



Minireview

Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation

Author for correspondence:
William R. L. Anderegg
Tel: +1 970 739 4954
Email: anderegg@princeton.edu

William R. L. Anderegg

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08540, USA

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Summary

Plant hydraulics mediate terrestrial woody plant productivity, influencing global water, carbon, and biogeochemical cycles, as well as ecosystem vulnerability to drought and climate change. While inter-specific differences in hydraulic traits are widely documented, intra-specific hydraulic variability is less well known and is important for predicting climate change impacts. Here, I present a conceptual framework for this intra-specific hydraulic trait variability, reviewing the mechanisms that drive variability and the consequences for vegetation response to climate change. I performed a meta-analysis on published studies ($n = 33$) of intra-specific variation in a prominent hydraulic trait – water potential at which 50% stem conductivity is lost (P50) – and compared this variation to inter-specific variability within genera and plant functional types used by a dynamic global vegetation model. I found that intra-specific variability is of ecologically relevant magnitudes, equivalent to *c.* 33% of the inter-specific variability within a genus, and is larger in angiosperms than gymnosperms, although the limited number of studies highlights that more research is greatly needed. Furthermore, plant functional types were poorly situated to capture key differences in hydraulic traits across species, indicating a need to approach prediction of drought impacts from a trait-based, rather than functional type-based perspective.

Introduction

Water transport in plants enables photosynthesis and influences the productivity of ecosystems globally, affecting hydrological and carbon cycles (Brodribb, 2009). Plant hydraulic traits are important for understanding and forecasting climate change impacts on woody plants (Choat *et al.*, 2012). Climate projections predict increased dry period length and more intense droughts in many regions (Dai, 2013), exacerbated by rising temperatures leading to higher vapor pressure deficit and subsequently higher water stress in forest trees (Williams *et al.*, 2013). Indeed, incidences of

widespread, drought-induced forest die-off have been observed globally in recent decades (Allen *et al.*, 2010). In addition, many woody plant species appear to operate relatively close to their hydraulic safety margins – the quantifiable margin between observed xylem water potentials and those potentially leading to catastrophic hydraulic failure from embolism – with many taxa experiencing minimum water potentials that risk embolism in the xylem (Choat *et al.*, 2012), although lethal levels of embolism are not well known and recovery from embolism is possible in some cases.

Plant traits – morphological or physiological differences across species – hold promise for capturing critical dimensions of vulnerability and response to drought across species and ecosystems (Maherali *et al.*, 2004; Engelbrecht *et al.*, 2007), with the major aim of informing projections of climate impacts (Soudzilovskaia *et al.*, 2013). Traits hold the potential to link community ecology and physiological ecology by delineating the trade-offs that define

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life-history strategies, particularly across environmental gradients, that can influence population demographic rates (McGill *et al.*, 2006). Recent work has shown that these traits can be used to predict plant population abundance changes with climate change (Soudzilovskaia *et al.*, 2013) and that global trade-offs in plant traits translate into life-history trade-offs that influence growth, fecundity, and survival rates (Adler *et al.*, 2013).

Hydraulic traits, such as the water potential at which 50% of hydraulic conductivity is lost (P50), play an important role in these life-history trade-offs regionally and globally (Maherali *et al.*, 2004; Chave *et al.*, 2009). P50 provides an indicator of the resistance of xylem to embolism and has considerable adaptive variation across species and biomes (Maherali *et al.*, 2004). P50 has been linked to life-history strategies and demographic rates following drought and fire (Pratt *et al.*, 2007, 2008). P50 has also been used to predict cross-species levels of drought-induced woody plant mortality, making it potentially relevant for modeling of forest die-off under climate change scenarios (Hoffmann *et al.*, 2011; Nardini *et al.*, 2013).

