Trait velocities reveal that mortality has driven widespread coordinated shifts in forest hydraulic trait composition

Anna T. Trugman1,2*, Leander D. L. Anderegg3, John D. Shaw4, and William R. L. Anderegg5*

1Department of Geography, University of California, Santa Barbara, CA 93106; 2Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106; 3Department of Integrative Biology, University of California, Berkeley, CA 94720; 4Rocky Mountain Research Station, US Forest Service, Ogden, UT 84401; and 5School of Biological Sciences, University of Utah, Salt Lake City, UT 84112

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Understanding the driving mechanisms behind existing patterns of vegetation hydraulic traits and community trait diversity is critical for advancing predictions of the terrestrial carbon cycle because hydraulic traits affect both ecosystem and Earth system responses to changing water availability. Here, we leverage an extensive trait database and a long-term continental forest plot network to map changes in community trait distributions and quantify “trait velocities” (the rate of change in community-weighted traits) for different regions and different forest types across the United States from 2000 to the present. We show that diversity in hydraulic traits and photosynthetic characteristics is more related to local water availability than overall species diversity. Finally, we find evidence for coordinated shifts toward communities with more drought-tolerant traits driven by tree mortality, but the magnitude of responses differs depending on forest type. The hydraulic trait distribution maps provide a publicly available platform to fundamentally advance understanding of community trait change in response to climate change and predictive abilities of mechanistic vegetation models.

Significance

Tree hydraulic traits determine plant water use and tree vulnerability to drought stress thereby affecting forest productivity and the movement of water between the land surface and the atmosphere. Here, we leverage an extensive trait database and a long-term continental forest plot network to map changes in the hydraulic traits of tree communities across the United States. We find evidence for shifts toward communities with more drought-tolerant traits driven by tree mortality. This trait compositional change may buffer forest productivity and water fluxes in the near term from the effects of climate change.


The authors declare no competing interest.

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Data deposition: Gridded trait maps are publicly available at Figshare, https://doi.org/10.6084/m9.figshare.11962710.

1To whom correspondence may be addressed. Email: att@ucsb.edu.

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Results and Discussion
We quantified spatial patterns in three hydraulic traits and one photosynthetic trait that collectively represent metrics of species’ hydraulic efficiency and safety (2, 28, 33). Specifically, we considered water potential at which 50% of stem xylem conductivity is lost (P50), hydraulic safety margin (HSM), or the difference between the P50 and the minimum stem water potential typically experienced, xylem conductivity per area of leaves distal to the measured xylem segment (Kx), and maximum photosynthetic rate (A_max) (Fig. 1). We calculated community-weighted mean trait values based on high-resolution species distribution and abundance data from the FIA (approximately one plot for every 2,428 ha of land). We found that photosynthetic and hydraulic traits varied substantially depending on regional climatic and edaphic factors. Trait spatial patterns revealed drought-tolerant traits throughout water-limited regions: strongly negative community-weighted P50 values in juniper (Juniperus species) monocultures in central Texas and piñon (Pinus edulis)–juniper woodlands in the Mountain West region of the United States co-occurring with large HSMs (red and dark orange in Fig. 1A and dark blue Fig. 1B). A notable exception to this high HSM pattern in water-limited systems is that of velvet mesquite (Prosopis velutina)-dominated woodlands in the Mountain West region of the United States co-occurring with large HSMs (red and dark orange in Fig. 1A and dark blue Fig. 1B). A notable exception to this high HSM pattern in water-limited systems is that of velvet mesquite (Prosopis velutina)-dominated woodlands in the Mountain West region of the United States co-occurring with large HSMs (red and dark orange in Fig. 1A and dark blue Fig. 1B).

We further analyzed our trait maps to quantify changes in community-weighted P50 and HSM, two traits shown to be predictive of cross-species drought mortality patterns (26, 27). Since FIA plots are typically too small to capture topographic detail, we hypothesize that both spatial and temporal heterogeneities facilitate the co-occurrence of different physiological strategies (37). However, since FIA plots are typically too small to capture topographic variation (and Fig. 2 shows only within-plot α diversity), temporal heterogeneity (climate seasonality) may be particularly important.

