

Variation and trade-off in drought versus frost resistance in trees

³ Maximilian Larter ^{1,2}, Guillaume Charrier ², Sylvain Delzon ¹, Anne Baranger ³, and Georges Kunstler ³

⁴ ¹Univ. Bordeaux, INRAE, BIOGECO, 33600 Pessac, France

⁵ ²Univ. Clermont Auvergne, INRAE, PIAF, 63000 Clermont-Ferrand, France

⁶ ³Univ. Grenoble Alpes, INRAE, LESSEM, 38400 St-Martin-d'Hères, France

⁷ Drought and frost stresses play important roles in determining species distributions, especially at the range margins. Understanding how stress resistance related functional traits interact to determine species vulnerability to climate change is increasingly critical. Despite similarities in how drought and cold stress affect plant physiology, these stresses and associated resistance traits are typically studied separately.

¹¹ We developed a global database of published data and new measurements and investigated evolutionary trade-offs between drought resistance (xylem embolism resistance; P_{50}) and frost resistance (cell mortality; LT_{50}). Across all woody biomes, embolism resistance ranged from -1 to -19 MPa, and frost resistance from 0 to below -80 °C. We found a weak trade-off between drought and frost resistance: drought-resistant species tend to be less frost hardy, and frost-resistant species are vulnerable to drought. Very few species are extremely resistant to both stresses (e.g. junipers) but many species are vulnerable to both stresses.

¹⁷ Although drought-resistant species tended to be shorter with tougher leaves, had denser wood and narrower xylem conduits, we found no trade-off between growth related functional traits and frost resistance. We find that specialist "survivors" on the global fast-slow economics spectrum are not necessarily great at resisting both stresses, and don't necessarily sacrifice growth potential relative to "fast" but vulnerable species.

²¹ drought stress | embolism resistance | xylem | frost | trade-off |

²² Correspondence: *maximilian.larter@gmail.com*

23 Introduction

24 Climate extremes like freezing temperatures and severe droughts play a leading role in determining tree species
25 distributions, which are mainly limited at the cold margins by frost tolerance and on the warm margins by drought
26 resistance (Richardson and Bond, 1991; Hampe and Petit, 2005; Chaot et al., 2018; Körner, 2021; Baranger
27 et al., 2024). Climate change has already deeply modified rainfall and temperature patterns in many areas of
28 the world, and increased the stochasticity and duration of extreme climate events such as droughts and heatwaves
29 (Masson-Delmotte et al., 2021). It is causing large-scale tree mortality events following droughts, documented in
30 all forested ecosystems (Allen et al., 2010; Anderegg et al., 2015). A general warming pattern could also increase
31 vulnerability to sudden autumn and winter cold snaps and spring frosts (Matusick et al., 2014; Greco et al., 2018;
32 Körner, 2021; Vanoni et al., 2016). From boreal to Mediterranean ecosystems, forests are therefore likely to be
33 exposed to more frequent, alternating frost and drought stresses, with compounding effects on productivity and
34 survival (Charrier et al., 2021; Vitasse et al., 2019). By their sessile nature, woody perennial plants must survive
35 seasonal frost and drought, and compete for resources with other species in order to grow and reproduce. This leads
36 to balancing selection pressures: 1) between different stress resistance traits (e.g. frost vs. drought resistance), and
37 2) between stress resistance and growth or reproduction traits on the other (Grime, 1977; Reich, 2014). In particular,
38 direct and indirect fitness costs and benefits of functional traits related to frost and/or drought resistance can result in
39 trade-offs within the plant, in turn determining their ability to compete and survive, especially at the margins of their
40 species' distribution (Sanchez-Martinez et al., 2023). Understanding how tree functional traits interact to determine
41 species-specific response to extreme frost and drought is crucial in order to be able to predict climate change impact
42 on forest dynamics at local and continental scales (Aubin et al., 2016; Pollock et al., 2012; Stahl et al., 2014; Wiens,
43 2016).

44 From a mechanistic point of view, we can expect either synergies or antagonisms between drought- and
45 frost-resistances in woody plants, depending on the compartment and process considered. Both stresses trigger
46 shared signaling pathways, and induce similar regulatory and molecular responses, impact xylem water transport
47 and induce tissue dehydration (Charrier et al., 2021; Beck et al., 2007; Zhang et al., 2020), ultimately leading to
48 cell death (Mantova et al., 2023; Sakai and Larcher, 1987b). Additionally, exposure to drought has been shown
49 to promote frost resistance in some species (Medeiros and Pockman, 2011; Sierra-Almeida et al., 2016; Sumner
50 et al., 2022), but not all (Fernández-Pérez et al., 2018). Finally, some comparative studies have shown that
51 drought and frost resistance traits can be correlated across species (Visakorpi et al., 2024; Pescador et al., 2016),
52 or not so (Charra-Vaskou et al., 2012; Francescantonio et al., 2020; Rueda et al., 2017). Across populations of
53 Douglas-fir, drought and frost resistance are positively correlated along a winter temperature gradient, but negatively
54 across a summer precipitation gradient (Bansal et al., 2016). When examining species ranges and associated
55 site characteristics to define a species stress tolerances, the relationships between abiotic stressors also appear
56 complex, with a drought-frost resistance trade-off modulated by interaction effects with other stresses such as