While the vast majority of research examines inter-species differences in functional traits, the intra-species variation is less understood, particularly for hydraulic traits, and is important for modeling climate impacts on vegetation. The degree of intra-specific trait variation has important consequences for the sensitivity of species to climatic shifts and required migration rates to track these shifts. Variance of hydraulic characteristics within a single species could have a major impact on population demographics and responses to changes in climate extremes, such as a given population's ability to survive a drought, as well as spatial patterns and thresholds in drought-induced mortality (Martínez-Vilalta *et al.*, 2009; L. D. L. Anderegg *et al.*, 2013). Partitioning the spatial and temporal variance in hydraulic traits across individuals, populations, species, and plant functional types (PFTs) will be critical for next-generation dynamic global vegetation models (DGVMs) (Scheiter *et al.*, 2013). Finally, it is largely unknown whether current PFTs used in DGVMs capture meaningful differences in drought resistance traits, which will influence and constrain their ability to simulate drought impacts on vegetation.

In this review, I provide a spatio-temporal framework for partitioning the intra-specific variation in plant hydraulic traits, focusing on stem P50 as a relevant and useful metric of drought resistance across species, as well as one of the most widely quantified hydraulic traits (Maherali *et al.*, 2004; Brodribb, 2009; Choat *et al.*, 2012). I discuss the mechanisms that give rise to variation, as well as issues in scale and inference. I conduct a meta-analysis of intra-species variation in hydraulic traits and place this variation in context with inter-species differences. Considering inter-species hydraulic trait variation, I test whether PFTs in vegetation models are well situated to capture drought impacts on plant populations. Finally, I discuss the implications of both intra- and inter-species hydraulic variation for predicting climate change impacts on vegetation.

A spatio-temporal framework for variation in hydraulic traits

There are numerous sources of spatial and temporal variation of hydraulic traits (Fig. 1). Within a tissue such as a branch,

individual growth rings can have different hydraulic properties (Corcuera *et al.*, 2004), including differential xylem anatomy and vulnerability to cavitation (Melcher *et al.*, 2003). This array of vulnerabilities of different xylem elements and growth rings integrates to generate the tissue-level response (Melcher *et al.*, 2003) (Fig. 1a, #1). This observation is powerful because it provides a set of mechanisms, such as vessel diameter, pit membrane characteristics, and ring width, that can mediate many of the other sources of spatial and temporal variation. Much ecophysiological work has also quantified the variation and coordination of plant hydraulics at the organism scale, where substantial differences in hydraulic characteristics can exist across tissues and within tissues as a function of height or canopy location (Domec & Gartner, 2002; Pratt *et al.*, 2010) (Fig. 1a, #2). Variation across trees (Fig. 1a, #3), when tissue, canopy location, etc. are constant, within the same population is less well explored but potentially substantial across microenvironments. The paucity of the literature is striking, given that many trees seem to exhibit greater within-population than across-population genetic variation (Hamrick, 2004). Studies have found some evidence of substantial within-population variation in hydraulics as a consequence of different microenvironments, such as a riparian area versus a nearby slope (Alder *et al.*, 1996). Importantly, ecophysiological studies that quantify hydraulic traits often sample from smaller spatial extents (typically 'a stand') than the genetic population (typically 'a population'), and therefore capture less variability than the true breeding population given the large dispersal distance of many species' pollen. Finally, hydraulic traits can vary across populations within a species' range (Fig. 1a, #4).

Temporal variation in plant hydraulics is typically studied within three general contexts. First, as a result of the potential for different abiotic and biotic constraints at different life stages within woody plants, some variation of hydraulic traits is expected across ontogeny (Mencuccini, 2002) (Fig. 1b, #5 and #6). For example, seedlings can be more vulnerable to hydraulic-driven mortality than adults, indicating that seedling hydraulic traits may be important in modeling vegetation change with climate change (Pratt *et al.*, 2013). Secondly, hydraulic architecture and traits can vary seasonally (Jacobsen *et al.*, 2007) (Fig. 1b, #6). Thirdly, previous environmental factors such as extreme drought or a biotic attack such as defoliation can trigger temporal changes in plant hydraulic characteristics (Anderegg & Callaway, 2012) (Fig. 1b, #7). Similarly, the hydraulic traits of resprouting trees may differ from those of undisturbed individuals, suggesting important interactions between disturbances such as drought and fire (Pratt *et al.*, 2013). Dendrochronology studies that analyze the time-course of xylem anatomy and characteristics may unravel these temporal changes in response to environmental fluctuations; see Fonti *et al.* (2010) for a detailed review. These temporal changes may lower vulnerability to the stressor, or increase vulnerability, which may hasten tree decline.

