Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe

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Drought-induced tree mortality has been observed globally and is expected to increase under climate change scenarios, with large potential consequences for the terrestrial carbon sink. Predicting mortality across species is crucial for assessing the effects of climate extremes on forest community biodiversity, composition, and carbon sequestration. However, the physiological traits associated with elevated risk of mortality in diverse ecosystems remain unknown, although these traits could greatly improve understanding and prediction of tree mortality in forests. We performed a meta-analysis on species' mortality rates across 475 species from 33 studies around the globe to assess which traits determine a species' mortality risk. We found that species-specific mortality anomalies from community mortality rate in a given drought were associated with plant hydraulic traits. Across all species, mortality was best predicted by a low hydraulic safety margin—the difference between typical minimum xylem water potential and that causing xylem dysfunction—and xylem vulnerability to embolism. Angiosperms and gymnosperms experienced roughly equal mortality risks. Our results provide broad support for the hypothesis that hydraulic traits capture key mechanisms determining tree death and highlight that physiological traits can improve vegetation model prediction of tree mortality during climate extremes.

meta-analysis | climate change | carbon cycle | climate extremes | biodiversity

Forests assimilate and sequester ~2.4 Pg carbon per year (1), equivalent to 25% of anthropogenic emissions, and provide manifold goods and services to society (2). Climate extremes, such as severe drought, could trigger abrupt and irreversible changes in Earth's forests (3, 4), which would have profound implications for their biodiversity, ecosystem services, and carbon storage (5). Episodes of widespread tree mortality in response to drought and/or heat stress have been observed across the globe in the past few decades (4). In addition, drought severity and frequency are projected to increase with temperature-driven rises in evaporative demand (6). There is fundamental concern that increased climate-induced mortality of trees (7) could offset carbon sinks currently yielded in old growth and regrowth forests alike (8).

Predicting plant demographic rates, such as mortality, using physiological traits is a central aim of ecology with critical importance for modeling climate change impacts and the carbon cycle (9). Drought-induced tree mortality has been particularly challenging to model and predict because of uncertainty in traits and mechanisms underlying the physiology of tree death (10, 11). Despite this uncertainty (12, 13), the failure of the plant vascular hydraulic transport system is considered to be a central pathway to mortality (7, 14–17). This failure happens through embolism of a tree's water transport elements by air bubbles during high xylem tensions induced by low soil moisture and/or high atmospheric evaporative demand during drought (14–16). The point at which individual species experience high levels of embolism is determined by a suite of plant hydraulic, allometric, and stomatal traits. Identifying which unique plant traits predict mortality in diverse plant communities will be crucial toward unraveling the mechanisms of mortality and incorporating them into Earth system models to improve predictions of forests in a rapidly changing climate (11, 12).

We performed a meta-analysis of published studies that documented cross-species patterns in tree mortality in mixed forests, where multiple species coexist, after a severe drought and examined whether drought-related physiological traits can explain species' tree mortality anomalies. We analyzed 33 studies that observed tree mortality linked to drought and heat stress spanning >760,000 individual trees and 475 species across a range of biomes, including tropical rainforest, temperate deciduous and evergreen forests, boreal forests, and savanna woodlands (Fig. 1). For each study, we compiled the mortality rates for individual species after severe drought and calculated the species-specific deviations—which we term "mortality anomalies"—from the mean community-averaged tree mortality rate at each site (Fig. S1). For each species, we collected a number of physiological traits that have been hypothesized as important to predicting mortality from global trait databases (18, 19), analyzing both absolute trait values and relative values to the ecological community at each site. Specifically, we examined (*i*) wood density, (*ii*) maximum branch stem hydraulic conductivity, (*iii*) the water potentials at which 50% and 88% of hydraulic conductivity is lost because of embolism (P50 and P88, respectively), (*iv*) the hydraulic safety margin (HSM) between the typical minimum xylem water potential and P50 or P88, (*v*) the water potential at leaf turgor loss point, (*vi*) the water potential at

Significance

Predicting the impacts of climate extremes on plant communities is a central challenge in ecology. Physiological traits may improve prediction of drought impacts on forests globally. We perform a meta-analysis across 33 studies that span all forested biomes and find that, among the examined traits, hydraulic traits explain cross-species patterns in mortality from drought. Gymnosperm and angiosperm mortality was associated with different hydraulic traits, giving insight into the relative weights of different traits and mechanisms in mortality prediction. Our results provide a foundation for more mechanistic predictions of drought-induced tree mortality across Earth's diverse forests.

