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# Rooting depth and xylem vulnerability are independent woody plant traits jointly selected by aridity, seasonality, and water table depth

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## Summary

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- Evolutionary radiations of woody taxa within arid environments were made possible by multiple trait innovations including deep roots and embolism-resistant xylem, but little is known about how these traits have coevolved across the phylogeny of woody plants or how they jointly influence the distribution of species.

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**Key words:** cavitation, drought avoider, drought resistant, embolism, species distribution modeling, trees, water availability.

- We synthesized global trait and vegetation plot datasets to examine how rooting depth and xylem vulnerability across 188 woody plant species interact with aridity, precipitation seasonality, and water table depth to influence species occurrence probabilities across all biomes.
- Xylem resistance to embolism and rooting depth are independent woody plant traits that do not exhibit an interspecific trade-off. Resistant xylem and deep roots increase occurrence probabilities in arid, seasonal climates over deep water tables. Resistant xylem and shallow roots increase occurrence probabilities in arid, nonseasonal climates over deep water tables. Vulnerable xylem and deep roots increase occurrence probabilities in arid, nonseasonal climates over shallow water tables. Lastly, vulnerable xylem and shallow roots increase occurrence probabilities in humid climates.
- Each combination of trait values optimizes occurrence probabilities in unique environmental conditions. Responses of deeply rooted vegetation may be buffered if evaporative demand changes faster than water table depth under climate change.

‘Species that show deviations from statistical correlations (and there are always many such species) may tell us more about the adaptive value of particular characteristics than species that fit the correlation.’

(Carlquist, 1975, p. 1)

## Introduction

Hotter droughts are expected to become more frequent and severe under most climate change scenarios (Spinoni *et al.*, 2018; Hammond *et al.*, 2022), and they have already resulted in widespread tree mortality (Bauman *et al.*, 2022; Hartmann *et al.*, 2022; McDowell *et al.*, 2022). Understanding which plant species are winners and losers under scenarios of decreasing water availability is critical for improving predictions of vegetation dynamics (Hammond *et al.*, 2019) and ecosystem restoration success (Laughlin *et al.*, 2017). Rooting depth and xylem vulnerability to drought-induced embolism are strongly linked to how woody plant species respond to moisture availability (Aubin *et al.*, 2016; Volaire, 2018) because the physiological link between water uptake and xylem conductance is vital to maintaining photosynthesis in arid climates and during dry seasons. Rooting depth and xylem vulnerability have each been separately investigated in woody species (Canadell *et al.*, 1996; Choat *et al.*, 2012), but little is known about how these traits have coevolved within woody taxa, nor do we know the joint effects of these traits on species distributions and potential responses to global change.

Survival in water-limited landscapes can be achieved by resisting, avoiding, or escaping dehydration caused by low soil water potentials (May & Milthorpe, 1962; Fischer & Maurer, 1978; Levitt, 1980; Volaire, 2018). First, drought resistance (also called drought tolerance) is achieved by constructing xylem that can resist embolism formation and maintain water conductance to enable CO<sub>2</sub> uptake even under extreme negative xylem pressure. Woody plants vary widely in their vulnerability to embolism (Hacke *et al.*, 2001; Maherali *et al.*, 2004; Choat *et al.*, 2012), which can be quantified by P<sub>50</sub>, the xylem pressure (MPa) at which xylem conductance is reduced to 50% of its maximum, where species with lower P<sub>50</sub> values (i.e. more negative values) are

more resistant to embolism. Second, drought avoidance can be achieved by constructing root systems that access soil water in the unsaturated deep vadose zone or directly from the water table in the saturated zone (Loheide *et al.*, 2005; Ryel *et al.*, 2008). Maximum rooting depth varies widely among woody plants (Canadell *et al.*, 1996; Jackson *et al.*, 1996) and deep roots evolved for a variety of reasons, including anchorage, support, and increasing the available soil volume in deep soil. Here, we focus on its vital role in water uptake. Shallow-rooted species rely on rainfall directly, whereas deep-rooted species can access water from deeper and older sources of water (Miguez-Macho & Fan, 2021). Both phreatophytic species that tap into water tables and deeply rooted xerophytic plants that access soil water in the deep vadose zone can avoid the drought-induced reductions in soil water potential near the soil surface (Ryel *et al.*, 2008; Miguez-Macho & Fan, 2021). In arid climates, species that develop only shallow roots confront drought directly and must be able to resist embolism formation. If ‘roots grow only as deeply as needed’ (Schenk & Jackson, 2002, p. 481), then plants will develop shallow roots in humid climates, and if the water table is shallow, they may restrict their roots to the oxygenated zone to prevent anoxia (Jackson *et al.*, 1996; Fan *et al.*, 2017; Tumber-Dávila *et al.*, 2022). Third, drought escape can be achieved by completing a short life cycle during the wet growing season or by deciduous leaf senescence during the dry season. Data are limited for drought deciduous species, so this paper focuses on xylem vulnerability and rooting depth.

The large investments into the growth and maintenance of deep roots must be offset by fitness advantages made possible by having such deep roots (Seyfried *et al.*, 2005). The construction costs of deep roots could possibly be offset by lower stem xylem construction costs, and evidence for a trade-off between functional rooting depth (estimated using isotopes) and xylem resistance to embolism was demonstrated across 12 species in a humid tropical forest, where shallow-rooted species were more tolerant of low water potentials (Brum *et al.*, 2019). However, the relationship between maximum rooting depth and xylem vulnerability across global-scale climatic gradients has never been rigorously quantified. There are well-known examples of deep-rooted species in arid climates that exhibit remarkably resistant

stem xylem (Jackson *et al.*, 2000; Seyfried *et al.*, 2005), suggesting that the costs of constructing both deep roots and resistant xylem are offset by the fitness gains that are achieved by simultaneously avoiding and resisting dehydration.

Rooting depth and xylem vulnerability may jointly influence species distributions along gradients of water availability in complex ways. Water limitation in plants is affected by climatic aridity, which includes both the regional macroclimate (i.e. atmospheric aridity) and precipitation seasonality, and by local topography and drainage gradients (Fig. 1a) (Schwinning & Ehleringer, 2001; Fan *et al.*, 2017; Grossiord *et al.*, 2020). From a hydrological perspective, water from ‘uplands’ (defined as well-drained topographic positions independent of elevation above sea level) flows into local topographic depressions creating shallow water tables in ‘lowlands’ (defined as poorly drained topographic depressions independent of elevation above sea level) (Fig. 1a) (Nobre *et al.*, 2011; Fan *et al.*, 2017). Rooting depth is predicted to occur at intermediate water table depth on well-drained mid-slopes (in arid and seasonally arid climates), where plants tap into capillary rise from groundwater (Fan *et al.*, 2017). Water table depth is largely independent of regional climate because it is primarily under hydrologic control (Sousa *et al.*, 2022), and plant species responses to regional drought may depend on water table depth (Sousa *et al.*, 2020). For example, phreatophytic plants growing in arid riparian areas experience severe atmospheric vapor pressure deficits yet have ample access to soil water. Conversely, plants growing in coarse, shallow, or excessively drained soils within humid regions will experience local soil water deficits despite receiving high amounts of precipitation. In previous studies, species with low  $P_{50}$  were associated with arid regional

climates (Larter *et al.*, 2017; Laughlin *et al.*, 2020a) and upland topographical positions (Oliveira *et al.*, 2019). Plants with shallow roots tend to occur in humid climates and waterlogged soil, whereas both shallow and deep-rooted species occur in well-drained soil in arid climates (Schenk & Jackson, 2005; Fan *et al.*, 2017). Yet, ‘humid’ and ‘arid’ are relative terms, since the water available to plants also depends on precipitation seasonality, and the length of the dry season can be a more defining feature of the climate than mean annual rainfall. Therefore, determining the joint response of both traits to gradients of regional aridity, precipitation seasonality, and local water table depth will improve our understanding of vegetation response to drought.