water-logging or shade (Puglielli et al., 2021; Laanisto and Niinemets, 2015). At the vascular level, both stresses can lead to reductions in water flow through the xylem, through drought- and freeze-thaw-induced embolism (Charrier et al., 2021), leading to potential synergies between frost and drought stress resistance. During drought, the increase in xylem tension in the sap stream causes air-bubbles to be pulled into functional conduits through pores in the cell walls (Sperry and Tyree, 1988; Tyree and Sperry, 1989; Delzon et al., 2010). In winter, temperature fluctuations cause xylem sap to cycle between solid and liquid phase, whereupon dissolved gases can come out of solution and form air bubbles, which in turn can nucleate cavitation and expand to embolize the conduit. Wider vessels result in larger air bubbles less likely to redissolve into solution on thawing, therefore, vulnerability to freeze-thaw embolism is known to scale with increasing xylem conduit diameter (among other factors) (Charrier et al., 2014; Pittermann and Sperry, 2003; Hacke and Sperry, 2001; Sperry and Sullivan, 1992; Davis et al., 1999). While the mechanism of air-seeding is not identical, both are linked to the presence of air dissolved in functional conduits or at atmospheric pressure in embolized ones (Tyree and Zimmermann, 2002). Strategies for resisting summer embolism could make winter embolism less likely - and the reverse is also true - leading to an indirect correlation (Torres-Ruiz et al., 2016; Christensen-Dalsgaard and Tyree, 2013). Furthermore, because drought resistant species tend to have xylem conduits with thicker cell walls relative to lumen size to maintain hydraulic function under very negative xylem pressures (Sperry et al., 2006; Pittermann et al., 2006; Bouche et al., 2014; Larter et al., 2017), we could expect smaller conduits to favor both resistance to drought and freeze-thaw embolism (Mayr et al., 2006) but see (Zhang et al., 2024). On the other hand, carbon costs of xylem anatomical changes associated with establishing resistance to either type of stress could limit resources available for resisting the other type of stress. On top of higher carbon investment in cell wall thickness woody tissue of species in dry environments tend to be denser with a higher proportion of fibers, due to increased mechanical stress during drought. This high demand for structural carbon in dead cell walls, and a reduced carbon storage compartment could reduce the availability of non-structural carbohydrates necessary for the energy intensive cellular and molecular changes that occur during early winter hardening (Baffoin et al., 2021; Charrier et al., 2021; Charrier and Améglio, 2011; Sakai and Yoshida, 1968; Sakai and Larcher, 1987a). However, the xylem of drought-resistant woody species can also have a higher proportion of axial and ray parenchyma (Morris et al., 2016; McDowell et al., 2022), which plays a role both in water storage (i.e. hydraulic capacitance) and non-structural carbohydrate (NSC) storage. This interdependency between water and carbon economies likely plays a role in mortality during drought or cold snaps (Bond and Midgley, 2001; Trueba et al., 2024; McDowell et al., 2022), and a shared, albeit limited pool of NSCs necessary for drought and cold stress responses could facilitate surviving hot dry summers and harsh winters (Blumstein et al., 2023). Conversely, mild summer drought can actually cause an increase in carbohydrate reserves, because growth stops before photosynthesis (McDowell et al., 2011; Muller et al., 2011; McDowell, 2011), and drought stress can induce an increase in frost hardness in some species, with lower water content and higher solute concentration lowering the freezing point (Charrier et al., 2021). However, prolonged summer drought induces carbon starvation, when respiration outpaces photosynthesis, thereby depleting NSC reserves (McDowell et al., 2011, 2022), critical for

winter frost response (but see ([Harbol et al., 2023](#))). Similarly, cold snaps consume NSCs, decreasing growth and summer resilience to drought ([Camarero et al., 2023](#); [Alderotti et al., 2024](#); [D'Andrea et al., 2020](#); [D'Andrea et al., 2021](#)).