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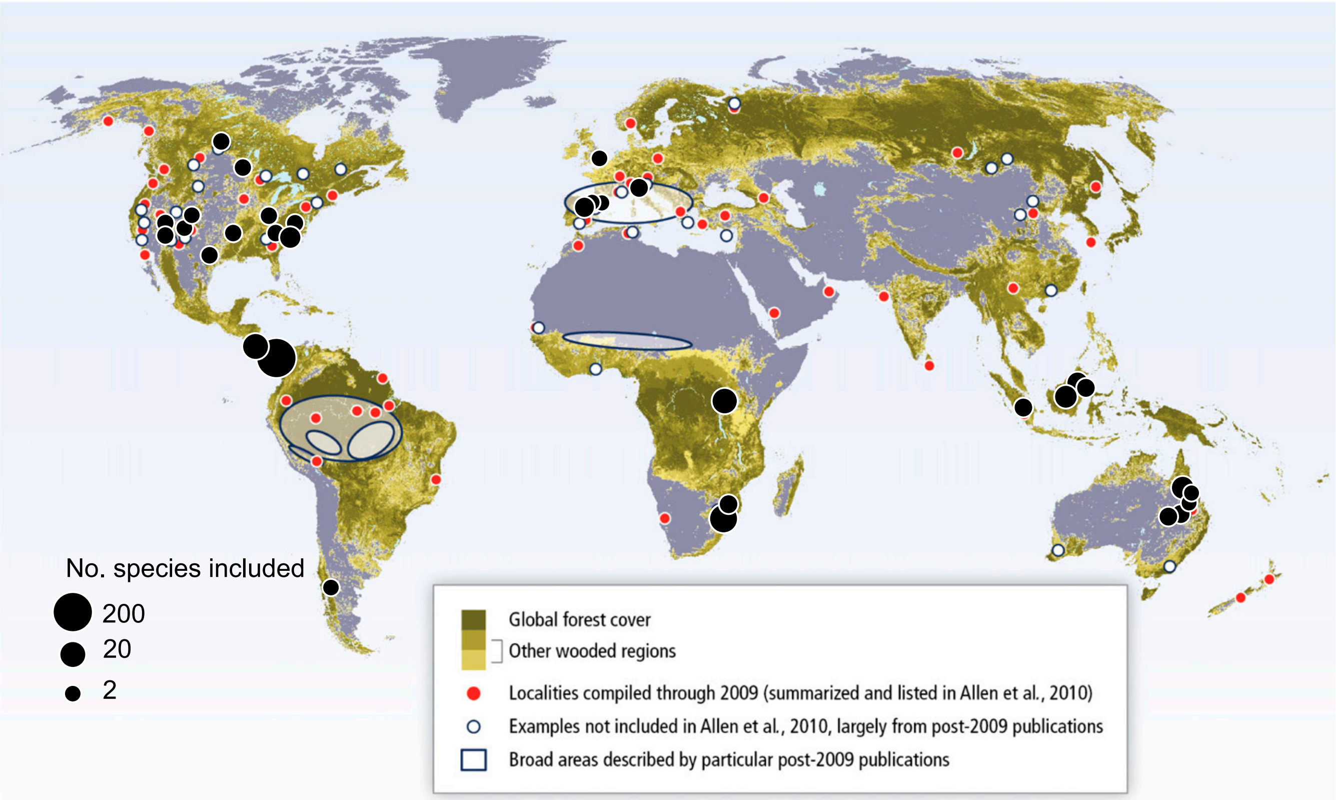

Fig. 1. Drought- and heat-induced regional tree mortality events around the world. Black dots indicate the cross-species mortality rates examined here, with dot size proportional to the number of species reported (n = 475 unique species). Red dots indicate pre-2009 mortality studies synthesized in the work by Allen et al. (4); white dots indicate the updated studies presented in ref. 73, and polygons are broad regions described by post-2009 studies.

50% stomatal closure, (*vii*) maximum rooting depth, (*viii*) wood anatomy category (coniferous, diffuse-porous, or ring-porous xylem), (*ix*) angiosperm–gymnosperm, and (*x*) evergreen–deciduous leaf habit. We used multilevel mixed effects models, weighting mortality anomalies by study precision and including study as a random effect to account for site and drought characteristics, to examine which physiological traits influence which species will succumb to drought.