In this paper, we combined species-level trait data with three gradients in water availability to ask the following research questions: (1) Do  $P_{50}$  and maximum rooting depth exhibit an interspecific trade-off across the phylogeny of woody plants? And (2) do each of the four combinations of the two trait values optimize occurrence probabilities in unique environmental conditions? We demonstrate that there is no evidence for an interspecific trade-off between resistance and avoidance strategies and that each combination of trait values optimizes occurrence probabilities in unique conditions of water availability.

## Materials and Methods

### Dataset compilation

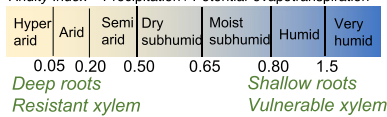
We combined the Xylem Functional Traits (XFT) database (Choat *et al.*, 2012) with recently published data to quantify

### (a) Three drivers of water limitation

Green text: Predictions of optimal trait values in each environment

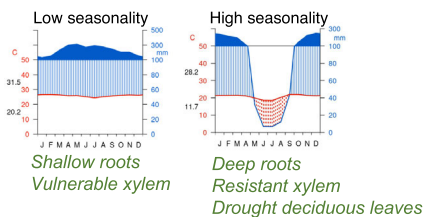
#### 1) Regional macroclimate

Aridity Index = Precipitation / Potential evapotranspiration

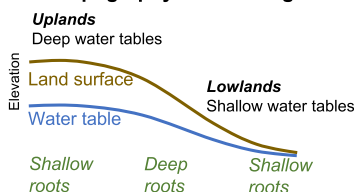


#### 2) Precipitation seasonality

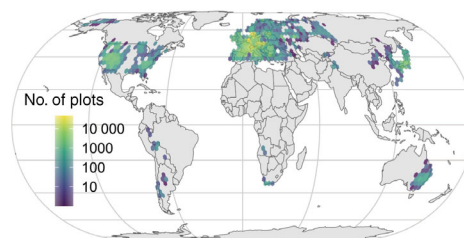
Seasonality = Coefficient of variation of monthly precipitation



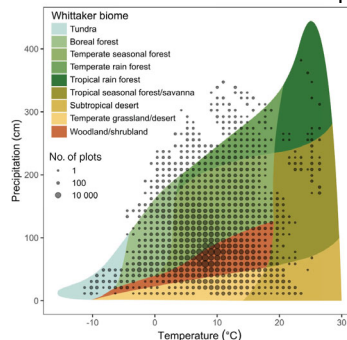
#### 3) Local topography and drainage



### (b) Geographic distribution of plots



### (c) Whittaker biome distribution of plots



**Fig. 1** (a) Gradients of atmospheric aridity (regional macroclimate) (Trabucco & Zomer, 2018), precipitation seasonality (Fick & Hijmans, 2017), and local water table depth (Fan *et al.*, 2017) drive water limitation in plants. Green text reports predictions of optimal trait values along each environmental gradient (see text). (b) Biogeographic distribution of vegetation plots from the sPlot 3.0 database around the planet illustrated as density of plots per hexagonal grid cell. (c) Bioclimatic distribution of vegetation plots within Whittaker biome defined by mean annual temperature and total annual precipitation (Whittaker, 1975).

average  $P_{50}$  trait data at the species level (Supporting Information Table S1). We discarded vulnerability curves that were nonsigmoidal in shape or were generated using the air-injection method (Cochard *et al.*, 2013). We merged this  $P_{50}$  dataset with the Root Systems of Individual Plants (RSIP) database joined by species (Tumber-Dávila *et al.*, 2022). We calculated maximum rooting depth for each species as the absolute maximum rooting depth recorded for that species in the database. This estimates the potential rooting depth of a species and is analogous to maximum height, another size-dependent trait and key indicator of plant ecological strategies (Díaz *et al.*, 2022). Maximum rooting depth is meaningful because it captures the potential for individuals of a species to construct deep roots. This rooting depth potential may be more informative than highly plastic individual trait values for explaining species occurrence across large-scale climatic gradients. Maximum rooting depth was strongly correlated with the median of individual plant rooting depths across species ( $r=0.85$ ), and models that used median rooting depth were qualitatively indistinguishable from models that used maximum rooting depth. After standardizing species names according to the World Flora Online taxonomic backbone (Miller & Ulate, 2017) and filtering out two outlying measurements of maximum rooting depth that were  $< 0.3$  m, the database contained 903 species (2458 observations) with average  $P_{50}$  and 1089 species (2716 observations) with maximum rooting depth. We merged the datasets based on species names and found that both traits have been measured on 207 woody species (Table S1). For these 207 species, there were 871 observations of  $P_{50}$  and 950 observations of rooting depth (Table S1).

We extracted vegetation plots from the sPLOT 3.0 database (Bruehlheide *et al.*, 2019) that had a location uncertainty of 1 km or less. Of the 207 species, 188 were present on 508 443 plots (1733 795 occurrences). The selected plots were broadly distributed worldwide and throughout Whittaker's bioclimatic space (Fig. 1b,c) (Whittaker, 1975). Vegetation plots were assigned to ecoregions using Olson's updated ecoregion map (Olson *et al.*, 2001; Dinerstein *et al.*, 2017). We defined regional species pools as all of our species that were detected within an ecoregion, and we defined species absences as species that were present in the regional species pool but not detected in the plot itself (Laughlin *et al.*, 2021). For each plot, we extracted the aridity index (the ratio of precipitation-to-potential evapotranspiration) from the Global Aridity Index and Potential Evapotranspiration Climate Database (Zomer *et al.*, 2008; Trabucco & Zomer, 2018), water table depth (WTD) from the WTD database (Döll & Fiedler, 2008; Fan *et al.*, 2013), and precipitation seasonality (Coefficient of Variation of monthly precipitation) from the WorldClim database using climate normals from 1970 to 2000 (Fick & Hijmans, 2017). The aridity index estimates macroclimatic water availability, where low ratios indicate arid climates and high ratios indicate humid climates (Fig. 1a-1). Water table depth varies independently of climate (in this dataset, the correlation coefficient between aridity and WTD is  $r=0.13$ ) and is thought to be a major driver of rooting depth distributions (Fan *et al.*, 2017).

