directly through changes in surface energy and momentum fluxes, which come about through changes in surface energy budget terms (latent heat, sensible heat, longwave radiation, and shortwave radiation). A change in tree cover is likely to change surface albedo (and thus shortwave energy absorption), latent heat fluxes through evapotranspiration, and sensible and longwave fluxes through changes in surface temperatures. Given that these direct impacts of forests on the atmosphere are the proximate cause for triggering atmospheric responses to forest loss, one might expect that the impact of forest loss should scale with area. However, across all of our experiments we find that continental-scale impact does not scale with area alone (figure 2(c)). Thus, in addition to the magnitude of forest loss, the location of forest loss plays an outsized role in determining the continental-scale impact. This is consistent with prior findings, where individual experiments may have specific mechanisms through which trees impact the atmosphere and ecosystems elsewhere (e.g. Garcia *et al* 2016), including significant impacts from atmospheric feedbacks and cloud responses (Laguë and Swann 2016). Given that atmospheric feedbacks play a central role in the response of climate to forest loss in the continental US, the importance of the location of forest loss could be due either to the sensitivity of the local atmosphere

Figure 5. Response of climate and gross primary productivity (GPP) to forest loss and response of GPP to local climate. The response of annual mean GPP (*a*), summertime near surface air temperature (*b*), and summertime precipitation (*c*) is shown for each domain listed on the *y*-axis due to forest loss in each domain listed on the *x*-axis. Domains are ordered from most overall negative impact on US GPP to most overall positive impact. Small white circles indicate that the change in a variable is considered significantly different from zero at 95% confidence. Panel D shows a map of domains labeled with their abbreviations. Panels E and F show the response of annual mean GPP to local changes in summertime near surface air temperature (*e*) and summertime precipitation (*f*). Data plotted in panels *A–C* is available in tables S2–S4.

in responding to surface forcing, or the sensitivity of larger-scale circulation to surface forcing in a particular location.

Constraints and caveats on predictions

Our investigation was limited in a few important ways, which stand as points for future transformations of the study of ecoclimate teleconnections. First, even extreme tree die-off events are unlikely to occur homo-

geneously within a domain as we implemented in our experiments. Nonetheless, our simulations provide important upper bounds for the degree to which a given domain is potentially sensitive to tree loss or is affected by tree loss in another domain; these initial estimates can be further refined with more detailed patterns of tree loss in future simulations. Second, as detailed in the Methods section, the NEON domains reflect neither climate alone nor vegetation alone, but

rather an intersection of the two. Therefore, our implementation of tree mortality strictly on a domain by a domain basis is unlikely to exactly match the boundaries of actual mortality events. Tree die-off may in some cases cross domain boundaries. However, given that NEON domains are reflective of intersections of climate and vegetation patterns, our estimates can be viewed as reasonable initial estimates within boundaries where major die-off events may occur (e.g. Breshears *et al* 2005, Moore *et al* 2016, Young *et al* 2017). In addition to providing general insights about potential modes of connectivity at regional-to-global scales, by implementing simulated experiments corresponding to NEON domains, we also begin developing a foundation for using NEON, in association with related networks (Peters *et al* 2008, Peters and Okin 2017), as a tool for testing predictions about specific ecoclimate teleconnections. Third, our simulations use a simplified representation of ocean circulation which does not represent long time scale ocean dynamics, and so will not capture any feedbacks driven by deep ocean circulation responding to forest changes. Our simulations are also limited in length, representing a compromise between simulations long enough to average over multi-decadal internal climate variability (Deser *et al* 2012, 2014, Kay *et al* 2015) yet still computationally achievable. Fourth, die-off may happen in more than one place at the same time and this can cause synergies or even teleconnected feedbacks. In these cases, the individual impacts of die-off from two different areas evaluated separately do not necessarily reveal the ecoclimate teleconnection impacts that can occur when die-off occurs in two regions simultaneously (Garcia *et al* 2016). Approaches for addressing these caveats in the future include conducting scenarios of tree die-off using case studies of recent events, including incomplete or partial die-offs (e.g. Breshears *et al* 2005, Moore *et al* 2016, Young *et al* 2017) testing simulations of forest loss via their components using data on microclimate change, atmospheric moisture trajectories, and vegetation responses in disparate locations to historical and ongoing vegetation change through the use of tree ring and other time-series or historical data.