Results and Discussion

We found that the HSM from P50, P50 itself, and P88 were the only significant predictors of cross-species patterns of mortality anomalies across all species combined ($p_{\mathrm{HSM50}} = 0.01$; $p_{\mathrm{P50}} = 0.04$; $p_{\mathrm{P88}} = 0.048$) (Fig. 2 and Table S1). A tree's HSM integrates the "safety" of xylem to drought-induced embolism and some elements of stomatal response to leaf water potential, thereby capturing a number of key components in a plant's integrated drought response (16, 18). Our results provide support for the hypothesis that the HSM is likely to be one of the most useful traits in predicting tree mortality across species within individual ecosystems. Critically, a global synthesis found that species' HSMs were relatively small across a wide range of biomes (18), indicating vulnerability to drought, and our results tie this vulnerability directly to risk of mortality and extend the importance of HSMs in predicting relative vulnerability within communities. Species with less negative (closer to zero) P50 values, on average, experienced higher rates of mortality, consistent with the link of this trait to drought tolerance. Other hydraulic traits, including native branch conductivity, the water potential at leaf turgor loss point, and wood density, were not associated with cross-species patterns in mortality across all species (Fig. 2 and Table S1). Furthermore, maximum documented rooting depth and stomatal traits alone were not associated with cross-species patterns in mortality (Fig. 2). Although these traits are known to strongly influence certain species' abilities to tolerate drought (15, 20), they did not capture the strong species variation in responses within given communities, possibly because species-level mean trait values might miss intraspecific trait variation present at a given site.

Across all studies, angiosperms and gymnosperms were equally likely to die during a given drought (Fig. 2). We observed a moderate increase in mortality anomalies for diffuse-porous angiosperms, although only statistically significant in some cases (Table S1), and no difference in mortality anomalies between deciduous and evergreen species (Fig. 2). We found no support for the recently published predictions based on a very simple model using a steady-state equation of water transport (21), including that there should be higher mortality in gymnosperms, species with low specific hydraulic conductivity, or species with conservative stomatal responses. In our view, that model did not capture observed mortality patterns for at least three reasons. First, equations for water transport assuming constant conductivity are not likely to be applicable during severe drought. Second, that model's assumption that low stomatal conductance will hasten mortality was problematic, because the opposite may, in fact, be true if stomatal closure increases the HSM (18), and third, we contend that models of mortality need to account for species' or plant functional types' differences in resistance to drought-induced embolism, such as P50 (22).

The specific hydraulic traits determining mortality anomalies differed across major plant lineages. Thus, considering angiosperms and gymnosperms separately showed that the HSM influenced mortality anomalies of gymnosperms but not angiosperms (Fig. 3). By contrast, low wood density was a significant predictor of mortality anomalies in angiosperms but not gymnosperms (Fig. 3). These different explanatory variables may be because of fundamentally different wood anatomy in

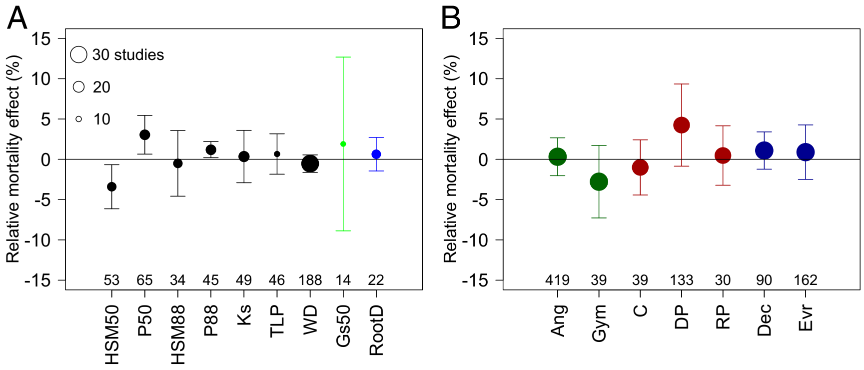

Fig. 2. Hydraulic traits predict mortality anomalies among species. (*A*) Effect size across all studies of change in mortality anomaly per unit change in *z* value of the predictive trait: hydraulic safety margin (HSM) from P50, P50, HSM from P88, P88, specific branch conductivity (Ks), water potential at leaf turgor loss point (TLP), wood density (WD), water potential at 50% of maximal stomatal conductance (Gs50), and maximum documented rooting depth (RootD). (*B*) Effect size across all studies of change in mortality anomaly per unit change in *z* value of the predictive category: angiosperm (Ang), gymnosperm (Gym), conifer wood type (C), diffuse porous wood type (DP), ring porous wood type (RP), deciduous leaf habit (Dec), and evergreen leaf habit (Evr). Mortality anomaly (*y* axis) refers to the species-specific deviation in percentage of mortality (typically number of stems per year) relative to the mean community-averaged mortality in the same drought event. Thus, a negative anomaly of 5% indicates that a 1-SD increase in trait *x* in species *i* leads to a 5% lower mortality rate of species *i* relative to the plant community. Error bars are 95% confidence intervals. Colors highlight different groupings of traits. Numbers below indicate the number of species included.

angiosperms and gymnosperms, with the latter generally having more negative P50 values, more conservative stomatal responses, and larger HSMs (18, 23). The importance of HSM in gymnosperms suggests a critical role of stomatal response in gymnosperms for maintaining xylem water potentials above damaging levels. By contrast, wood density may be a valuable proxy for mortality risk among angiosperms in particular; as has been observed previously in tropical biomes (24), it provides general tolerance of stresses, likely because of correlations with other traits not captured here, such as defense traits and the ability to regrow xylem after embolism (25).