Of the 207 species for which rooting depth and  $P_{50}$  were available, 105 were evergreen and 102 were deciduous (Table S1). We focus on drought resistance and avoidance in this paper because only a few deciduous species in our dataset were drought-deciduous escapers; the vast majority were cold-deciduous species. Nevertheless, we evaluate deciduous and evergreen species to understand their effects on the overall model results.

## Data analysis

To answer Question 1 (Do  $P_{50}$  and maximum rooting depth exhibit an interspecific trade-off across the phylogeny of woody plants?), we extracted a fully resolved phylogeny based on the PhytoPhylo megaphylogeny (Qian & Jin, 2016) using the R package *V.PHYLOMAKER* v.0.1.0 (Jin & Qian, 2019). We calculated Pagel's  $\lambda$  under a Brownian motion model of evolution to quantify the phylogenetic signal for each trait (Pagel, 1999) using the *phylosig* function in the R package *PHYTOOLS* v.1.2.0 (Revell, 2012). Ancestral state reconstruction used maximum likelihood estimates under a Brownian motion model of evolution. The phylogeny was plotted using the R package *PHYTOOLS* (Revell, 2012). We quantified the phylogenetic interspecific covariance between the two traits by fitting phylogenetic generalized least squares (PGLS) regression and a phylogenetic correlation structure to account for the nonindependence of species across the phylogeny (Revell & Harmon, 2022). To evaluate the sensitivity of the phylogenetic correlation between maximum rooting depth and mean  $P_{50}$ , we sampled observed values of rooting depth and  $P_{50}$  from our database (with replacement because some species only had single observations) and computed the interspecific PGLS slopes and associated  $P$ -values 10 000 times. This test evaluates the consistency of the interspecific correlation, but we note that neither this test nor the available data can evaluate whether an intraspecific trade-off exists between drought resistance and avoidance.

To answer Question 2 (Do each of the four combinations of the two trait values optimize occurrence probabilities in unique environmental conditions?), we compared two generalized linear mixed-effects models of species presence-absence data using the binomial family and logit link. Both models included species as random intercept terms to account for the fact that trait data were species-level averages and not measured at the intraspecific level at each location. We also added ecoregions as random intercept terms to account for the different numbers of observations in each ecoregion. Model 1 was an environment-only model that included linear and quadratic fixed effects terms for aridity ('arid'), precipitation seasonality ('ps'), and WTD, and interactions among their linear terms. Model 2 included both the environment and traits, where  $P_{50}$ , rooting depth, aridity, seasonality, and WTD, their squared terms, and interactions among linear terms up to a five-way interaction, were included as fixed effects. Aridity index and the absolute value of  $P_{50}$  were square root-transformed, seasonality, WTD, and rooting depth were log-transformed, and all predictors were mean-centered and scaled to a standard deviation of 1 prior to fitting the models.

For example, Model 1 can be written as

$$y_i \sim \text{Bernoulli}(p_i)$$

$$p_i = \text{logit}^{-1} \left( \beta_0 + \beta_1 \text{arid}_i + \beta_2 \text{arid}_i^2 + \beta_3 \text{WTD}_i + \beta_4 \text{WTD}_i^2 + \beta_5 \text{ps}_i + \beta_6 \text{ps}_i^2 + \beta_7 \text{arid}_i \text{WTD}_i + \beta_8 \text{arid}_i \text{ps}_i + \beta_9 \text{WTD}_i \text{ps}_i + \beta_{10} \text{arid}_i \text{WTD}_i \text{ps}_i + \eta_{j[i]} + \gamma_{k[i]} \right)$$

where  $y_i$  is the  $i^{\text{th}}$  presence–absence record,  $p_i$  is the expected occurrence probability, the  $\beta$ 's are regression coefficients,  $\eta_j$  is a random intercept for species  $j$  drawn from a normal distribution,  $N(0, \sigma_\eta)$ , and  $\gamma_k$  is a random intercept for ecoregion  $k$  drawn from a normal distribution,  $N(0, \sigma_\gamma)$ .

Model 2 includes traits and their linear interactions to model a two-dimensional surface of  $P_{50}$  and rooting depth and its interaction with a three-dimensional surface of aridity, seasonality, and WTD. The shape of the trait surface changes in relation to aridity, seasonality, and WTD, accounting for trait-by-environment interactions that cause different trait combinations to be selected in different environments. We compared Models 1 and 2 using a likelihood ratio test to determine the importance of traits for explaining species occurrences when environmental variables were already in the model. The R syntax of the binomial Model 2 using the `bam` function in the R package `mgcv` 1.8.41 (Wood, 2011) was as follows: `presence ~ arid * WTD * ps * p50 * rd + arid^2 + WTD^2 + ps^2 + p50^2 + rd^2 + s(spp, bs = 're') + s(eco, bs = 're')`. We plotted 90% confidence intervals using posterior simulations from the fitted model.

We plotted model predictions of occurrence probabilities at different combinations of environment and trait values to facilitate model interpretation. We plotted conditional effects of each trait by illustrating the effects of one trait, while holding the other trait at its mean value, at different combinations of high (95<sup>th</sup> percentile) or low (5<sup>th</sup> percentile) aridity, seasonality, and water table depth. To illustrate trait-by-trait interactions, we plotted landscapes of occurrence probabilities across a two-dimensional surface of  $P_{50}$  and rooting depth at different combinations of aridity, seasonality, and water table depth. We fixed the two traits at their 5<sup>th</sup> and 95<sup>th</sup> percentiles to represent four plant strategies and plotted landscapes of occurrence probabilities along a two-dimensional surface of aridity and WTD at two levels of seasonality. The average occurrence probability across this large dataset is *c.* 5%, so predicted probabilities vary above and below this mean value. All analyses used R v.4.2.2.

## Results

### Phylogenetic correlation

Mean  $P_{50}$  and maximum rooting depth exhibited significant phylogenetic signal (Fig. 2), although the signal was weaker for rooting depth ( $P_{50}$ : Pagel's  $\lambda = 0.91$ ,  $P < 0.001$ ; rooting depth: Pagel's  $\lambda = 0.58$ ,  $P < 0.01$ ). These two traits were uncorrelated

(Fig. 3) across the phylogeny of woody plants (PGLS slope = 0.06, SE = 0.07,  $t = 0.95$ ,  $P = 0.35$ ). Interspecific variation accounted for 79% of the total variation in  $P_{50}$  and for 43% of the total variation in rooting depth, so we tested the sensitivity of this intraspecific variation on our evaluation of the interspecific correlation. Inspection of the ranges of intraspecific trait variability provided no indication that these traits were correlated across species (Fig. S1A) and random samples drawn from the observed trait values exhibited a consistent lack of correlation between these two traits (Fig. S1B,C). Deciduous and evergreen species were well-distributed throughout this two-dimensional trait space, but deciduous species had on average more vulnerable xylem than evergreen species (Fig. 3). Given the orthogonal nature of these traits, the bivariate trait space can be divided into four nominal strategies: resistant avoiders, resistant confronters, vulnerable avoiders, and vulnerable confronters (Fig. 3).

