ANALYSIS OF THE U.S. FOREST TOLERANCE PATTERNS DEPENDING ON CURRENT AND FUTURE TEMPERATURE AND PRECIPITATION

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Abstract— Forested ecosystems are shaped by climate, soil and biotic interactions, resulting in constrained spatial distribution of species and biomes. Tolerance traits of species determine their fundamental ecological niche, while biotic interactions narrow tree distributions to the realized niche. In particular, shade, drought and waterlogging tolerances have been well-characterized at the species level in the Northern hemisphere tree species. Species distribution models explore fundamental niches and current geographic distributions with respect to environmental factors, but their ability to capture and predict the community-level patterns is limited. Here, we analyze the Forest Inventory and Analysis Database and show that the tolerances of forest stands are directly linked with annual temperature, precipitations, and soil features in mainland USA. Using temperature and precipitation as two major predictors, we developed a model of tolerance distributions at forest patch-mosaic level, that we call the Tolerance Distribution Model (TDM). Using 17 climate change models from CMIP5, we delineate forested ecosystems vulnerable to drought, and we show that high elevation areas, and Midwest as well as Northeast US are at a high risk under future climate. We also predict changes of forest type over much of the land surface along the Southern and Western borders of the conterminous US. Our TDM provides a scaling of species tolerances to the community level and improves our understanding of how terrestrial ecosystems develop over large spatial scales shaped by climate. In particular, the direct connection we elucidate between temperature, precipitation and stand-level tolerances provides a new tool to quantitatively assess the impact of climatic changes in forested ecosystems.

INTRODUCTION

Understanding and predicting how forest distributions will respond to ongoing and anticipated climate change is a challenge with great ecological, economic, and cultural implications (Levin, 1999). It is well established that environmental stressors increase mortality of intolerant trees (e.g. Hanson and Weltzin, 2000, Lienard et al. 2015a). However, our ability to scale up individual plant traits such as growth/mortality characteristics to the ecosystem level has been limited due to ecosystem biocomplexity, including numerous non-linear functional relationships and feedback loops between different organisms (Strigul, 2012).

Although it is widely recognized that climate change will require a major spatial reorganization of forests on the landscape, our ability to predict what this will look like has been quite limited. Current modeling efforts to predict future distribution of forested ecosystems as a function of climate include species distribution models (for precise, local scale predictions) and potential vegetation climate envelope models (for coarse-grained, large scale predictions). In this work we bridge these approaches by considering an intermediate level of complexity, using stand-level tolerances.

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METHODS

The USDA Forest Inventory and Analysis database was used to compute the tolerance indices of current US forests. The connection between soil moisture and waterlogging tolerance was investigated using the FIADB and USFWS National Wetlands Database. Two independent databases were employed to link vegetation patterns and climate: Worldclim (using a spatial resolution of 30 seconds) and PRISM (using a spatial resolution of 800 meters). The 17 climate change models from CMIP5 were bias-corrected with a baseline extracted from the Worldclim dataset.

To establish the drought tolerance model, annual temperatures and precipitations occurring in forested plots were gridded into cells of 0.5 °C and 60 mm/month. To validate the model, we compared the drought tolerance index computed from the FIADB (i.e. current forest) with the model's predictions based on current temperature and precipitations. To extrapolate expected values of drought tolerance index to future climate, we computed the model's prediction over the conterminous US, with a spatial resolution of 30 seconds. We relied on projected climatic data using two representative concentration pathways adopted on the Fifth Assessment Report from the Intergovernmental Panel on Climate Change: moderate forcing (RCP4.5) and severe forcing (RCP8.5).

RESULTS

Shade, drought and waterlogging tolerance indices show distinct landscape level patterns (Fig. 1A), demonstrating that these stand-level indicators can effectively describe forests in the US (Lienard et al, 2015a, 2015b, Lienard and Strigul, 2015). Waterlogging tolerant plots are located mainly on hydric soils (Fig. 1B), along the Mississippi river or its tributaries, and along the Southwestern US coast (Fig. 1A). Spatial distributions of shade and drought tolerance were strongly correlated with mean annual temperature and precipitation (Fig. 1C-D), while waterlogging tolerance displayed no clear relationship with climate parameters except for demonstrating very low values when the mean annual temperature was higher than 20°C (Fig. 1E). The shade tolerance index demonstrated fully opposite climate response to the drought tolerance index (Fig. 1C-D), and good correlation with basal area (Fig. 1C,F).