We calculated differences between the community-weighted P50 and HSM from the initial to the final FIA censuses divided by the length of the census period to quantify the trait velocity (trait

Fig. 1. Hydraulic and photosynthetic traits vary substantially across the continental United States. Spatial variations in community-weighted (A) water potential at which 50% of stem xylem conductivity is lost (P50), (B) HSM, or the difference between the minimum stem water potential typically experienced and the P50, (C) xylem conductivity per total area of leaves distal to the measured xylem segment (Kx), and (D) maximum photosynthetic rate (A_max). White space indicates nonforested regions or regions where trait coverage was less than 80% by stand basal area.
change per year) in a given community and diagnosed the underlying drivers of trait change. We first examined if there were significant shifts in P50 and HSM and if changes depended on forest type (angiosperm- versus gymnosperm-dominated). We found strong evidence for a significant decrease in the inventory mean P50, driven predominantly by decreases in P50 in gymnosperm forests (SI Appendix, Table S1). Additionally, we found some evidence for a significant increase in the inventory mean HSM in all forests for one data filtering method and for angiosperm forests with multiple data filtering methods (SI Appendix, Table S1). Trait velocities of P50 and HSM are consistent with selection for more drought-tolerant communities.

We next quantified and diagnosed the P50 and HSM trait velocities over the past two decades by relating the rate of change in P50 and HSM (in MPa y\(^{-1}\)) to mortality rates (basal area in m\(^2\) ha\(^{-1}\) y\(^{-1}\)) and year of final census in the FIA. We found significant decreases in P50 and increases in HSM in most regions and forest types were associated with local mortality rates (Fig. 3 A–C). Interestingly, we found evidence for significant decreases in P50 and increases in HSM in gymnosperm-dominated and western forests with measurement year, with larger changes in stands censused more recently, which could be indicative of an acceleration in the rate of change in P50 and HSM (39, 40) (SI Appendix, Table S2 and Methods).

We further examined the regional climatic drivers associated with changes in community-weighted P50 and HSM using the Terra-Climate dataset (32, 41, 42). Of the environmental drivers tested (see Methods), we found that CWD was most predictive of both changes in P50 and HSM over the past two decades (Fig. 3 D and E and SI Appendix, Table S3). Specifically, regions with a higher growing season CWD (higher aridity) experienced significant shifts over the past two decades toward community-weighted P50s that are more negative and significant shifts toward community-weighted HSMs that are larger (e.g., more drought-tolerant communities). Although broad trends existed across forest types and geographic regions, some interesting differences were apparent. For example, gymnosperm-dominated forests and forests in the western United States exhibited significant shifts toward more negative P50 and larger HSMs with increased CWD, whereas this trend was not apparent in less water-limited eastern forests (Fig. 3 D and E).

Significant decreases in P50 and increases in HSM associated with mortality were robust, even when species known to be suffering nonclimate related mortality due to pests/pathogens, or declines related to fire suppression were excluded from the analysis. We performed sensitivity tests where we examined the trait velocity-mortality relationship while excluding, in turn, P. edulis (piñon pine) and Pinus contorta (lodgepole pine), which suffered from bark beetle mortality, Quercus alba and Quercus rubra (white and red oak), which have been reported to suffer mortality resulting from due to long-term fire suppression (43), Tsuga canadensis (eastern hemlock), which has suffered mortality due to wooly adelgid, and Fraxinus pennsylvanica and Fraxinus americana (green and white ash), which have been attacked by the emerald ash borer, and found no significant change between the rate of change in P50 and HSM relative to mortality rates (SI Appendix, Table S2). Although our analysis does not preclude other drivers from influencing forest demographic rates and traits, it indicates that climate and water availability are important drivers. Given that traits have changed more in dry places (with higher CWD), and that trait changes are associated with nonspecific mortality, our results indicate that climate-driven mortality (either proximately or through interactions with pest outbreaks, see refs. 44–46) is likely behind these trait shifts. Indeed, a similar relationship between community drought tolerance and water limitation has been observed even in the wetter eastern forests of the United States after accounting for confounding factors, such as forest age and anthropogenic harvesting (47). We cannot rule out nonclimatic factors, such as rising CO\(_2\), invasive pests, and legacies of fire suppression. However, if nonclimate factors are the main drivers of P50 and HSM trait velocities, they, at least, appear to be making US forests more drought tolerant.