The contrasting importance of HSM and wood density in gymnosperms and angiosperms, respectively, is also consistent with other divergent aspects of their hydraulic architecture and life history. Thus, the relatively narrow, "safe" tracheids of the gymnosperm conducting system are thought to be unable to recover from water potentials close to their P50 values because of their limited amount of parenchyma in wood and their monopodial growth; conifers rarely show resprouting and refilling, and may have lethal water potentials around P50 (23, 26, 27). Angiosperms, however, are, on average, more susceptible to embolism (less negative P50 values and narrow safety margins), may quickly lose conductivity at relatively low levels of water stress, and are more likely to be able to recover from drought because of the potential for embolism refilling, resprouting from branch nodes below dead segmented tissues, and regrowth from a sympodial architecture. The higher amount of parenchyma in angiosperm wood (tissue fractions around 20–30%) could be linked to their higher storage capacity (e.g., for water and nonstructural carbohydrates), symplastic connectivity, and positive root pressure but also, various mechanisms related to defense and resilience to disturbance (23). The differential trait influences on mortality in angiosperms and gymnosperms may help guide mortality algorithms across plant functional types, because angiosperms and gymnosperms are often simulated as different plant functional types in global vegetation models.

Improved understanding of cross-species mortality patterns during drought will be critical to predicting the impacts of climate change on biodiverse ecosystems and whether drought could drive shifts in dominant tree species. Despite much recent research advancing our understanding, we still cannot predict which species will live or die in a given drought based on first principles. Our results highlight which traits and species' attributes were associated with mortality across a range of studies, but the proportion of explained variation was modest. The multitrait hydraulic statistical model explained ~27% of the variance in mortality rates (Fig. S2). Within studies of individual ecosystems with fewer potential confounding factors, however, the predictive power of the HSM has explained much higher amounts of variation in some cases ($R^2 = 0.73$) (16). Some of the unexplained variation may be caused by our inability to include topoedaphic and plant community effects as well as other potentially useful traits because of lack of data. In particular, it would be valuable to examine the level and utility of carbon reserves during drought, which were related to mortality in some studies (28, 29) but not in others (14, 30). Currently, however, enormous methodological uncertainty with nonstructural carbohydrates measurements prohibits cross-study comparison (31). Although most of our analyses focused on species' relative mortality anomalies compared with the overall community mortality rate within a study, drought intensity was marginally significantly correlated with overall absolute mortality rate within a study ($F = 3.17$; df = 30; $P = 0.08$) (Fig. S3).

Interactions of drought effects with biotic agents and their feedbacks can also significantly change the demographic patterns of tree mortality, especially in cases where pathogens are host-specific. Although we examined only studies that identified drought as a critical driver of observed mortality rates, biotic agents were reported as present in 8% of species analyzed. In cases where major roles of biotic agents have been noted, such as in bark beetle attacks during drought in western North America, physiological traits concerning tree defenses, such as resin duct size and density, may be crucial to incorporate (32) as well as the effects of climate on insect populations.

Tree species drought responses are often affected by multiple and interacting traits (11, 12, 15). Although several of our traits, such as HSM, synthesize complex drought responses that involve integration of stomatal and hydraulic responses and although we analyzed the predictive capability of a multiple hydraulic trait model (Fig. S2), limited data overlap among traits necessitated conducting most of our meta-analyses on single-trait models, which are an oversimplification of drought responses. Several of the studies included here account for such interactions between traits and complex mortality mechanisms at a local scale and they corroborate our findings of the importance of the same hydraulic traits in these local events (14–16). Tree mortality studies at the global scale have been so far descriptive (4) or theoretical (20); thus, our approach shows the importance of synthesizing cross-species mortality rates of mature trees in situ, and it provides

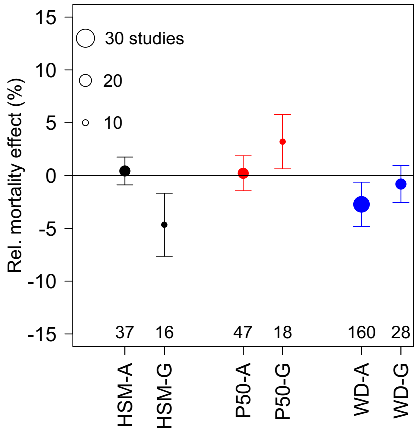

Fig. 3. Hydraulic traits' influence on mortality differs between gymnosperms and angiosperms. Effect size across all studies of change in mortality anomalies per unit change in *z* value of the predictive trait in gymnosperms (G) and angiosperms (A) as a function of HSM, P50, and wood density (WD). Mortality anomaly (*y* axis) refers to the species-specific deviation in percentage of mortality (typically number of stems per year) relative to the mean community-averaged mortality in the same drought event. Thus, a negative anomaly of 5% indicates that a 1-SD increase in trait *x* in species *i* leads to a 5% lower mortality rate of species *i* relative to the plant community. Error bars are 95% confidence intervals. Numbers below indicate the number of species included. Rel., relative.

insights into how and why trees die in drought-affected forests across the globe and which species are at higher risk than others.