### Models of occurrence probabilities

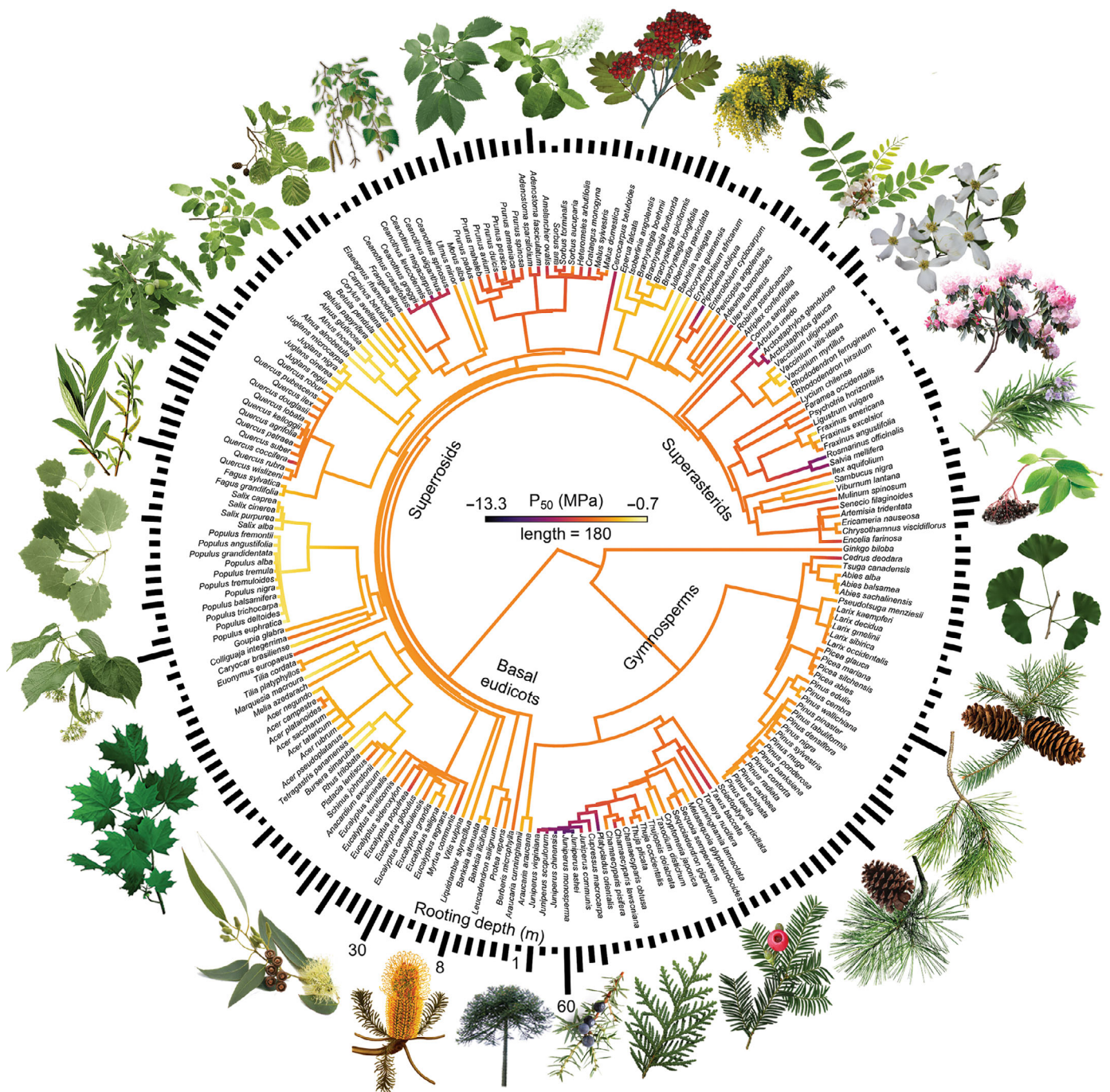
The generalized linear mixed-effects model that included traits (see Model 2 results in Table S2) explained 16.7% of the deviance (marginal  $R^2 = 0.24$ ; conditional  $R^2 = 0.70$ ). A likelihood ratio test (LRT) determined that traits were a significant improvement to the model that only included environmental data as predictors (LRT  $\chi^2_{21} = 188\ 143$ ;  $P < 0.0001$ ) (see Model 1 results in Table S3). Traits exhibited no significant main linear effects (i.e. the trait effects depended on the environment), and the quadratic term for rooting depth was not significant. Nearly all trait-by-environment interactions were significant (Table S2).

Xylem vulnerability ( $P_{50}$ ) interacted with aridity, seasonality, and water table depth (Fig. 4; Table S2). The effect of  $P_{50}$  on probability of occurrence switched from negative to positive from arid to humid climates, where the probability of occurrence of species resistant to embolism increased in more arid climates (Fig. 4a,b). In arid climates with shallow water tables, low  $P_{50}$  values increased occurrence probability in seasonal environments, whereas high  $P_{50}$  values increased occurrence probabilities in nonseasonal environments (Fig. 4c).

Rooting depth interacted weakly with aridity, seasonality, and water table depth (Fig. 4, Table S2). The effect of rooting depth on the probability of occurrence switched from positive to negative in arid to humid climates, where the probability of occurrence of species that construct deep roots increased in more arid climates (Fig. 4e,f). The interaction was weak because the importance of shallow roots in humid climates increased slightly in sites with shallower water tables (Fig. 4f,h).

Trait-by-environment interactions generated highly contingent occurrence landscapes. Landscapes of probabilities illustrate the trait values and environments that optimize species occurrence probabilities and can be viewed through two perspectives: first, as functions of aridity, seasonality, and water table depth for each of the four plant strategies (Fig. 5); and second, as functions of  $P_{50}$  and rooting depth in different combinations of aridity, seasonality, and water table depth (Fig. 6).