Finally, we found that changes in HSM and P50 were coordinated, regardless of forest type such that forests with a decrease in community-weighted P50 also often saw an increase in HSM (Fig. 4 and SI Appendix, Table S4). Given that HSM is defined as the difference between the P50 and the minimum stem water potential typically experienced, coordinated shifts in community mean HSM and P50 are indicative that minimum stem water potential tends to decrease proportionally with P50. Globally, P50 and HSM are only partially correlated across
species ($\rho = -0.54$ across 577 species in the XFT database with measures of both traits), meaning that increased drought tolerance (P50) and increased relative safety (HSM) do not necessarily go hand in hand. However, among dominant North American forest tree species, there is a strong correlation between P50 and HSM ($\rho = -0.78$ across 55 species with measures of both traits), which, no doubt, drives the coordinated shifts in community mean P50 and HSM found here. Persistent changes toward more negative community-weighted P50s and larger community-weighted HSMs have important implications for the resilience of US forest communities in coming decades. P50 is indicative of the amount of hydraulic stress a tree can sustain before suffering hydraulic damage, so communities with more negative P50s are expected to be more resilient to increased routine water stress. Communities with larger HSMs may additionally be more able to withstand increased variability in water stress because of a larger buffer between the expected seasonal water stress and the amount of stress that induces costly and potentially lethal hydraulic damage. Coordination between HSM and P50 trait velocities indicates that forests may be more able to withstand both a more stressful mean climate and increased climate variability and/or extremes.

While our results quantify trait velocities associated with shifts in species composition documented in forest inventory plots, we note that substantial intraspecific variation in plant traits exists (48–50) and could be important to include in future regional trait distribution estimates. We hypothesize that the mechanisms driving intraspecific variation in traits, such as trait plasticity and/or genetic variation have the potential to further buffer ecosystems to novel climate conditions on top of changes in species composition. Furthermore, HSM can be a challenging trait to quantify because the minimum water potential measurement (used in the calculation of HSM) is influenced by individual study context and design, such as whether annual or interannual minimum water potentials were reported and the severity of water limitation during the period over which measurements were collected. In our analysis, we were limited to the definition used by the database compilers who define HSM as “the difference between the P50 and the minimum stem water potential observed for a species” (51) rather than the difference between the P50 and the minimum stem water potential during a period of extreme water limitation as would occur during a drought. Thus, interpretation of HSM results, particularly, between the eastern and the western US forests, should be performed with caution.

Fig. 3. Shifts in community trait composition toward more drought-resistant forests are associated with mortality and aridity but differ substantially depending on region and forest type. (Top) Schematic of the mechanisms resulting in shifts in community weighted mean (CWM) trait composition and the subsequent trait velocities including trait change through selective recruitment and growth or through selective mortality of trees with particular traits (A). Different colors represent different species with distinct trait values. (Middle) Response coefficient between forest basal area mortality and community-weighted changes (final minus initial inventory divided by inventory interval length) in key drought tolerance traits including (B) water potential at which 50% of stem xylem conductivity is lost (P50) and (C) HSM for the inventory as a whole (Total), angiosperm forest types (Angio), gymnosperm forest types (Gymno), the eastern United States (East), and the western United States (West). (Bottom) Standardized response coefficients between climatic water deficit (CWD) and community-weighted changes (final inventory minus initial inventory) in (D) P50 and (E) HSM. CWD is calculated for mean growing season (May–August) for the inventory interval. For B–E, grouped points are response coefficient estimates using different data gap filling and outlier screening methods (see Methods). Similar forest types are grouped by color, error bars show 95% confidence intervals, and associated significance levels are in SI Appendix, Tables S2 and S3.
caution because long-term trends indicate a stronger intensification in water limitation in the western United States compared to the eastern United States over the past several decades (52), potentially resulting in a systematic bias in HSM estimates.