What mechanisms shape spatial and temporal variation of plant hydraulics? More than 250 yr of 'common garden' or provenance trials on trees have detailed the range of possible variability for many plant traits, particularly phenology and timing of growth and, to a lesser extent, resistance to drought and cold stress (Alberto *et al.*,

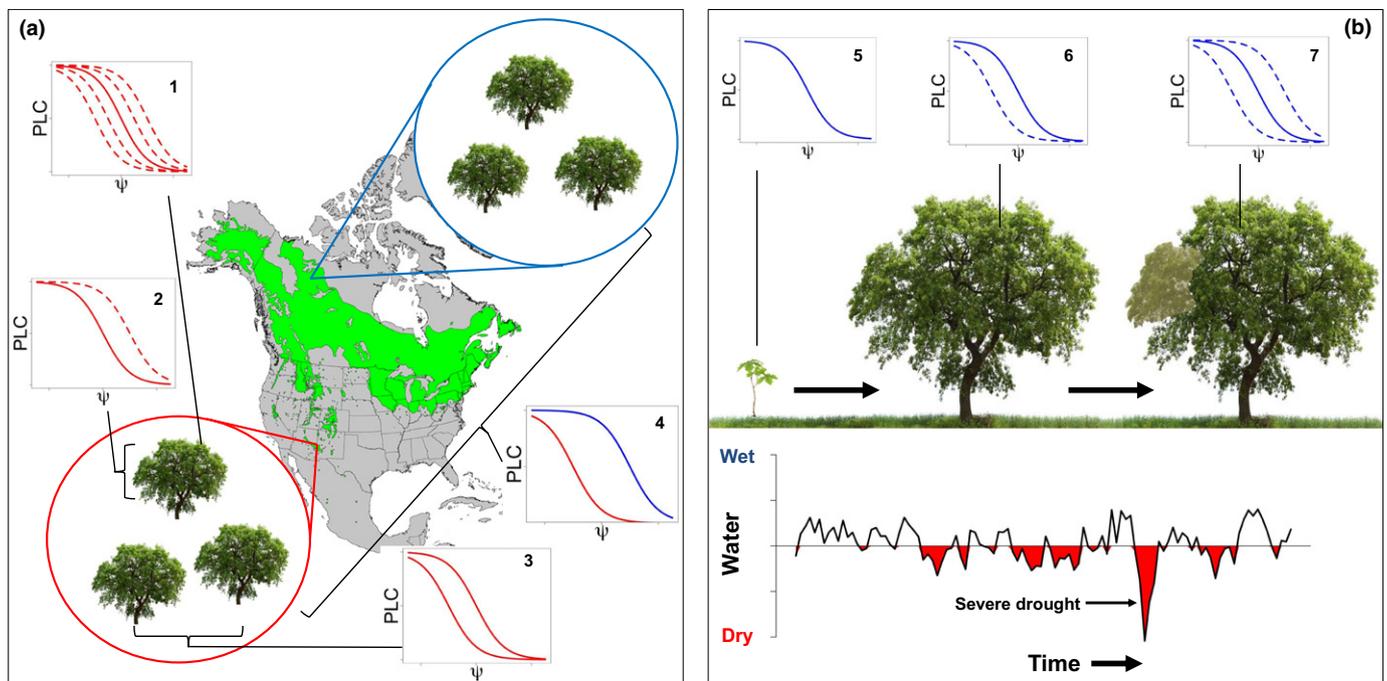


Fig. 1 Conceptual framework covering the spatial (a) and temporal (b) variation of plant hydraulic traits, shown via a hydraulic vulnerability curve linking per cent loss of conductivity (PLC; %) with plant water potential (Ψ ; MPa). Subpanels illustrate: 1, differential vulnerability across growth rings within a given branch; 2, differential vulnerability across branches within the same crown; 3, differential vulnerability across individual trees within the same population; 4, differential vulnerability across populations; 5, the vulnerability of a seedling; 6, differential vulnerability across ontogeny and/or seasons; 7, differential vulnerability following a climatic extreme such as drought.