Each strategy was most likely to occur in different environments. First, resistant avoiders (species with low  $P_{50}$  and deep

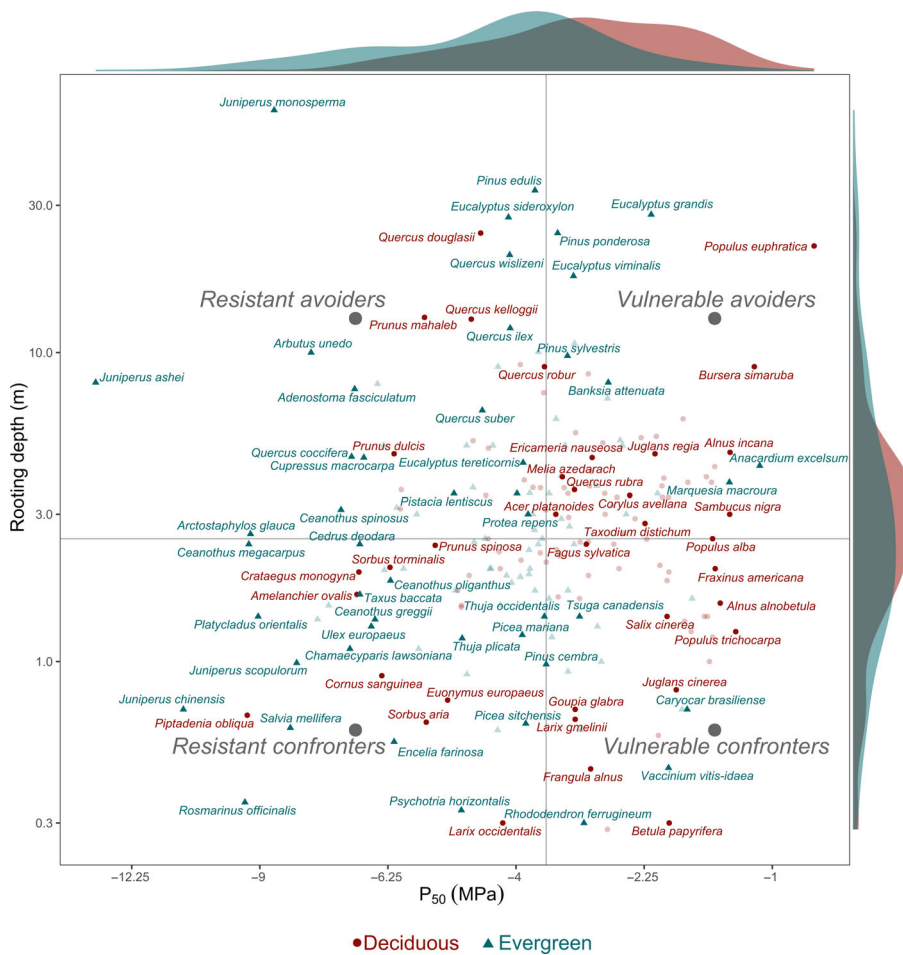


**Fig. 2** Xylem vulnerability to embolism ( $P_{50}$ ) mapped onto the phylogeny of woody plants, where the color of the internal tree branches show vulnerability based on maximum likelihood-based ancestral state reconstruction. Dark colors indicate more resistant xylem and light colors indicate more vulnerable xylem (see key in the center). The outer bars represent maximum rooting depth (log-scale) for each species, where longer bars represent deeper roots (see lower left for rooting depth scale legend). Pictures of representative species of major clades are illustrated around the phylogeny.

roots that avoid drought) were most likely to occur in arid and seasonal climates in sites with deep water tables (Figs 5a, 6a). Second, resistant confronters (species with low  $P_{50}$  and shallow roots that confront drought) were most likely to occur in arid and non-seasonal environments in sites with deep water tables (Fig. 5c). Third, vulnerable avoiders (species with high  $P_{50}$  and deep roots that avoid drought) were most likely to occur in arid and

nonseasonal climates in sites with shallow water tables (Figs 5b, 6c). Fourth, vulnerable confronters (species with high  $P_{50}$  and shallow roots that confront drought) were most likely to occur in humid climates at any water table depth (Figs 5d, 6b,d).

Trends in occurrence probabilities for deciduous species were qualitatively similar to full model results (Fig. S2). However, resistant confronters and vulnerable avoiders with evergreen



**Fig. 3** Distribution of species in the bivariate trait space defined by maximum rooting depth and mean  $P_{50}$ . Vertical and horizontal lines denote the 50<sup>th</sup> percentiles of the traits. Species names associated with bold symbols were selected by an algorithm to represent as much of the occupied trait space as possible because not all names could easily fit. The four gray points represent the 5<sup>th</sup> and 95<sup>th</sup> percentiles of the trait distributions ( $-7.0$  and  $-1.5$  MPa for  $P_{50}$ ;  $12.9$  and  $0.6$  m for rooting depth) to represent each of the four plant strategies. The curves depict the distribution of values across each of the two trait axes for each leaf type.

leaves exhibited relatively flat occurrence landscapes, suggesting that the full model results for these two strategies were driven by deciduous species (which comprised *c.* 50% of the species in this dataset). Rooting depth did not differ among soil texture classes, although rooting depth was significantly shallower in water-logged soil (Fig. S3).

## Discussion

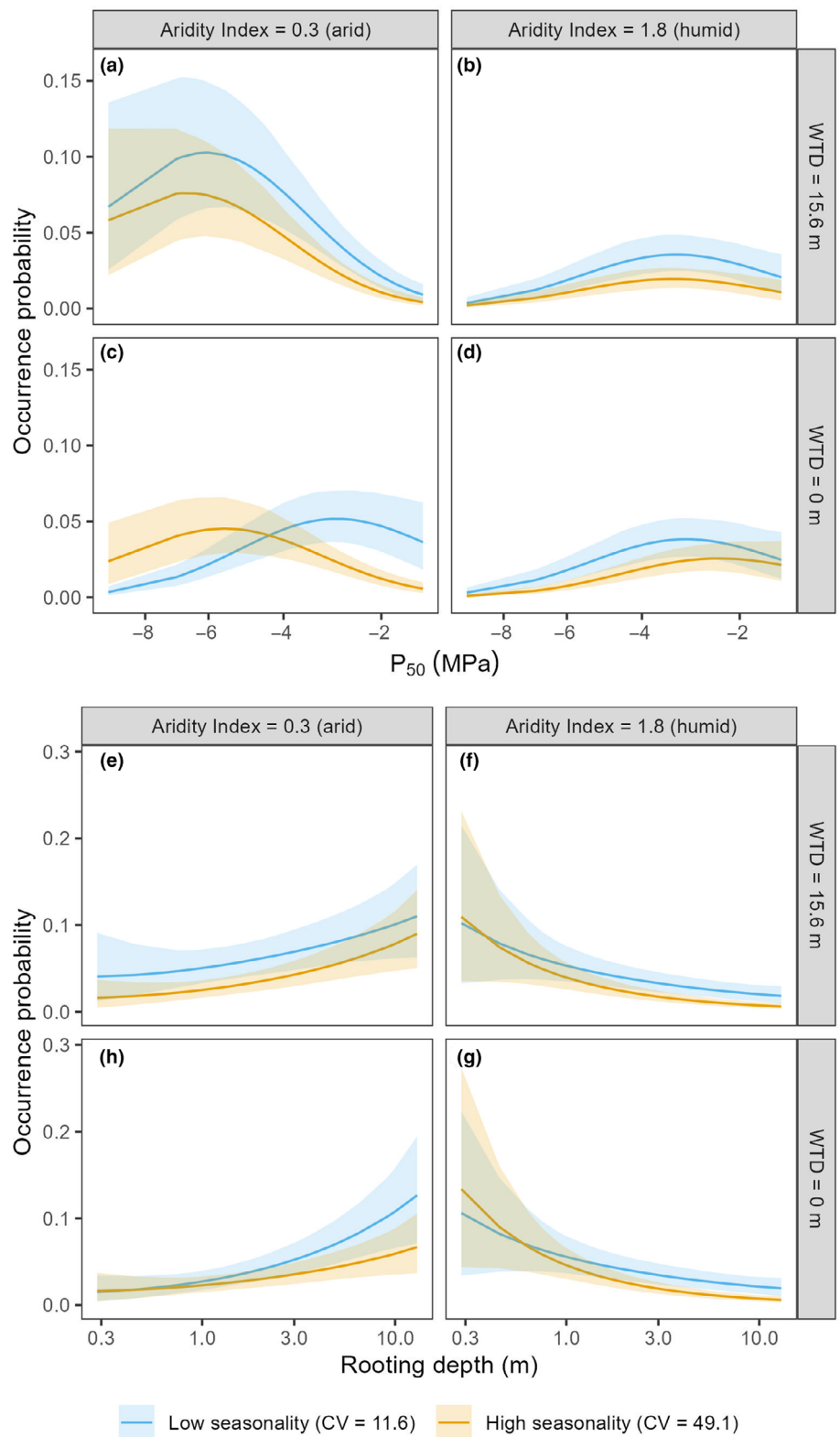
Xylem vulnerability to drought-induced embolism and maximum rooting depth have each been separately investigated as drivers of drought resistance and avoidance in woody species (Canadell *et al.*, 1996; Choat *et al.*, 2012), yet their phylogenetic correlation and the joint effect of these traits on species distributions were unknown until now. Here, we have shown that: (1) drought resistance and avoidance are independent woody plant strategies; and (2) each of the four combinations of  $P_{50}$  and rooting depth values optimizes occurrence probabilities in unique conditions of water availability.