With this analysis, we developed open source trait maps that can serve as a platform for mechanistic vegetation models to improve geographic trait distributions for the continental United States (53). Furthermore, we provide quantitative evidence for coordinated changes in community-weighted mean P50 and HSM across the United States over the past two decades, indicating that forest communities have experienced compositional shifts toward more drought-tolerant ecosystems since 2000. We found that these shifts were larger in drier regions and were associated with tree mortality. The concept of trait introduced in this analysis has utility beyond quantifying the degree to which functional change has occurred in a given community. Trait velocities have the potential to mechanistically link communities’ “trait space” with the prediction of forest mortality risk by identifying mismatches in the rate of community trait adaptation and the rate of climate change (54). Through the use of trait velocities and plant hydraulic trait maps in hydraulically enabled trait-based vegetation models, it should now be possible to rigorously partition the relative importance of ecology (i.e., shifts in species composition and the impact on community hydraulic traits) versus environment (changes in mean climate and climate variability) on the terrestrial carbon cycle. Such partitioning could inform both future conservation efforts as well as climate change adaptation and mitigation strategies.

**Methods**

**Forest Inventory and Analysis Data.** We used the US Forest Service FIA long-term permanent plot network to generate high-resolution hydraulic and photosynthetic trait maps for the continental United States based on species composition and abundance and to document and diagnose the evolution of trait distributions across the United States from 2000 (when FIA protocols were standardized nationwide) to the present. The FIA plots are set up on a stratified systematic sampling design using a hexagonal cell grid (55). The network contains >160,000 permanent plots sampling forests where tree status (living/dead) is measured on a plot return interval that varies by state, typically, every 5 to 10 y. Within plots, different condition classes can be mapped and recorded separately, representing different land cover class types, size classes, or other distinguishing characteristics. In our analysis, we excluded plot-condition groupings with fire damage, human damage, or other treatments so that we could isolate the effects of climate on the dynamics of community trait compositions. Given that condition classes with a small plot fraction can overinflate forest basal area, we examined a plot of forest basal area as a function of condition class plot fraction and found that a forest condition class threshold >30% of an individual plot’s area was the minimum threshold that filtered large basal area anomalies. Thus, we required a forest condition class to occupy >30% of a given plot’s area to be included in the analysis.

**Maps of Community-Weighted Trait Distributions and Trait Diversity.** We calculated community-weighted mean trait values, community trait range, and quantified decadal-scale changes in community-weight traits between the final and the initial inventory census by pairing plot-level species basal area abundance derived from the FIA with plant hydraulic and photosynthetic trait data from the XFT database (30). Plant hydraulic traits included the water potential at 50% loss of hydraulic conductivity (P50), HSM, and xylem conductivity per area of leaves distal to the measured xylem segment (Ks). We mapped hydraulic traits in conjunction with maximum photosynthetic rate (Amax; μmol m⁻² s⁻¹). For species with multiple trait observations within the XFT (SI Appendix, Fig. S2), we computed species’ means and included a number of sensitivity analyses to account for method uncertainties in hydraulic trait measurements (see below). This methodology neglects intraspecific variation due to environment or tree life stage (48–50). While maps based on species mean values will not capture the full spectrum of hydraulic and photosynthetic trait variabilities, they offer considerable added information above basic species composition and provide an important platform for understanding how and why traits vary across space and time. Furthermore, it has been shown that species-level averages are predictive of plant performance during and after drought (2, 3).

In our analysis, we included several measurement screening criteria for data quality control in the XFT, data gap filling techniques, and to address ongoing uncertainties in the plant hydraulics literature related to measuring P50 (56). For the majority of analyses of P50, the calculation of HSM, and phylogenetic imputing (described below), we performed the following additional quality control on the data available in the XFT. We i) only used P50s derived from branches (no petioles, leaves, or roots) and ii) filtered for strongly R-shaped vulnerability curves (where we excluded P50 measurements –0.75 MPa, measurements with HSM <–2 MPa, and any measurements where gravitational effects due to tree height were within 0.5 MPa of P50). We refer to this, subsequently, as our “base-version trait dataset.” Additionally, we performed a separate analysis on a conservative end-member estimate of P50 measurements where we strictly selected for sigmoidal vulnerability curves to avoid any artifacts associated with long-veseled species (57) resulted in coverage of only 91 species. We refer to this, subsequently, as the “strict quality control version.” Finally, given the evidence for a considerable phylogenetic signal in many plant traits (58, 59), we developed a separate trait dataset where we phylogenetically imputed missing traits based on genus means for genera with more than two measured species to increase trait coverage. Subsequently, we refer to this version as the “phylogenetically imputed trait dataset.” As a slightly more conservative imputation, we removed imputed values in genera with the top 25% highest within-genus CVs for each trait (SD was used for HSM), under
the assumption that these genera likely showed the least phylogenetic signal useful for trait imputation. Results were qualitatively identical when using imputed traits for the FIA dataset. We also observed the range (min and max) in species mean and trait values for each location with adequate trait coverage. Summary of trait data coverage for each trait are included in Supplementary Table S5.