2013). This extensive literature allows quantification of ‘response functions’ of populations (i.e. the change in a trait’s value as a function of transfer distance or environmental factors), which can be very valuable for forecasting climate change impacts (Rehfeldt *et al.*, 2002). Yet common garden experiments often do not measure hydraulic traits (but see Sparks & Black, 1999; Pratt *et al.*, 2008; Lamy *et al.*, 2013), and they are predominantly focused on commercially valuable species, which limits their utility for many natural ecosystems (Alberto *et al.*, 2013).

Variation of traits arises from a combination of genetic variation and phenotypic plasticity, which is the variation in phenotype within a single genotype. Regarding genetic variation, meta-analyses suggest that local adaptation in tree populations appears to be very common, but not universal (Leimu & Fischer, 2008; Hereford, 2009; Alberto *et al.*, 2013), and more common in trees than in most plants (Kawecki & Ebert, 2004). Indeed, genetic differentiation and clinal genetic variation across elevation were observed in 90% and 78% of studies, respectively (Alberto *et al.*, 2013). Despite this prevalence of local adaptation, other syntheses provide evidence that trees tend to have much higher within-population than across-population genetic diversity, although this varies by mating system and degree of fragmentation of a tree species’ distribution (Hamrick, 2004). Mechanisms that can dampen or erase local adaptation include high gene flow, genetic drift, lack of reliable environmental signals, especially with regard to temporal variation, lack of genetic variation, and genetic architecture of the underlying trait (Kawecki & Ebert, 2004).

Phenotypic plasticity, which may be adaptive, neutral, or maladaptive, is the second major mechanism through which traits

vary across environments and over time. Theoretical work indicates that adaptive plasticity should arise in spatially heterogeneous environments where the selective pressures are constant in time but not space (Nicotra *et al.*, 2010). Many forest trees show extensive clinal variation of phenotypic traits (Neale & Kremer, 2011), although the relative influence of plasticity versus adaptation on this variation differs both by trait and by species (Franks *et al.*, 2013) and plasticity can be strongly genotype-dependent (Fichot *et al.*, 2010). An extensive body of research has examined the limits of phenotypic plasticity, which generally fall into two categories: (1) ‘internal limits’ such as genetic costs, allocation, ontogeny, plasticity history, developmental constraints, and phenotypic integration, and (2) ‘ecological limits’ such as reliability of environmental cues, abiotic stress, herbivory, competition, multi-species interactions, and multiple simultaneous stressors (Valladares *et al.*, 2007; Nicotra *et al.*, 2010). In general, more stressful environments appear to lead to higher phenotypic integration – tighter coordination among functional traits – which constrains phenotypic plasticity (Valladares *et al.*, 2007).

Observed spatial and temporal variation in drought traits

I performed a meta-analysis using linear fixed-effects models on published studies that quantified intra-specific spatial or temporal variation in P50. A literature search revealed 33 studies that quantified P50 variation for 46 species (Supporting Information Table S1). From each study, I calculated the coefficient of variation (CV) of P50 across space (which includes both within-population

and across-population variation) or time periods, analyzing space and time separately, as the effect size for meta-analysis. I then compared these intra-specific CV values to CV values obtained for P50 values in the global data set presented in Choat *et al.* (2012) across species in the same genus. Finally, to compare these sources of variability to the variation present in classifications for global vegetation models, I assigned each species in the Choat *et al.* data set to a plant functional type (PFT) from the Community Land Model (CLM3.0), based on the classification presented in (Lawrence & Chase, 2007). For full details, see Methods S1.

The intra-specific CV of P50 varied both in time and in space, with more negative P50 values generally found in more xeric environments over space and slightly higher variability temporally than spatially (z -value = 2.3; $P = 0.02$) (Fig. 2a), although the relatively small number of studies examining temporal variation ($N_{\text{time}} = 7$ versus $N_{\text{space}} = 26$) suggests caution in drawing broad conclusions. There was no relationship between spatial and temporal CVs of P50 in species present in both analyses ($n = 14$) ($r^2 = 0.03$; $P = 0.6$). The observed spatial variation presented here, however, almost certainly underestimates the true variability. This is because (1) there are relatively few studies that quantify variation across a species' full geographic range (e.g. Herbet *et al.*, 2010; Wortemann *et al.*, 2011; Lamy *et al.*, 2013) and (2) a substantial number of studies (63%) included only a few populations. Finally, temporal variability was less well studied and often measured in response to a given stress, such as an induced pressure in a centrifuge (Hacke *et al.*, 2001) or a severe drought (W. R. L. Anderegg *et al.*, 2013). Thus, the timescales over which temporal variability in vulnerability curves persists are largely unknown.