Across gymnosperm and angiosperm trees, xylem embolism resistance, i.e. the xylem pressure inducing a 50% drop of hydraulic conductance (P_{50}) has been identified as a key functional trait directly linked to mortality ([Brodribb and Cochard, 2009](#); [Urli et al., 2013](#); [Anderegg et al., 2016](#)) and broadly correlated to aridity and species distributions ([Delzon et al., 2010](#); [Larter et al., 2017](#); [Skelton et al., 2021](#); [Brodribb and Hill, 1999](#); [Maherali et al., 2004](#)). Although additional parameters are needed to determine time to death during drought (PsiTLP, Sureau paper), and other strategies regarding extreme drought exist (such as avoidance through deep rooting systems or succulence), it is considered a good proxy of drought resistance in trees. In spite of this broad consensus, some methodological issues have brought into question many old and more recent measurements, making the aggregation of large databases challenging. Negative temperatures induce the formation of intra- and extra-cellular ice crystals, inducing intensive dehydration and disrupts cell membranes, all of which are lethal to plant cells ([Sakai and Larcher, 1987b](#)). At the onset of winter, environmental cues trigger woody plants acclimation for the coming freezing temperatures, notably by lowering the freezing point of the intracellular compartment, mobilizing internal carbon resources and decreasing bulk water content, synthesizing anti-freeze proteins, and changing the composition of their cell membranes ([Weiser, 1970](#); [Sakai and Larcher, 1987c](#); [Charrier et al., 2021](#); [Baffoin et al., 2021](#)). These processes allow them to tolerate the formation of extra-cellular ice-crystals, and living cells to survive negative temperatures for the winter months. Hardened tissues of some species can survive in a deep frozen state for several months, in some cases for boreal species even recovering from the temperature of liquid nitrogen ([Sakai and Larcher, 1987b](#)). By quantifying cell damage of winter-hardened tissues after exposure to extreme negative temperatures, we can measure a species maximum frost resistance. Different methodologies have been used since the 1960 ([Dexter et al., 1932](#); [Anisko and Lindstrom, 1995](#); [Kovaleski and Grossman, 2021](#)), and to our knowledge global unifying databases are lacking (but see ([Lancaster and Humphreys, 2020](#))). While trees' ability to withstand drought without reaching damaging xylem embolism levels and extreme cold temperatures without cell death are recognized as critical traits for plant survival, they have seldom been studied together in a comparative framework ([Charrier et al., 2021](#); [McCulloh et al., 2023](#)), limiting our understanding of how drought and frost resistance traits evolve in stress-tolerance syndromes (ref).

From an evolutionary perspective, woody angiosperms are thought to have moved poleward into seasonally freezing environments from frost-free tropical forests by co-opting adaptations to seasonal drought, such as deciduousness, herbaceousness or narrow embolism-resistant conduits ([Zanne et al., 2014](#); [Preston and Sandve, 2013](#)) (but see ([Stolsmo et al., 2024](#))). Conifer physiology and anatomy is thought to allow them to tolerate both cold and dry environments explaining in part how they were able to persist in the face of the radiation of angiosperms, competing successfully at least in harsh and nutrient-poor habitats ([Augusto et al., 2014](#); [Bond, 1989](#)). Plant species traditionally assigned to "slow" ecological strategy are often thought of as slow growing, long-lived, stress resistant species, based either on their performance in a given habitat or their traits ([Volaire et al., 2022](#)). These traits, e.g. long lived

leaves with high dry matter content and high wood density, should both be positively correlated with drought and frost resistance. Conversely, in this framework, investment in resistance traits (either frost or drought resistance, or both) should limit allocation to growth, resource acquisition and reproduction, which is sometimes called a physiological or allocation trade-off ([Grime, 1977](#); [Stearns, 1992](#); [Willi and Van Buskirk, 2022](#)). Therefore, even if not functionally directly linked, we can expect positive evolutionary correlations between functional traits linked to drought resistance and frost resistance, which could be in turn negatively correlated to functional traits of "fast" ecological strategies.

Evolutionary constraints between functional traits could be restricted to the tails of trait distributions, and not be apparent if using means-based regression methods. For example, in dry environments, embolism resistance could exert constraints on the evolution of frost resistance, whereas frost resistance is constrained by other factors in more humid environmental conditions (e.g. nutrient availability or shade tolerance). Furthermore, we

In this study, we constructed an unprecedented global database of embolism resistance and frost resistance in woody plants, building on existing knowledge and adding a large number of new measurements. We tested whether (1) there is no trade-off between drought resistance and cold resistance traits, and therefore some trait combinations exist that allow woody plants to be adapted to both extreme cold and extreme drought, or if (2) there is a strong direct trade-off between drought resistance and frost resistance, with the absence of poly-stress resistance traits combinations ([McCulloh et al., 2023](#)). In this case, we further expected (3) a trade-off between stress-resistance traits on the one hand and traits enhancing resource acquisition or competitive ability, such as maximum height, hydraulic efficiency, leaf area or wood density on the other.