Our meta-analysis indicates that hydraulic traits are a promising avenue for modeling mortality and lend additional support to hydraulic mechanisms mediating die off. Simulations of the dynamics of plant water transport, conductivity, and drought-induced embolism are now possible at regional scales (7), although model validation is crucial and must also be conducted regionally, and appropriate validation datasets are relatively sparse. More measurements of rooting, stomatal, and defense traits during drought-induced mortality events will improve our understanding of how coordinated trait syndromes and their plasticity can influence demographic outcomes during climate extremes. Our study paves the way for multispecies prediction of drought impacts and better understanding of how climate change will alter Earth's forests in the 21st century.

Methods

We performed a two-pronged search of the drought and tree mortality literature. First, we drew on references presented in several extensive peer-reviewed syntheses in the past 5 y that aimed to comprehensively document studies that reported drought-induced tree mortality at a regional scale (4, 8). Because these studies include literature up through 2015 and were global in nature, they likely include most of the available literature. We considered all references in these studies that met the criteria below. As a second prong, we performed multiple Google Scholar and Web of Science searches using permutations of keywords drought, forest, tree mortality, vegetation, and dieback. To be included in the meta-analysis, the study had to (*i*) present mortality rates, with drought having been attributed as a prominent or the dominant driver; (*ii*) indicate that no other major disturbance (e.g., fire or harvest) had occurred that could drive mortality; and (*iii*) present mortality rates for more than one species or genus. These searches led to the identification of 33 studies (15, 16, 33–63) that spanned 475 unique species and covered all vegetated continents (Fig. 1 and Table S2). Three studies presented mortality rates only at the genus level, and thus, we included those studies only for angiosperm–gymnosperm comparisons (Table S2). Although attribution of mortality to drought is not always straightforward, we included only studies that stated or showed that drought had driven elevated mortality rates of at least some species in the study. In our sample of studies, 31 of 33 studies focused on a single specific drought event, suggesting higher confidence that drought was the dominant signal in these studies. We ran all analyses below with the full 33 studies and this subset of 31 studies, and all results were robust to which group was analyzed.

We compiled trait data for each species from the peer-reviewed literature and climate data for each study's location or geographic centroid if the study spanned a larger region. Hydraulic and stomatal traits came from recent cross-species syntheses (18, 19, 64, 65). P50 and P88 are defined as the water potentials at which a given species loses 50% and 88%, respectively, of hydraulic conductivity in a given tissue, and all of our analyses used stem measurements. We use the definition of HSM proposed in ref. 18, which is the minimum water potential observed in a given species minus either the P50 or P88 value. Wood density is commonly defined as the dry weight per unit volume of wet wood. Wood density was drawn from the Global Wood Density Database (66) and averaged where multiple values were present per species. Maximum rooting depth came from the TRY database (67). Use of global trait values for a given species at specific sites or regions presents challenges, and thus, we used the study-specific trait values for species, where they were presented in the original studies, to improve accuracy. The agreement of our findings about the central role of hydraulic traits in predicting cross-species mortality patterns with those of detailed site-specific studies across multiple biomes that measured traits on trees at those sites (15, 16, 68) indicates that our approach is reasonable. To estimate a common metric of drought stress across studies, we downloaded monthly precipitation data from 1901 to 2013 from the University of East Anglia Climatic Research Unit (CRU) dataset (69) and calculated the *z* scores of precipitation anomaly during the reported drought years in each study for each study's geographic location. We used the most negative precipitation anomaly observed during a 5-y window around the mortality-inciting drought year reported by the study, making sure that no part of this window occurred after the study publication date, as a metric of drought intensity for each study.