Angiosperms exhibited higher intra-specific spatial variability than gymnosperms in P50 (z -value = -4.0 ; $P < 0.0001$) (Fig. 2b). Higher angiosperm variability aligns with theoretical expectations resulting from anatomical differences between angiosperms and gymnosperms (Johnson *et al.*, 2012). Angiosperms have xylem vessels, which allow broader variability in element size and wall thickness than that of tracheids (Brodribb *et al.*, 2006), and higher numbers of parenchyma cells, which allow response to climate variability through their potential roles in stem biomechanics, heartwood formation, xylem–phloem communication, reserve storage, and embolism refilling (Olano *et al.*, 2013). There was no relationship found between the spatial CV across populations and a

species' average P50 value for angiosperms ($r^2 = 0.03$; $P = 0.34$) or all species combined ($r^2 = 0.01$; $P = 0.5$).

Considering intra-specific hydraulic trait variation from a broader perspective, the intra-specific spatial CV of P50 (meta-analysis weighted average $c. 0.1$) was $c. 33\%$ of the CV of P50 within a genus (average 0.29) and 20% of the CV of P50 within a PFT (average 0.52) (Fig. 2c). The CVs of P50 were significantly different across these three groupings (one-way ANOVA, $F = 13.6$; $P < 0.0001$) and all three groups differed significantly from each other in post hoc tests (Tukey honest significant difference, $P < 0.03$). These findings indicate that the spatial variation in P50 within a species is substantial, and thus probably ecologically relevant for drought impacts, but in general lower than the cross-specific differences within genera or biomes. Data limitations prevent a full comparison of P50 variability to that of other traits, as only a handful of studies have quantified the variability of P50 and other key stem and leaf traits across a species' range (Martínez-Vilalta *et al.*, 2009; Wortemann *et al.*, 2011; Lamy *et al.*, 2013), mostly in *Pinus* species. A detailed study of Scots pine (*Pinus sylvestris*) found much higher variation of many other traits across populations (CV = 0.18–0.56), particularly sapwood to leaf area ratios (CV = 0.34) in response to aridity, than P50 (CV = 0.08) (Martínez-Vilalta *et al.*, 2009). The emergent picture of these studies indicates that within-population variability of P50 is generally larger than across-population variability (Wortemann *et al.*, 2011; Lamy *et al.*, 2013). Similarly, an analysis of 112 provenance studies on 19 plant traits found that population-level differentiation was much higher for growth and phenology traits ($Q_{ST} = 0.11$ –0.52) than ecophysiological traits ($Q_{ST} = 0.02$ –0.1) (Alberto *et al.*, 2013).

Implications for climate change and modeling

In reviewing the literature, I found that intra-specific spatial and temporal variability appears to be higher in angiosperms than gymnosperms and that this variability is on the order of 33% of the variability within a genus, or 20% of the variability within a PFT (Fig. 2). However, the limited number of available studies ($n = 33$) and limited common garden and comparative studies across a species' geographic distribution that assess P50 preclude a full characterization of the generality and magnitude of this variability.