We focused our modeling efforts on drought tolerance, for which the link with global warming impacts is straightforward and develop the drought TDM for the continental US. The TDM predicts forest drought tolerance as a function of temperature and precipitation (Fig. 1C). The drought TDM is able to reproduce the current overall drought tolerance patterns in the continental US (excluding wetland areas). In particular, a detailed inspection of drought tolerance patterns across geographical features shows that the model has a high accuracy, with the exception of the lower Mississippi river, which is the most noticeable wetland area. The TDM ignores history of stochastic disturbances associated with plots as it takes only climate variables as input. This results throughout the US in the prediction of smooth patterns compared to the realized drought tolerance. An analysis of errors further reveal a symmetric, non-skewed profile that follows an exponential decrease around the mean, consistent with a high predictive power of the TDM.

Because annual precipitation and the mean annual temperature are both expected to change over the coming century, we anticipate that the geographic distribution of drought tolerance will need to shift to accommodate this change. Projected climate trajectories for forested plots in climate space can be coupled with the drought tolerance model to provide the drought tolerance expected to be resilient to future projected conditions. Extrapolation of the model to future conditions using an ensemble of 17 climate models revealed a progression toward greater required drought tolerance. This progression was geographically ubiquitous and consistent across forcing scenarios (from RCP4.5 to RCP8.5). Furthermore, we identify a number of regions where major shifts in drought tolerance will be required. Northeastern US and Northern Great Plains are at high risk, as well as, to a lower extent, higher elevation areas in the Rocky mountains. Vulnerable forests are