First, it has been suggested that drought resistance trades-off with drought avoidance because species in a tropical forest were either shallow-rooted trees that built resistant xylem or were deep-rooted trees that built vulnerable xylem (Brum *et al.*, 2019). This proposed trade-off assumed that investment

in deep root systems comes at a cost of constructing vulnerable xylem. However, our large sample across the phylogeny of woody plants provides evidence that  $P_{50}$  and rooting depth are phylogenetically uncorrelated (Fig. 3). The many species that deviate from the proposed correlation provide insight into the independent adaptive value of these two traits (Carlquist, 1975). The large investment into growth and maintenance of deep roots and resistant xylem must be offset by the fitness gains that are made possible by deep roots and resistant xylem in dry environments. By contrast, other plant species construct shallow root systems and vulnerable xylem to make abundant leaves above their neighbors to maximize fitness in wet environments. Drought resistance and avoidance do not exhibit a trade-off and species representing most major clades of woody plants have been able to explore the full range of combinations of these two traits to occupy a broad range of environments (Fig. 1).

Second,  $P_{50}$  and rooting depth jointly explain species distributions across broad gradients in three measures of water availability. In fact, each combination of trait values optimizes occurrence probabilities in unique environments, thereby advancing our conceptual understanding of how species may respond to changing water availability under climate change. Our modeling results suggest that forecasting woody species

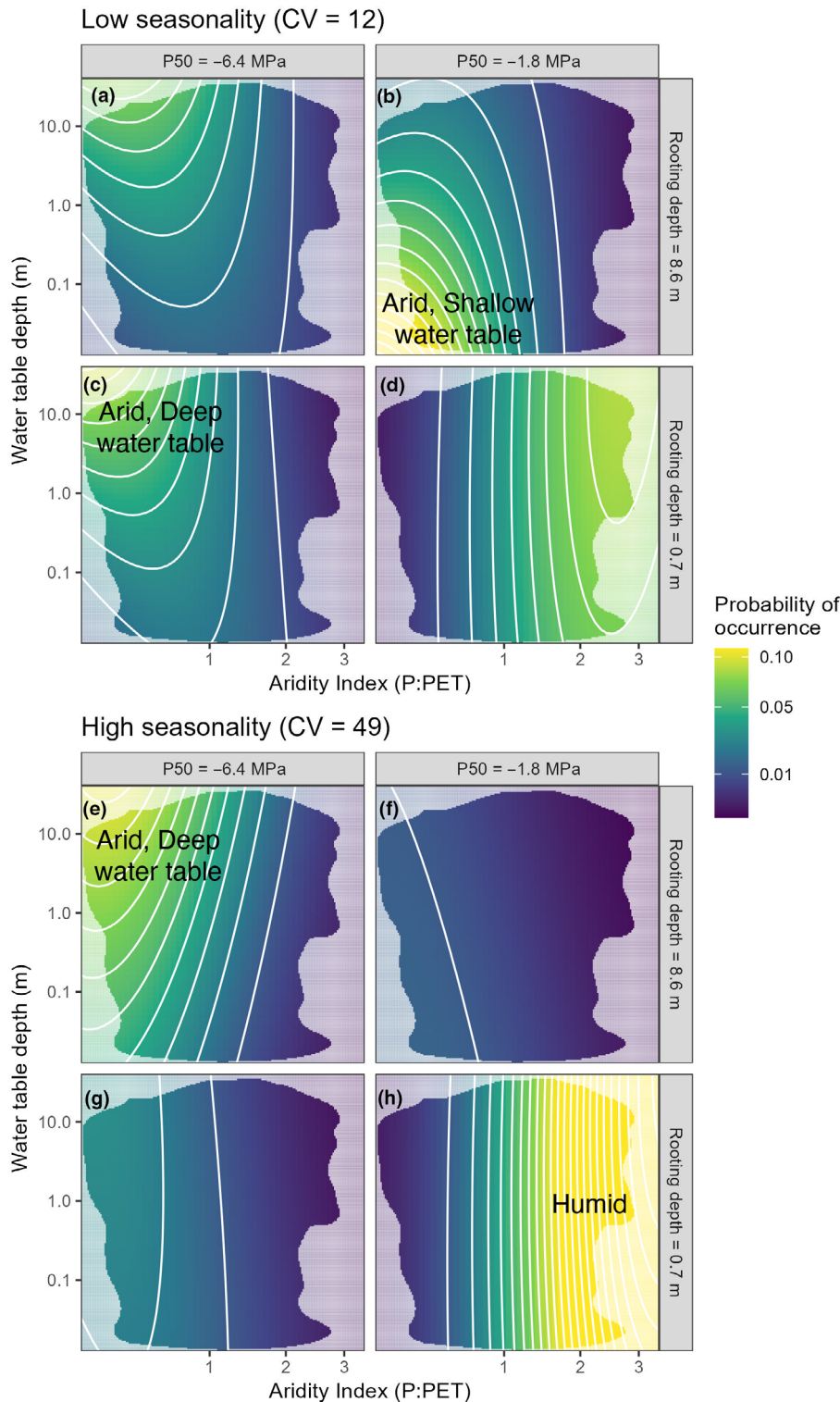




**Fig. 4** (a–d) Effects of  $P_{50}$  on occurrence probability (with rooting depth held at its average value, 2.6 m) at the 5<sup>th</sup> and 95<sup>th</sup> percentiles of the aridity index, seasonality, and water table depth (WTD). (e–h) Effects of rooting depth on occurrence probability (with  $P_{50}$  held at its average value, -3.6 MPa) at the 5<sup>th</sup> and 95<sup>th</sup> percentiles of the aridity index, seasonality, and water table depth (WTD). Note that the 5<sup>th</sup> percentile of WTD was close to zero meters.