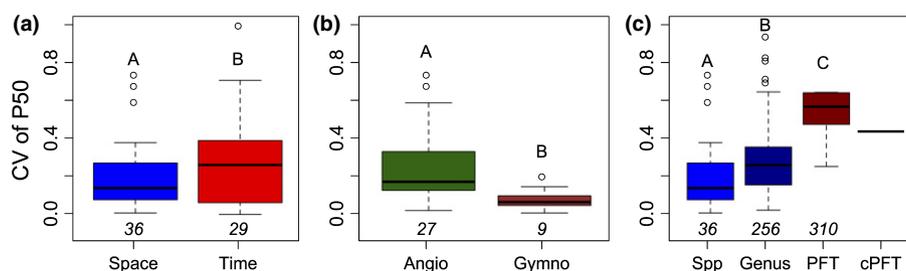


Fig. 2 Coefficient of variation (CV) of the water potential at which a plant stem reaches 50% loss of hydraulic conductivity (P50) (a) intraspecific variation across space versus time in angiosperms, (b) intraspecific variation spatially across angiosperms (Angio) versus gymnosperms (Gymno) within a given species, and (c) comparing within-species spatial variation, within-genus variation, within-plant functional type (PFT) variation (tree PFTs only), and across-PFT variation (cPFT). Box-plots show the median (dark line), interquartile range (box), and maximum/minimum value (whiskers), except where values exceeded 1.5 times the interquartile range (points). Numbers below bars indicate the sample size of the number of species included. Letters denote statistical significance at $P < 0.05$.

Xylem hydraulic traits are one element of a trait syndrome that species employ to survive and compete, operating in concert with other traits such as stomatal sensitivity and sapwood to leaf area ratios. Thus, a multivariate approach that includes other traits would be very informative but is beyond the scope of this review. Nonetheless, the degree of local adaptation and spatial variability in plant hydraulics within a given species are likely to have substantial effects on climate change impacts on woody plant species. If spatial variability is high and largely under genetic control (local adaptation), changes in climate would be expected to lead to increased risk of mortality in both wetter and drier portions of ranges, as has been observed in some cases (Allen *et al.*, 2010). Conversely, if temporal variability is high and largely driven by plasticity, rather than genetics, this would indicate a substantial capacity to adapt and buffer against environmental changes.

Two common garden experiments, which allow assessment of the relative roles of genetics versus plasticity, on the P50 values of the contrasting species *Fagus sylvatica* and *P. sylvestris* found relatively minor origin effects of source population, with the *F. sylvatica* study finding substantial plasticity and the *P. sylvestris* study finding little plasticity (Wortemann *et al.*, 2011; Lamy *et al.*, 2013). An extensive study on 16 chaparral shrub species found substantial effects of both temporal variation seasonally and population variation between wet and dry mountain ranges (Jacobsen *et al.*, in press). The potential for temporal plasticity, however, is constrained by the turnover time of sapwood, which is generally on the order of decades for gymnosperms and diffuse-porous angiosperms, and can be faster for ring-porous trees (Gebauer *et al.*, 2008), although faster plasticity via earlywood-latewood dynamics and other mechanisms may be possible. This anatomical constraint implies that hydraulic architecture and integrated traits such as P50 should have a slower response time than traits that can change on seasonal or yearly time-scales such as

many leaf traits. Furthermore, plastic responses that buffer against stress would need to occur more rapidly than the return interval of damaging climatic extremes such as drought.

Considering species' P50 and hydraulic safety margin (HSM) traits in ecosystem models, PFT was a significant factor in explaining variability across species P50 values both across all woody species (ANOVA, $F = 16.1$; $P < 0.0001$) and within tree PFTs alone (ANOVA, $F = 91.7$; $P < 0.0001$) (Fig. 3). PFT also was significant in explaining variability of HSM across woody species (ANOVA, $F = 47.5$; $P < 0.0001$) and tree species (ANOVA, $F = 39.2$; $P < 0.0001$). The number of species included in PFTs varied widely, from five species in Needleleaf Deciduous Boreal to 96 species in Broadleaf Deciduous Temperate (Fig. 3) with boreal species somewhat under-represented.

Despite these differences, however, P50 values among PFTs overlapped to a great extent and the within-PFT variability was greater than the cross-PFT variability (Fig. 2c). This indicates that PFT classifications do not accurately capture differences in plant hydraulic strategies and would therefore be poorly situated to capture hydraulically mediated drought impacts on vegetation (e.g. Hoffmann *et al.*, 2011; Anderegg *et al.*, 2012). While no current dynamic global vegetation models simulate plant hydraulics, it is an active area of research that may be incorporated into forthcoming models (McDowell *et al.*, 2011). The data I present here suggest that a PFT-based approach may encounter large difficulties in parameterization and simulation of hydraulic-mediated drought impacts. Recent modeling advances that incorporate plant traits and adaptive changes to traits (Scheiter *et al.*, 2013) and cohort-based models that allow demographic rates to respond to plant traits (Purves *et al.*, 2008) could allow the incorporation of drought response strategies, captured via traits such as P50, and spatial and temporal variability in traits. Additional common garden, distribution-spanning, and cross-trait studies that quantify the