Implications for carbon accounting

Notably, our results reveal the need to consider potential subcontinental-scale consequences of regional-scale tree die-off for coordination of carbon management across regions. Our findings point the way to new modes of carbon accounting and management, especially as confidence in the specific predicted spatiotemporal responses increases. First, the consequences of ecoclimate teleconnections such as we predict have important implications for accounting for carbon within a nation's or continent's carbon accounting. For example, an extreme die-off event in the Pacific Southwest domain (figure 1) affects the other NEON domains covering the US and therefore affects the US net carbon balance. International incentives for carbon sequestration through forest conservation currently ignore any potential for teleconnected effects (Jayachandran *et al* 2017, van der Gaast *et al* 2018). Second, the ecoclimate teleconnections we quantify reveal potential vulnerabilities in carbon storage of a given region to tree die-off in regions that are under other administrative control (e.g. die-off in the US could negatively affect Canada's or Mexico's net carbon budget; e.g. figure 3). We have focused this research on large-scale recent tree die-off events and the vulnerability of forests to rising temperatures, droughts, and other climate factors, however our results have relevance to other types of tree loss such as harvesting. For example, we found that a unit area of forest in the Pacific Southwest has a disproportionately large negative impact on GPP in several other domains (figure 3, figure 5, table S2) suggesting that Pacific Southwest forests might be a high conservation priority in addition to high GPP forests in general. While we do not yet have sufficient confidence in our specific predictions to advocate specific accounting and management actions at this time, our results provide high priority hypotheses that must be tested. Additionally, as confidence in them increases, their applicability to carbon accounting and management could be profound.

Conclusion

These results demonstrate the basic science of ecoclimate teleconnections by showing that forest loss in individual bioclimatic regions corresponding to NEON domains drives large-scale responses in atmospheric circulation. Through these atmospheric teleconnections, ecosystem changes in one region are able to influence the climate in remote regions across the US; these changes in remote climate in turn drive changes in GPP in regions far removed from the original vegetation change.

Notably, the continental-scale impact on GPP is not simply a function of the area of forest that is lost, and our findings demonstrate that the location of forest loss is of first order importance. It would be reasonable to expect that regional scale tree-loss may not cause climate impacts outside of the local area; however, we show here that forest loss even in small domains has an impact across the continent. Surprisingly, forest loss in the domain with the smallest area (the Pacific Southwest, PS, $279\,605\,\text{km}^2$) shows the largest continental-scale impact on GPP (figure 2(*a*)). This result is of particular relevance in light of forest mortality currently occurring in California where 100 million trees have died in the past few years following extreme drought (Asner *et al* 2016, Berner *et al* 2017, USDA 2017).

In addition to providing general insights about potential modes of connectivity at regional-to-global scales, by implementing simulated experiments corresponding to NEON domains, we also begin developing

a foundation for using NEON, in association with related networks (Peters *et al* 2008, Peters and Okin 2017), as a tool for testing predictions about specific ecoclimate teleconnections. The matrices we have developed (figures 5(*a*)–(*c*), figure S6, and tables S2–S5) specifically provide testable predictions for how broad-scale tree die-off in one NEON domain affect climate and vegetation in other domains. These of course need to be refined to reflect actual amounts of loss, but our predictions nonetheless provide initial insights on locations and magnitudes of potential ecoclimate teleconnections across NEON, where comparable data across the network can be complemented with such model simulation results to further evaluate continental scale connectivities.

In this context, the recent forest die off in the Western US may have broader concern than just local impacts and ecosystem services. This work suggests that remote impacts of the Western US die-offs are already being felt—as we expect that the last decade of forest die-off (Berner *et al* 2017) is reducing productivity of forests and croplands in the East. This critical hypothesis, that western forest loss could already be negatively impacting climate in eastern North America, must now be rigorously tested to advance understanding of ecoclimate teleconnections, carbon accounting, and economic connectivities across North America. However, the real-world climate system is noisy, and so detecting current ecoclimate teleconnections associated with forest loss in observational records is extremely challenging. Although actual tree loss to date has only covered a small fraction of any given domain, the collective tree loss in the Western US spans multiple domains, motivating future investigation of tree loss at finer scales and reflecting actual patterns of tree loss (e.g. Berner *et al* 2017). More generally, our work is the first to reveal that ecoclimate teleconnections associated with tree die-off in a warming word (as well as other types of tree loss) potentially impacts productivity across a continent (and beyond) even for tree loss from a small region, highlighting the need to further consider ecoclimate teleconnections as macrosystems biology develops to address continental-scale ecology.