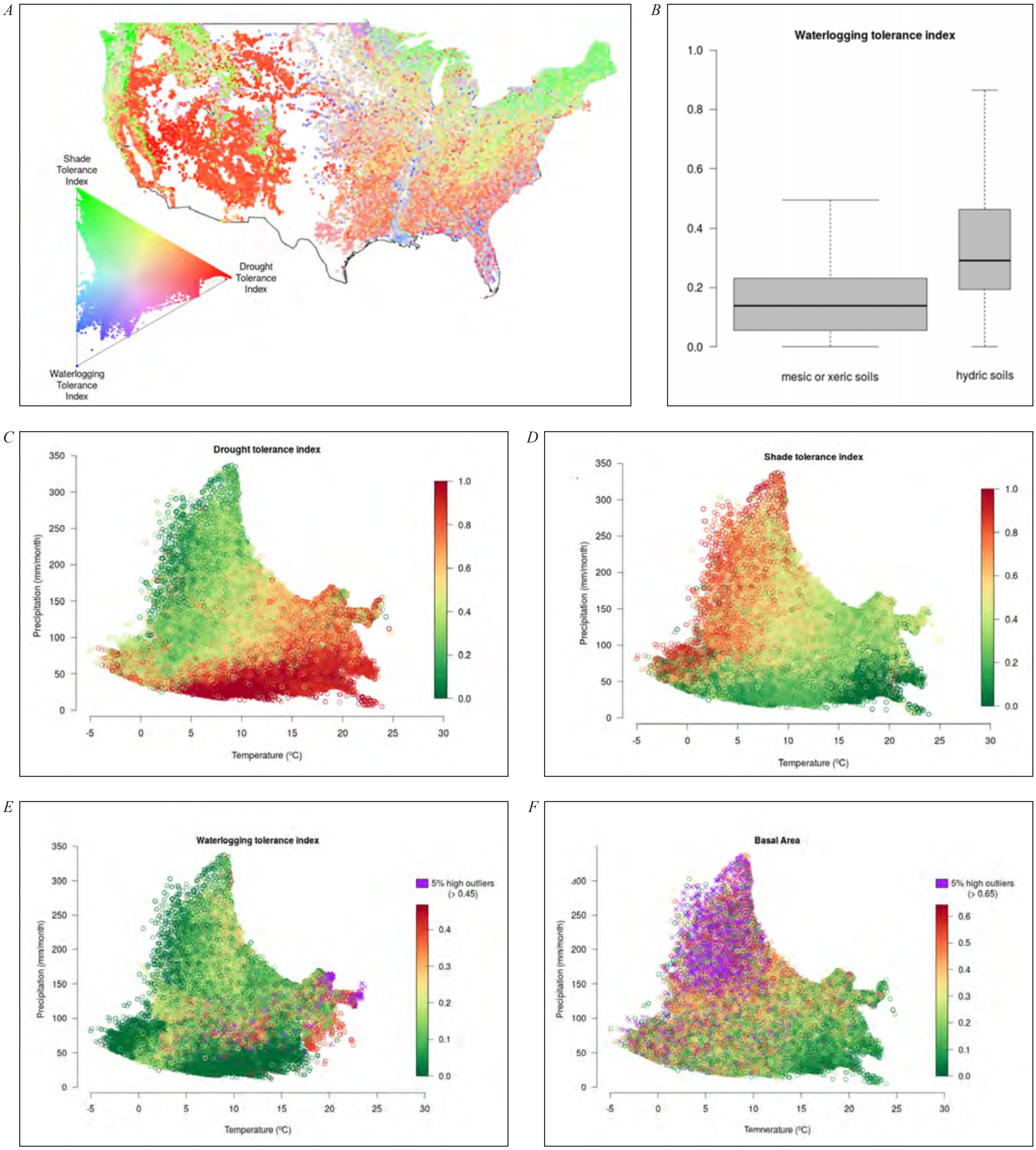

Figure 1—Overview of the tolerance indices in the conterminous US. A. Visualization of the tolerance index values in the US mapped onto the hue-saturation-value color space. In the color triangle key, plots where the shade tolerance (*respectively* drought tolerance and waterlogging tolerance) is high while all other tolerances are low are shown in green (*respectively* red and blue). Intermediate colors indicate plots with mixed tolerances (for example, yellow indicate plots resilient to both shade and drought). B. Waterlogging tolerance index as a function of soil moisture (boxplot widths are proportional to the number of plots, overall n=61,3275 total different locations are considered, two-tailed t-test is significant with $p<0.001$). C. to F., macroscopic variables describing forest stands plotted in the climatic system of mean annual temperature (x axis) and mean annual precipitation (y axis). The 5% high outliers for waterlogging tolerance index are represented by purple crosses.

overall evenly distributed in private, corporate, federal and state ownership. In the northeastern US, where the risks are the most pronounced, at-risk forest types include Maple/Beech/Birch, Spruce/Fir and White/Red/Jack Pine combination. Red pines (Pinus resinosa) and trembling aspens (Populus tremuloides), which are species with low to medium resistance to drought, have distributions overlapping the most vulnerable areas identified and are already considered to be endangered species. The predictions are robust with respect to the source of current climatic data (two databases used, Worldclim and PRISM) and to the climate change model choice (17 models considered).

DISCUSSION

One approach to predicting how vegetation distributions will change with climate is to associate certain biomes with certain climate envelopes (Olson et al., 2001) and assume that vegetation will migrate to fill potential vegetation niches. To a degree this approach is appealing as biome spatial distributions are strongly correlated with climatic variables, particularly temperature and precipitation (Olson et al., 2001). However, the discrete biome approach defines biomes into discrete entities at the landscape scale, which limits its ability to represent ecosystem transitions across space and time (Moncrieff et al., 2015). Alternatively, Species Distribution Models, SDMs also have been employed to study how plant communities respond to climate, albeit generally to examine plant presence or absence across environmental gradients, most often at small scales (Elith and Graham, 2009). The well-known shortcoming of SDMs is that they ignore biocomplexity and species interaction effects. In fact, species distributions depend not only on climatic factors, but also on biotic interactions within plant communities, disturbances and dispersal (Elith and Graham, 2009). Furthermore, upscaling the SDM approach is not possible as it requires too many predictors to model the large number of species present at continental or global scales (e.g. 38 environmental variables are used to predict the distribution of 134 tree species across Eastern USA in Iverson et al., 2008). Although the TDM approach provides a new insight over climate envelope models and SDMs, it shares a limitation with those models, which is an inability to predict rate of vegetation changes. Despite this limitation, the presented work substantially extends available tools for potential vegetation mapping as it offers a simple mechanistic explanation on how climatic variables affect landscape scale vegetation patterns.

LITERATURE CITED

Elith, J. and Graham, C. H. (2009) Do they? how do they? why do they differ? on finding reasons for differing performances of species distribution models. Ecography. 32:66–77.

Hanson P.J., Weltzin J.F. (2000) Drought disturbance from climate change: response of United States forests. Sci. Total Environ. 262:205–220.

Iverson, L.R., Prasad, A.M., Matthews, S.N., and Peters, M. (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manage. 254: 390-406.

Levin, S. A. (1999) Fragile Dominion: Complexity and the Commons. Perseus Publishing, Cambridge, MA.

Lienard, J., & Strigul, N. (2015). Linking forest shade tolerance and soil moisture in North America. *Ecological Indicators*, *58*, 332-334.

Lienard, J., Florescu, I., and Strigul, N. (2015a) An appraisal of the classic forest succession paradigm with the shade tolerance index. PLoS ONE. 10(2):e0117138 (2015).

Lienard, J. F., Gravel, D., & Strigul, N. S. (2015b). Data-intensive modeling of forest dynamics. *Environmental Modelling & Software*, *67*, 138-148.

Moncrieff, G.R., Hickler, T., and Higgins, S.I. (2015) Intercontinental divergence in the climate envelope of major plant biomes. Glob. Ecol. Biogeogr. 24:324–334.

Olson, D.M. et al. (2001) Terrestrial ecoregions of the world: A new map of life on earth a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience. 51:933–938.

Strigul, N. (2012). Individual-based models and scaling methods for ecological forestry: implications of tree phenotypic plasticity. In Garcia, J. and Casero, J., editors, Sustainable Forest Management, pages 359–384. InTech, Rijeka, Croatia.