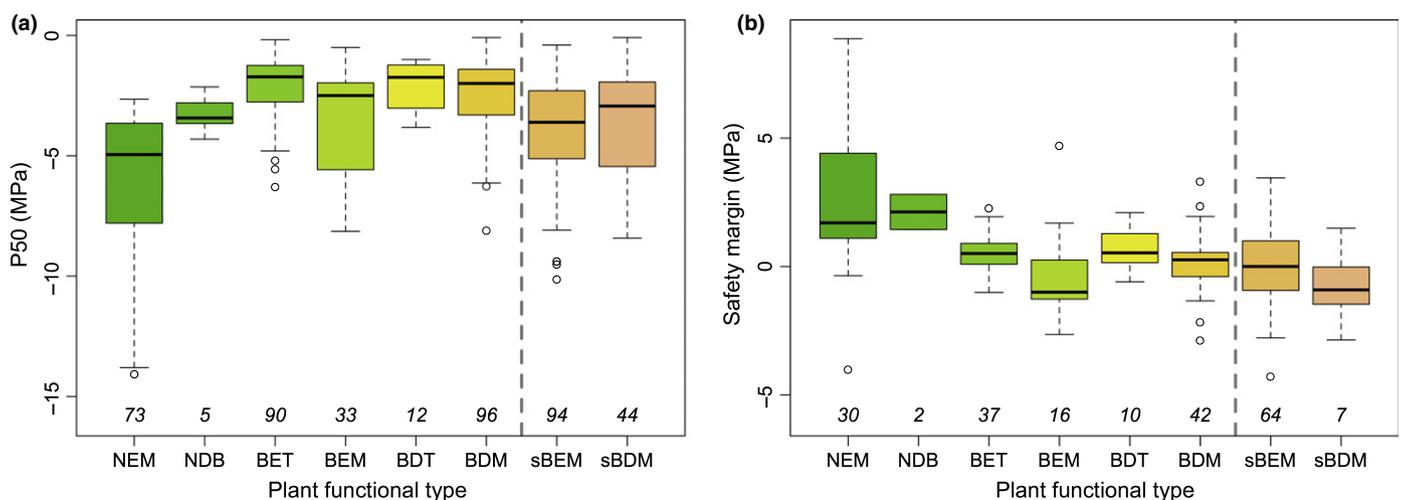


Fig. 3 Box-plots of (a) the water potential at which a plant stem reaches 50% loss of hydraulic conductivity (P50) and (b) the hydraulic safety margin (minimum observed midday water potential minus P50) of species globally, categorized by their respective plant functional type (PFT) of: NEM, Needleleaf Evergreen Temperate; NDB, Needleleaf Deciduous Boreal; BET, Broadleaf Evergreen Tropical; BEM, Broadleaf Evergreen Temperate; BDT, Broadleaf Deciduous Tropical; BDM, Broadleaf Deciduous Temperate; sBEM, shrub Broadleaf Evergreen Temperate; sBDM, shrub Broadleaf Deciduous Temperate. Box-plots show the median (dark line), interquartile range (box), and maximum/minimum value (whiskers), except where values exceed 1.5 times the interquartile range (points). Numbers below bars indicate the sample size of that PFT as the number of species included. The dashed line divides tree PFTs from shrub PFTs.

variability of plant hydraulic traits over space and time, and their respective genetic and plastic underpinnings, are greatly needed to assess the vulnerability of woody plant species to climate change.

Conclusions

A meta-analysis of intra-specific variability of P50 across 46 species revealed that intra-specific variability is substantial. This indicates an urgent need to quantify the magnitude, time-scales, and roles of genetic versus plastic mediation of intra-specific trait variability across species and environments, and to connect trait variation to mortality during climatic extremes. These results indicate that moving to a trait-based approach, rather than a PFT-based approach, particularly while accounting for trait variation in space and time, holds great potential for improving understanding and prediction of climate change impacts on vegetation.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 The species, study designs, and references of all studies incorporated into the meta-analysis

Methods S1 The text describes the literature search, methods, and statistics used in the meta-analysis.

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