We calculated the mortality anomaly of species *i* in study *j* as the difference between the reported mortality rate of that species and the whole community-averaged mortality rate in the study (Fig. S1). This metric provides a simple and robust "effect size" for meta-analysis that encapsulates the relative risk of mortality that each species experienced during the drought in that plant community. The advantage of this approach is that it can provide a comparable metric across studies and also, account for "site effects" that differ across studies (Fig. S1). Mortality rates were typically reported as the annualized percentages of mortality (percentages of stems per year) during or immediately after the drought. We included only mortality rates for mature trees (typically diameter at breast height > 10 cm), and where mortality information was reported for multiple size classes, we used mortality rates for only the largest size class. We included only species that had >10 individuals, and the median number of individuals per species was 109. Following other recent rigorous meta-analyses (19), we constructed single-trait statistical models with linear mixed effects models that included study identity as a random effect. Mixed effects models were performed using the lmer function in the lme4 (70) package in R. Per standard meta-analysis methods, weighted species by the study's measurement precision were quantified as log(*N* individuals of species *i*), because SDs or SEs were not presented in almost all studies, and precision should be proportional to the number of individuals in a species, with a log required because of a log-normal distribution of abundances across species. Including study identity as a random effect allows the slope and intercept to vary within each study, thereby explicitly accounting for differences in drought and site characteristics and their impacts across studies.

To compare effect sizes among traits, we normalized trait values to *z* scores relative to all species. As an alternate approach, we normalized traits within each study (thus, relative mortality could be compared with relative trait values within a plant community) and found that this approach yielded nearly identical results. Number of individuals per species was not available for a small number of studies ($n = 5$ studies), and those species were assigned the median number of individuals per species ($n = 109$ individuals) across all other studies. Weighting had relatively little effect on models (Table S1), and thus, we present unweighted values in Figs. 2 and 3 and both sets of values in Table S1. *P* values for fixed effects of traits were calculated using the Kenward–Roger approximation. In some models, data were transformed by arctangent and cube root transformations to meet assumptions of normality. To assess angiosperm–gymnosperm differences, we performed hydraulic trait models on subsetted data of either angiosperms or gymnosperms using the same procedures as above. We did not, however, test all traits against angiosperms and gymnosperms separately because of sample size limitations. Thus, in the separate angiosperm and gymnosperm analyses, we tested only the HSM from P50, P50, and wood density traits, which had enough sample size to make inferences and were suggested as important in the all-species analyses.

To assess the combined predictive capability of the three main hydraulic traits (HSM from P50, P50, and wood density), we used random forest regression, which avoids any problems with predictor variable colinearity, and included study identity and angiosperm–gymnosperm as covariates. The random forest algorithm produces multiple "trees," with each tree based off of a subset of the data and predictor variables. The final "forest" is a combination of these model trees, with the percentage variance explained based off of out of bag predictions. We compared predicted values vs. observed mortality data to generate an estimate of the proportion of variance explained by hydraulic traits. We did not examine other combinations of traits, because relatively limited overlap of other (nonhydraulic) trait datasets would have led to low sample sizes, such that the models could not be fit reliably. Ultimately, species drought responses, of course, are a function of a large number of traits and their interactions, and thus, more drought trait data will be needed across a broader breadth of species to test multitrait models in the future. All statistical analyses were conducted in R (71) using the lme4 (70) and randomForest (72) packages.

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Supporting Information

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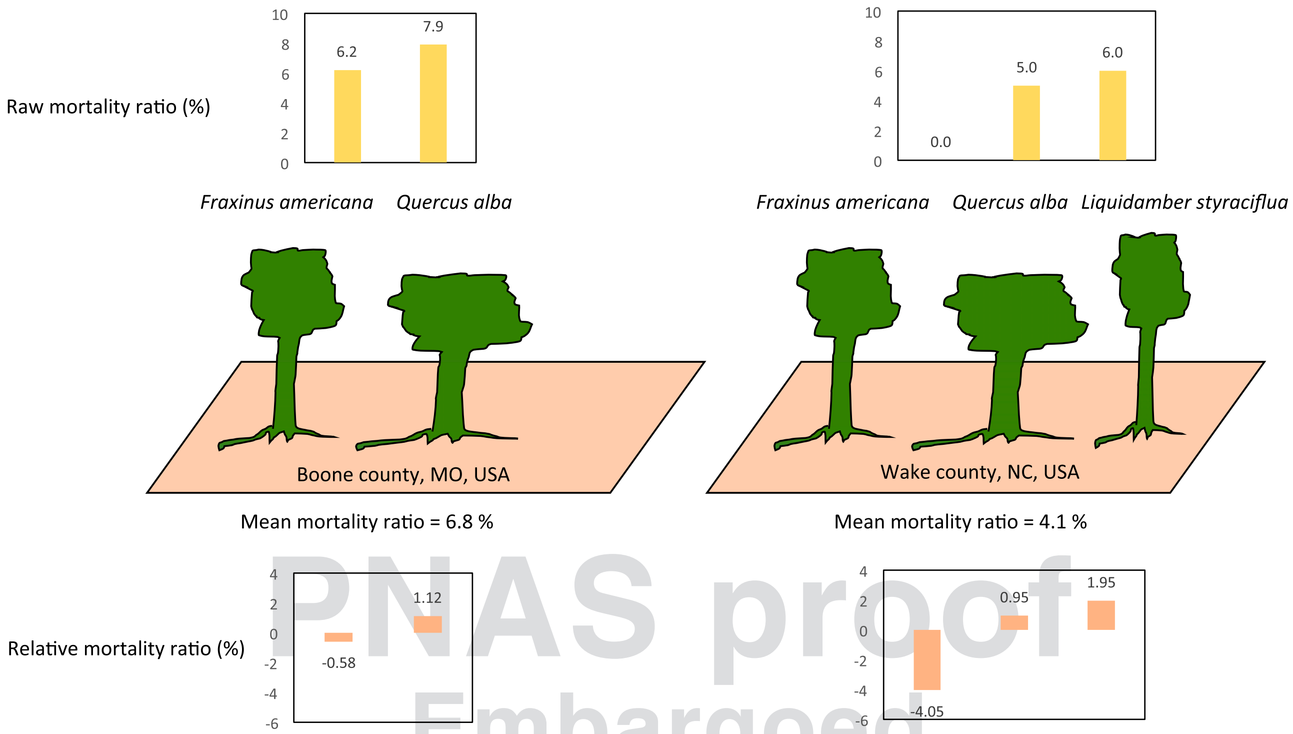