range shifts in response to changing climate must also consider topographically mediated hydrologic regimes. While both xylem vulnerability and rooting depth were more strongly related to aridity, they interacted with water table depth to

determine species occurrence probabilities. Given that water table depth is relatively independent of regional climate (Fan *et al.*, 2017), if evaporative demand changes faster than water table depth under climate change, then deeply rooted

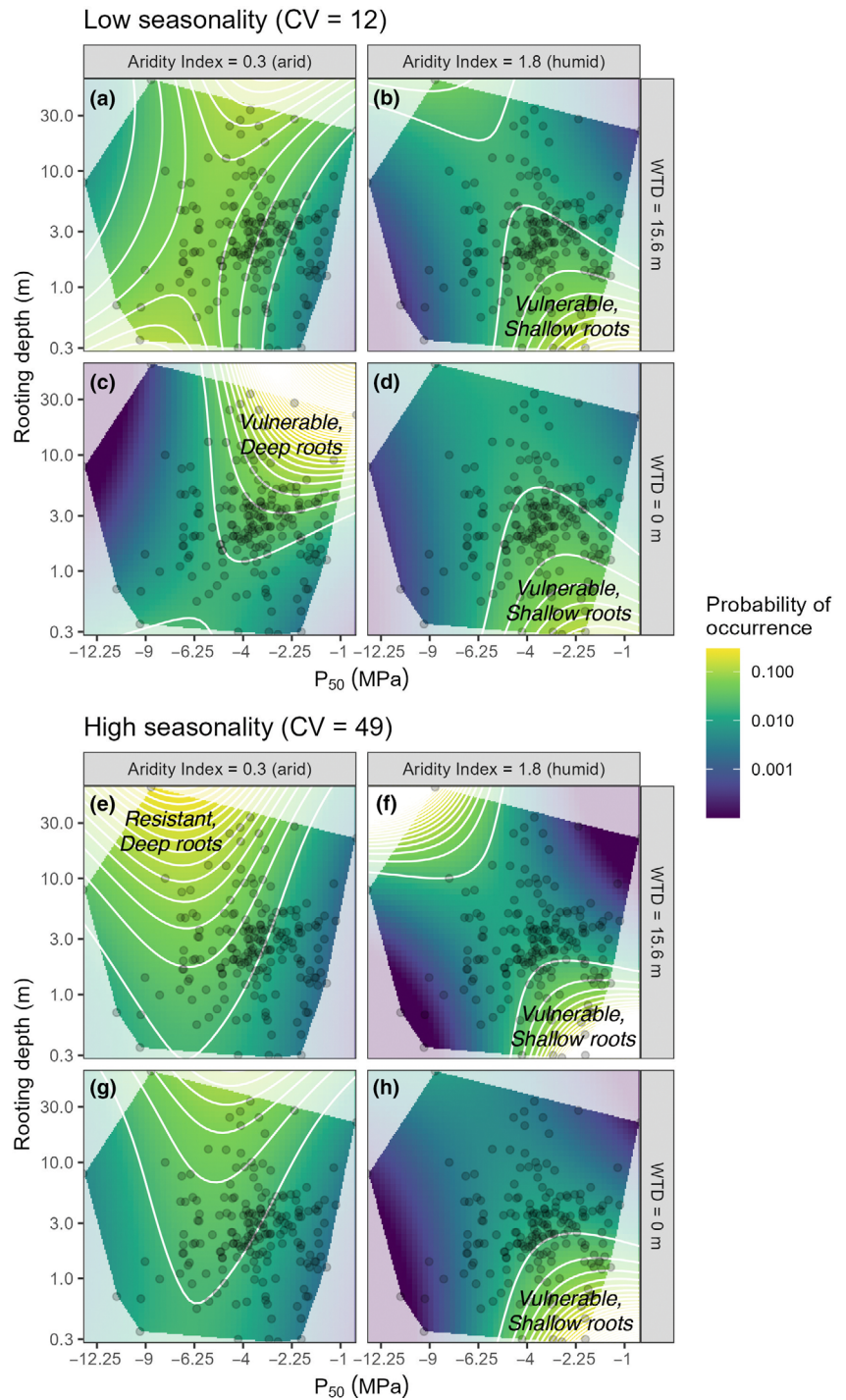


**Fig. 5** Occurrence probability landscapes illustrating changes in the probability of woody species occurrence for each of the four plant strategies (i.e. set as the 5<sup>th</sup> and 95<sup>th</sup> percentiles of  $P_{50}$  and maximum rooting depth) along continuous gradients of the aridity index and water table depth at the 5<sup>th</sup> and 95<sup>th</sup> percentiles of precipitation seasonality. (a) resistant xylem, deep roots, low seasonality; (b) vulnerable xylem, deep roots, low seasonality; (c) resistant xylem, shallow roots, low seasonality; (d) vulnerable xylem, shallow roots, low seasonality; (e) resistant xylem, deep roots, high seasonality; (f) vulnerable xylem, deep roots, high seasonality; (g) resistant xylem, shallow roots, high seasonality; (h) vulnerable xylem, shallow roots, high seasonality. Warm colors indicate higher probability of occurrence and cool colors indicate lower probability of occurrence. Black text highlights the environmental conditions where occurrence probabilities are maximized for each trait combination. The environmental space is masked to emphasize the 99<sup>th</sup> percentile of observed environmental variation. Contour interval = 0.01.

vegetation responses may be buffered in the near-term by stable water table depths and soil moisture in the deep vadose zone.