In all statistical analyses, except where noted, we independently analyzed our base-version trait dataset, the phylogenetically imputed version, and, for P50 only, the strict quality control version. In all cases, only plots locations with trait coverage of at least 80% by basal area in the initial census were included in the analyses so as to not bias results due to poor species coverage. Our results are robust to these different levels of quality control and inventory coverage (Supplementary Table S5 and Table S2).

Sensitivity of Community Traits to Climate and Demographic Drivers. Given that HSM and P50 have been shown to be key traits for predicting species mortality risk and productivity during periods of water limitation (2, 3), we further analyzed the change in community traits over the duration of the inventory period. We calculated the change in community-weighted mean P50 and HSM between the first and the last plot census to get ΔP50 and ΔHSM and looked at trait sensitivities for the inventory across the entire United States as well as by forest type (angiosperm versus gymnosperm) and geographic location (eastern versus western United States). To categorize plots as angiosperm-dominated or gymnosperm-dominated, we used the FIA “field type code” variable. Eastern and western plots were divided by state with the dividing line running west of Minnesota to Louisiana. Finally, we performed a series of sensitivity tests to see if factors other than climate, such as pest, pathogen, or anthropogenic fire suppression, were major drivers of tree mortality by excluding plots dominated by species known to be associated with these factors. Specifically, plots dominated by P. edulis (pinion pine), P. ponderosa (limber pine), Q. albida (white and red oak), T. canadensis (eastern hemlock), and F. pennsylvanica and F. americana (green and white ash) were excluded each, in turn, based on the plot FIA field type code. Collectively, these sensitivity tests help unmask if known species suffering from severe bark beetle outbreaks (pines), potential oak mortality due to long-term fire suppression (43), mortality due to wooly adelgid (hemlock), and mortality due to the emerald ash borer are driving significant relationships between HSM/P50 and mortality.

First, we looked for significant shifts in population mean trait distributions in P50 and HSM between the first and the last inventory using the Wilcoxon signed-rank test (given the lack of normality in trait distributions). Next, to analyze trait responses to climate, we used climate variables from the TerraClimate dataset (32), which includes a number of climate metrics from 1956 to 2018 at a monthly time step and 4-km spatial resolution globally. We initially used the CRCLIM dataset (32), which includes a number of climate metrics from 1956 to 2018 at a monthly time step and 4-km spatial resolution globally. We initially used the CRCLIM dataset (32), which includes a number of climate metrics from 1956 to 2018 at a monthly time step and 4-km spatial resolution globally. We initially used the CRCLIM dataset (32), which includes a number of climate metrics from 1956 to 2018 at a monthly time step and 4-km spatial resolution globally. We initially used the CRCLIM dataset (32), which includes a number of climate metrics from 1956 to 2018 at a monthly time step and 4-km spatial resolution globally. We initially used the CRCLIM dataset (32), which includes a number of climate metrics from 1956 to 2018 at a monthly time step and 4-km spatial resolution globally. We initially used the CRCLIM dataset (32), which includes a number of climate metrics from 1956 to 2018 at a monthly time step and 4-km spatial resolution globally.

Given the large sample size of FIA plots and the consensus that symmetric overdispersion does not tend to bias parameter estimates, only significance tests, we provide two estimates of response coefficient magnitude and significance for each dataset version, one estimate including the entire dataset, and one where we excluded outliers (identified as points with residuals >2σ from the mean). This methodology resulted in six estimates for response coefficients for P50 and four estimates for HSM. Coefficient estimates from each technique are grouped in Fig. 3 and recorded in Table S4.

Data and Code Availability. All forest inventory plot data are publicly available at the US Forest Service’s FIA program website https://www.fia.fs.fed.us/. Gridred trait maps are publicly available at Figshare (DOI: 10.6084/m9. figshare.11962710).

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