Fig. S1. Two examples of the relative mortality anomaly approach. Raw species-specific mortality anomalies depend on local site conditions and species composition. This approach derives species-specific anomalies from the local mean mortality and hence, aims to neutralize these site effects. In turn, this approach allows for cross-site comparison and correlations with species trait data. Here, *Quercus alba* had higher drought-related mortality in Missouri than in North Carolina, but considering the generally higher mortality after the Missouri drought and the contrasting effects on coexisting species, its relative mortality ratio was similar across sites (around 1% above the local mean). Missouri and North Carolina data were adapted from Gu et al. (54) and Hoffmann et al. (15), respectively.

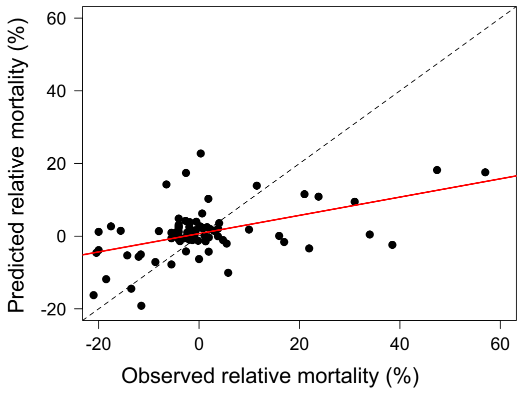

Fig. S2. Hydraulic traits predict relative mortality risk. Predicted mortality of the combined model of HSM, water potential at 50% conductivity loss, and wood density (including angiosperm–gymnosperm and study identification as random effects) vs. observed model. The red line is the best fit for predicted vs. observed ($F = 28.84$; df = 84; $P < 0.0001$), and the black line is the 1–1 line.

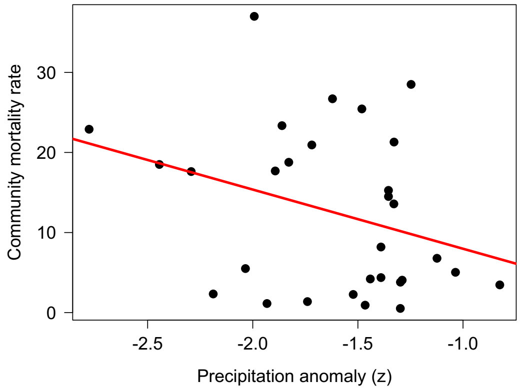

Fig. S3. Precipitation anomaly severity (most negative *z* score during the drought period described in the study) compared with total mortality rate averaged across all species in a given study. The red line is the best linear fit for predicted vs. observed ($F = 3.17$; df = 30; $P = 0.08$).

Table S1. Summary of trait-specific mixed effects models, with trait as a fixed effect and study identity as a random effect, both weighted and unweighted by a species' accuracy [quantified here as log(*N* individuals of species *i*)]