To facilitate the interpretation of model results based on a complex five-way interaction of continuous traits and environments, we discuss each of the four strategies that represent low and high values of each trait in turn (Figs 1b, 3, 5). First, resistant avoiders (low  $P_{50}$  and deep roots) exhibit, in theory, the most

drought-tolerant strategy because they can withstand substantial negative pressure in their xylem and at the same time are also able to avoid these strongly negative pressures when accessing deep soil water reservoirs (Hammond *et al.*, 2019; Tumber-Dávila *et al.*, 2022). This strategy is most likely to occur in arid, seasonal climates over deep water tables (Figs 5e, 6e). This result was consistent for deciduous and evergreen species, but most resistant



**Fig. 6** Occurrence probability landscapes illustrating changes in the probability of woody species occurrence in different environments (i.e. set as the 5<sup>th</sup> and 95<sup>th</sup> percentiles of the aridity index and water table depth (WTD) at the 5<sup>th</sup> and 95<sup>th</sup> percentiles of precipitation seasonality along continuous gradients of  $P_{50}$  and maximum rooting depth. (a) arid, deep water table, low seasonality; (b) humid, deep water table, low seasonality; (c) arid, shallow water table, low seasonality; (d) humid, shallow water table, low seasonality; (e) arid, deep water table, high seasonality; (f) humid, deep water table, high seasonality; (g) arid, shallow water table, high seasonality; (h) humid, shallow water table, high seasonality. Warm colors indicate higher probability of occurrence and cool colors indicate lower probability of occurrence. Black text highlights the trait combinations that maximize occurrence probabilities in each environmental condition. The trait space is masked to illustrate the convex hull of observed trait values. Contour interval = 0.01.

avoiders were evergreen (Fig. S2E). For example, the evergreen angiosperm *Arbutus unedo*, a small tree that grows in Mediterranean chaparral on dry slopes and ridges, and the evergreen gymnosperm *Juniperus monosperma*, a small tree that grows in arid deserts, illustrate how resistant xylem and deep roots optimize growth and survival in arid uplands. Constructing both deep roots and resistant xylem is the optimal strategy to survive in the driest environments on earth.

Second, resistant confronters (low  $P_{50}$  and shallow roots) are most likely to occur in arid, nonseasonal climates over deep and

inaccessible water tables. This agrees with previous empirical work that arid environments contain both deep and shallow-rooted species (Fan *et al.*, 2017) yet clarifies that shallow roots are more adaptive in nonseasonal arid climates where more consistent precipitation (albeit modest amounts) wets the top soil layers throughout the year. This result appeared to be driven by deciduous species, such as *Amelanchier ovalis*, which grows in open sites in drier climates, but evergreen species, such as *Encelia farinosa* and *Juniperus scopulorum*, also grow in dry habitats with well-drained soils (Ehleringer, 1993).

Third, vulnerable avoiders (high  $P_{50}$  and deep roots) are most likely to occur in arid, nonseasonal climates over shallow and likely accessible water tables. This result was also most evident in deciduous species. This strategy may be emblematic of deep-rooted, phraetophytic species that occur in desert riparian zones (Loheide *et al.*, 2005), where they can easily extend their root system to the shallow water tables (but no deeper than needed (see Fan *et al.*, 2017)) to access water from the saturated zone to drive the high transpiration rates that are associated with deciduous leaves and high-capacitance xylem. For example, the deciduous *Populus euphratica* grows in central Asian river flood plains in arid regions (Bruehlheide *et al.*, 2010). This combination of traits is likely to also occur in humid tropical climates with a dry season over deep water tables, where plants access water in the deep vadose zone (Brum *et al.*, 2019; Miguez-Macho & Fan, 2021). Our model did not detect this latter effect because the dataset included few observations of species that occur in these environments (Fig. 1b,c), highlighting the need for more measurements of these traits in tropical regions.

Fourth, vulnerable confronters (high  $P_{50}$  and shallow roots) present, in theory, the least drought-tolerant strategy because root-to-shoot conductance can decline under weak negative xylem pressure that cannot be overcome by access to deep soil water (Hammond *et al.*, 2019; Tumber-Dávila *et al.*, 2022). This strategy is most likely to occur in humid climates, regardless of water table depth. This result was consistent for deciduous and evergreen species. For example, the deciduous angiosperm *Salix cinerea* is a medium-sized shrub that grows in wetlands in humid climates, and *Juglans cinerea* is a deciduous angiosperm tree that grows in humid climates ranging from streambanks to well-drained slopes. Other drought-related traits that were not measured here, such as leaf turgor loss point, could further explain how species that are vulnerable confronters such as *Juglans cinerea* can survive in well-drained dry soil, yet turgor loss point was not available for most of the 188 species in this dataset.

Our work represents the first systematic analysis of the combined effect of drought resistance and avoidance on the global distribution of woody species. Yet, some limitations of the study deserve attention. First, maximum rooting depth is underestimated due to the logistical difficulty of measuring this trait, and rooting depth within species responds plastically to variation in soil water depth (Schenk & Jackson, 2005; Fan *et al.*, 2017). Given the low number of replicated trait observations within species (Table S1; Fig. S1), our analysis was unable to evaluate the phenotypic plasticity of each trait and whether individual species could acclimate to changing vapor pressure deficits and soil water availability. We urge researchers to develop methods to simultaneously measure xylem vulnerability and rooting depth on individual plants in their environments to refine predictions of drought sensitivity and adaptive capacity. This new data would be the only way to test for an intraspecific trade-off between drought resistance and avoidance. Second, our analysis does not predict the growth, survival, and reproduction of different ontogenetic stages of trees, and these are the fitness components that are

important to population dynamics that lead to range shifts (Merow *et al.*, 2017). Our analysis is an important first step to determine the joint effect of these critical traits on species responses to changing aridity, seasonality, and water table depth, but future work should link these trait-by-environment interactions to demographic rates and population growth rates to improve forecasting generality (Laughlin *et al.*, 2020b). Third, the limited data availability for drought-deciduous species prevented us from understanding how the drought escape strategy relates to drought resistance and avoidance. Fourth, integrating empirical measurements of soil texture and depth will further clarify limitations on rooting depth. Future work should address these limitations.

The earliest plants to colonize the land emerged in humid tropical environments and likely did not stray too far from shorelines and streambanks in humid atmospheres with shallow water tables (Willis & McElwain, 2014; Bouda *et al.*, 2022). The evolution of increasing resistance to embolism and extension of roots deep into the soil profile permitted species to occupy increasingly drier environments, and these traits have retained their adaptive advantages to this day. Simultaneous understanding of drought resistance and avoidance strategies that have evolved across the phylogeny of woody plants will enhance our predictions of vegetation response to changing water availability and guide species selection in ecological restoration projects (Laughlin *et al.*, 2017; McDowell *et al.*, 2022).

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## Competing interests

None declared.

## Author contributions

DCL designed the study. AS, JRF and DCL conducted the data analyses. DCL and AS wrote the first draft, and SJT-D, WMH, FMS, GD, IA, RF, MZH, SJ, JL, FL, JKM, UN, OLP and HB provided data and contributed substantially to early drafts of the manuscript. FA, YB, HHB, CB, RC, JD,

MDS, JD, BJA, BH, JH, JK, PM, MM, JN, AN, JP, MS, ZS, FS and RMU provided data and contributed substantially to revising the manuscript.

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## Data availability

Data and code to reproduce the results are available at doi: [10.25829/ndiv.3555-akwd44](https://doi.org/10.25829/ndiv.3555-akwd44).

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Ranges of minimum and maximum rooting depth and  $P_{50}$  of species in the study, and sensitivity analysis of bivariate phylogenetic correlation.

**Fig. S2** Occurrence probability landscapes for deciduous and evergreen species.

**Fig. S3** Effects of soil texture on rooting depth on individual values.

**Table S1** Species-level trait values of species in this study.

**Table S2** Fitted model coefficients for the trait-by-environment model.

**Table S3** Fitted model coefficients for the environment-only model.

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