Acknowledgments

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References

Adams H and Macalady A 2010 Climate induced tree mortality: Earth system consequences *Eos. Trans.* **91** 2009–10

Adams H D, Barron-Gafford G A, Minor R L, Gardea A A, Bentley L P, Law D J, Breshears D D, McDowell N G and Huxman T E 2017 Temperature response surfaces for mortality risk of tree species with future drought *Environ. Res. Lett.* **12** 115014

Allen C D, Breshears D D and McDowell N G 2015 On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene *Ecosphere* **6** 1–55

Allen C D *et al* 2010 A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests *Forest Ecol. Manage.* **259** 660–84

Anderegg W R L, Flint A, Huang C, Flint L, Berry J A, Davis F W, Sperry J S and Field C B 2015 Tree mortality predicted from drought-induced vascular damage *Nat. Geosci.* **8** 367–71

Asner G P, Brodrick P G, Anderson C B, Vaughn N, Knapp D E and Martin R E 2016 Progressive forest canopy water loss during the 2012–2015 California drought *Proc. Natl Acad. Sci.* **113** E249–55

Avissar R and Werth D 2005 Global hydroclimatological teleconnections resulting from tropical deforestation *J. Hydrometeorol.* **6** 134–45

Badger A M and Dirmeyer P A 2015 Climate response to Amazon forest replacement by heterogeneous crop cover *Hydrol. Earth Syst. Sci. Discuss.* **19** 879–910

Bala G, Caldeira K, Wickett M, Phillips T J, Lobell D B, Delire C and Mirin A 2007 Combined climate and carbon-cycle effects of large-scale deforestation *Proc. Natl Acad. Sci.* **104** 6550

Berner L T, Law B E, Meddens A J H and Hicke J A 2017 Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States (2003–2012) *Environ. Res. Lett.* **12** 065005

Bonan G B 2008 Forests and climate change: forcings, feedbacks, and the climate benefits of forests *Science* **320** 1444–9

Breshears D D *et al* 2005 Regional vegetation die-off in response to global-change-type drought *Proc. Natl Acad. Sci. USA* **102** 15144–8

Bretherton C S, Smith C and Wallace J M 1992 An Intercomparison of methods for finding coupled patterns in climate data *J. Clim.* **5** 541–60

Cobb R C *et al* 2017 Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models *Ecosphere* **8** e02034

Chen G-S, Notaro M, Liu Z and Liu Y 2012 Simulated local and remote biophysical effects of afforestation over the southeast united states in boreal summer *J. Clim.* **25** 4511–22

Collatz G J, Ball J T, Grivet C and Berry J A 1991 Physiological and environmental-regulation of stomatal conductance, photosynthesis and transpiration—a model that includes a laminar boundary-layer *Agric. Forest Meteorol.* **54** 107–36

Deser C, Phillips A, Bourdette V and Teng H 2012 Uncertainty in climate change projections: the role of internal variability *Clim. Dyn.* **38** 527–46

Deser C, Phillips A S, Alexander M A and Smoliak B V 2014 Projecting North American climate over the next 50 years: uncertainty due to internal variability *J. Clim.* **27** 2271–96

Devaraju N, Bala G and Modak A 2015 Effects of large-scale deforestation on precipitation in the monsoon regions: remote versus local effects *Proc. Natl Acad. Sci.* **112** 3257–62

Garcia E S, Swann A L S, Villegas J C, Breshears D D, Law D J, Saleska S R and Stark S C 2016 Synergistic ecoclimate teleconnections from forest loss in different regions structure global ecological responses *PLoS ONE* **11** e0165042

Hargrove W W and Hoffman F M 2005 Potential of multivariate quantitative methods for delineation and visualization of ecoregions *Environ. Manage.* **34** S39–S60

Horel J D and Wallace J M 1981 Planetary-scale atmospheric phenomena associated with the southern oscillation *Mon. Wea. Rev.* **109** 813–29