Model	β_{trait}	SE	*t* Value	*P* value
HSM, unweighted	−3.56	1.40	−2.63	0.01*
HSM, weighted	−1.66	0.27	−6.07	<0.001*
P50, unweighted	3.13	1.25	2.51	0.04*
P50, weighted	1.27	0.20	6.69	<0.0001*
HSM88, unweighted	−0.37	0.46	−0.77	0.45
HSM88, weighted	−0.42	0.20	−2.02	0.04*
P88, unweighted	1.18	0.57	2.08	0.048*
P88, weighted	1.32	0.22	6.32	<0.0001*
Ks, unweighted	0.37	1.70	0.22	0.82
Ks, weighted	0.34	0.71	0.48	0.62
TLP, unweighted	0.02	1.32	0.01	0.98
TLP, weighted	0.68	0.54	1.24	0.21
WD, unweighted	−0.52	0.66	−0.78	0.45
WD, weighted	−0.19	0.30	−0.63	0.53
Gs50, unweighted	1.90	5.50	0.34	0.73
Gs50, weighted	1.57	2.11	0.74	0.46
RootD, unweighted	0.62	1.05	0.59	0.58
RootD, weighted	0.72	0.48	1.62	0.12
Ang, unweighted	0.31	1.19	0.26	0.80
Ang, weighted	0.33	0.54	0.82	0.42
Gym, unweighted	−2.77	2.29	−1.21	0.26
Gym, weighted	−2.46	2.09	−2.41	0.09
Con, unweighted	−1.00	1.75	−0.57	0.57
Con, weighted	−0.38	0.62	−0.61	0.55
DP, unweighted	4.24	2.60	1.63	0.11
DP, weighted	4.50	1.14	3.93	0.002*
RP, unweighted	0.47	1.88	0.24	0.81
RP, weighted	0.72	0.72	0.65	0.52
Dec, unweighted	1.08	1.18	0.92	0.38
Dec, weighted	1.01	0.51	1.96	0.06
Evr, unweighted	0.88	1.72	0.51	0.62
Evr, weighted	0.80	0.84	0.94	0.34

All traits were scaled to *z* scores, such that all slopes are comparable. Traits are HSM, P50, HSM from P88 (HSM88), P88, specific branch conductivity (Ks), water potential at leaf turgor loss point (TLP), wood density (WD), water potential at 50% of maximal stomatal conductance (Gs50), maximum documented rooting depth (RootD), angiosperm (Ang), gymnosperm (Gym), conifer wood type (C), diffuse porous wood type (DP), ring porous wood type (RP), deciduous leaf habit (Dec), and evergreen leaf habit (Evr).

*Statistically significant at $P < 0.05$.

Table S2. Studies included in the meta-analysis, their location, and the number of unique species for which mortality data were available

Study no.	Study authors	Location	No. of species
1	Condit et al., 1995 (34)	Barro Colorado Island, Panama	205
2	Suarez and Kitzberger, 2008 (33)	Patagonia, Argentina	2
3	Faber-Langendoen and Tester, 1993 (35)	Minnesota	2
4	Gitlin et al., 2006 (36)	Arizona	6
5	Olano and Palmer, 2003 (37)	North Carolina	4
6	Stringer et al., 1989 (38)	Kentucky	5
7	Kukowski et al., 2013 (39)	Texas	4
8	Floyd et al., 2009 (40)	Arizona, Colorado, and New Mexico	2
9	Klos et al., 2009 (41)	Alabama, Georgia, and Virginia	3*
10	Viljoen, 1995 (42)	Kruger National Park, South Africa	17
11	O'connor, 1999 (43)	Northern Province, South Africa	7
12	Lwanga, 2003 (44)	Kibale National Park, Uganda	27
13	Van Nieuwstadt and Sheil, 2005 (45)	East Kalimantan, Indonesia	10
14	Potts, 2003 (46)	Lamber Hills National Park, Sarawak, Malaysia	10*
15	Nakagawa et al., 2000 (47)	Lamber Hills National Park, Sarawak, Malaysia	11*
16	Newberry and Lingenfelder, 2009 (48)	Danum Valley, Sabah, Malaysia	34
17	Fensham and Holman, 1999 (50)	North Queensland, Australia	27
18	Fensham, 1998 (49)	North Queensland, Australia	3
19	Rice et al., 2004 (51)	North Queensland, Australia	2
20	Fensham et al., 2003 (52)	Great Basalt Wall, Queensland, Australia	10
21	Martínez-Vilalta and Piñol, 2002 (53)	Prades Mountains, Spain	2
22	Gu et al., 2015 (54)	Missouri	6
23	Ganey and Votja, 2011 (55)	Arizona	5
24	Hoffmann et al., 2011 (15)	North Carolina	23
25	Fensham et al., 2015 (56)	North Queensland, Australia	21
26	Camarero et al., 2015 (57)	Aragon, Spain	3
27	Cavin et al., 2013 (58)	Southern United Kingdom	2
28	Nardini et al., 2013 (16)	Trieste, Italy	6
29	Coll et al., 2013 (59)	Spain	17
30	Anderegg et al., 2015 (60)	Western United States	3
31	Chazdon et al., 2005 (61)	Sarapiqui, Costa Rica	28
32	Fensham et al., 2012 (62)	North Queensland, Australia	31
33	Peng et al., 2011 (63)	Southern Canada	5

*Studies presented only genus-level data and thus, were only used for the angiosperm–gymnosperm analyses.