Hunke E C, Lipscomb W H, Turner A K, Jeffery N and Elliott S M 2010 CICE: the Los Alamos Sea Ice Model Documentation and Software User's Manual Version 4.1 LA-CC-06-012 *T-3 Fluid Dynamics Group, Los Alamos National Laboratory,* 675

IPCC 2014 Change 2014: synthesis report *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* ed R K Pachauri and L A Meyer (Geneva: IPCC) p 151

Jayachandran S, De Laat J, Lambin E F, Stanton C Y, Audy R and Thomas N E 2017 Cash for carbon: a randomized trial of payments for ecosystem services to reduce deforestation *Science* **357** 267–73

Kay J E *et al* 2015 The community earth system model (CESM) large ensemble project: a community resource for studying climate change in the presence of internal climate variability *Bull. Am. Meteorol. Soc.* **96** 1333–49

Koven C D, Chambers J Q, Georgiou K, Knox R, Negron-Juarez R, Riley W J, Arora V K, Brovkin V, Friedlingstein P and Jones C D 2015 Controls on terrestrial carbon feedbacks by productivity versus turnover in the CMIP5 Earth system models *Biogeosciences* **12** 5211–28

Laguë M M and Swann A L S 2016 Progressive midlatitude afforestation: impacts on clouds, global energy transport, and precipitation *J. Clim.* **29** 5561–73

McDowell N G *et al* 2016 Multi-scale predictions of massive conifer mortality due to chronic temperature rise *Nat. Clim. Change* **6** 295–300

Medvigy D, Walko R L, Otte M J and Avissar R 2013 Simulated Changes in Northwest US climate in response to Amazon deforestation *J. Clim.* **26** 9115–36

Moore G W, Edgar C B, Vogel J G, Washington-Allen R A, March R G and Zehnder R 2016 Tree mortality from an exceptional drought spanning mesic to semiarid ecoregions *Ecol. Appl.* **26** 602–11

Neale R B *et al* 2012 Description of the NCAR community atmosphere model (CAM 5.0) *NCAR Tech. Note NCAR/TN-486+STR* 289

Oleson K W *et al* 2013 Technical description of version 4.5 of the Community Land Model (CLM) *NCAR/TN-503+STR* 434

Peters D P C, Groffman P M, Nadelhoffer K J, Grimm N B, Collins S L, Michener W K and Huston M A 2008 Living in an increasingly connected world: a framework for continental-scale environmental science *Front. Ecol. Environ.* **6** 229–37

Peters D P C and Okin G S 2017 A toolkit for ecosystem ecologists in the time of big science *Ecosystems* **20** 259–66

Phillips O L *et al* 2009 Drought sensitivity of the Amazon rainforest *Science* **323** 1344–7

Raffa K F, Aukema B H, Bentz B J, Carroll A L, Hicke J A, Turner M G and Romme W H 2008 Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions *Bioscience* **58** 501–17

Schimel D, Hargrove W, Hoffman F and MacMahon J 2007 NEON: a hierarchically designed national ecological network *Front. Ecol. Environ.* **5** 59

Stark S C *et al* 2016 Toward accounting for ecoclimate teleconnections: intra- and inter-continental consequences of altered energy balance after vegetation change *Landsc. Ecol.* **31** 181–94

Swann A L S and Fung I Y 2012 Mid-latitude afforestation shifts general circulation and tropical precipitation *Proc. Natl Acad. Sci.* **109** 712–6

Trumbore S, Brando P, Hartmann H, Gauthier S, Bernier P, Kuuluvainen T, Shvidenko A Z and Schepaschenko D G 2015 Forest health and global change *Science* **349** 814–18

USDA Forest Service 2017 Tree Mortality Aerial Detection Survey Results (www.fs.usda.gov/detail/catreemortality/toolkit/ ?cid=FSEPRD565838)

van der Gaast W, Sikkema R and Vohrer M 2018 The contribution of forest carbon credit projects to addressing the climate change challenge *Clim. Policy* **18** 42–48

Williams A P *et al* 2013 Temperature as a potent driver of regional forest drought stress and tree mortality *Nat. Clim. Change* **3** 292–7

Young D J N, Stevens J T, Earles J M, Moore J, Ellis A, Jirka A L and Latimer A M 2017 Long-term climate and competition explain forest mortality patterns under extreme drought *Ecol. Lett.* **20** 78–86