145 **Methods**

146 **Frost resistance database**

147 We obtained frost resistance data from the literature, using search terms 1) "frost", "cold" and 2) "resistance",
148 "tolerance", or "hardiness". We limited our search to trees, shrubs and woody species. Overall, we collected
149 data from around 200 references in tables, supplementary data or directly from figures when necessary using
150 WebPlotDigitizer ([Rohatgi, 2022](#)). From these papers, combined with unpublished data (Charrier, pers. comm.), we
151 accumulated a database of around 4000 measurements in over 600 species. We also recovered as much metadata
152 as possible regarding the experimental setup, including the date and location of the study, the age of the plant, which
153 organ/tissue was used, and other parameters of the experiment, such as which technique was used, the rate of
154 temperature change, and the duration of exposure at the lowest temperature. As a first step, based on the date of
155 the study, we removed from all measurements that were not from the middle of winter, so that natural hardening
156 had occurred, and the late-winter de-hardening process had not started. These measurements included data from
157 various plant organs (mainly leaves, stems, buds), and using different techniques. Briefly, two main methods exist in
158 the literature that both examine samples for damage after exposure to cold temperatures. Firstly, the visual scoring
159 technique (VS) is based on visual examination of multiple tissue samples exposed to different cold temperatures,
160 and LT_0 ($^{\circ}\text{C}$) is recorded as the coldest temperature at which the samples did not show cell damage, usually a visible
161 necrotic discoloration of the tissue ([Sakai and Larcher, 1987b](#)). The electrolyte leakage technique (EL) employs a
162 similar cold temperature gradient, and quantifies the release of electrolytes from plant cells as they die following
163 exposure to cold temperatures. From the sigmoid response curve of the relationship between the relative electrolyte
164 leakage (REL; equation 1) obtained and the minimum temperature of exposure, we can derive the inflection point
165 called LT_{50} ($^{\circ}\text{C}$), i.e. the temperature at which 50% of REL is reached (equation 2). These two techniques result
166 in critical temperature thresholds that describe the species frost resistance. Although measured differently, LT_0 and
167 LT_{50} were well correlated across species considering measurements across all organs ($R^2=0.34$; $p<0.001$; $n=110$
168 species; Suppl. Figure S??), with LT_0 at higher temperatures on average than LT_{50} for the same species and
169 organ, allowing us to keep data from both methods in subsequent analyses. Among branches, buds and leaves,
170 we found LT_0 and LT_{50} to be generally comparable (Suppl. Figure X). However, to ensure as much homogeneity
171 as possible while maximizing the number of species in the dataset, we proceeded as follows: within a species, we
172 averaged all data grouping by organ and by method, resulting in a maximum of six different values per species
173 (branch/bud/leaf by LT_0/LT_{50}). We prioritized measurements using the EL technique, which had protocols that are
174 more consistent across studies (notably regarding freezing rate, see below). Branch data was much more common
175 in the database, and we avoided a bias towards conifers (with fewer deciduous species, therefore with more leaf
176 frost resistance data than for angiosperms) by placing leaf data last. Thus, we selected which value to use based
177 on availability in this order: 1: LT_{50} in branches, 2: LT_{50} in buds, 3: LT_0 in branches, 4: LT_0 in buds, 5: LT_{50} in
178 leaves, 6: LT_0 in leaves. Finally, we also applied a selection criterion based on the age of the plants, selecting only

179 data collected using adult or mature individuals. This mainly excluded experiments on juvenile and/or potted plants,
 180 and data sources not reporting plant age. Additionally, slow freezing and/or thawing rates can artificially induce cold
 181 hardening whereas high rates can artificially increase the probability of intra-cellular ice formation (Weiser, 1970;
 182 Sakai and Larcher, 1987c). We chose arbitrary cut-offs, removing data with rates below 0.2°C h⁻¹ and over 9°C h⁻¹.
 183 This resulted in a "clean" dataset, that was used in the downstream analyses. Although the overall differences across
 184 all species in both datasets are not notable ($R^2 = 0.68$, $p < 0.001$; Suppl. Fig. SX), in some cases the full dataset
 185 over-estimated frost resistance by around 30°C relative to the clean dataset. We also added measurements for 79
 186 species (suppl. materials), focusing on adding species from drier areas (temperate and Mediterranean climates),
 187 which were underrepresented in frost hardness studies. We used the EL technique (Zhang and Willison, 1987),
 188 modified from the protocol described elsewhere (Baffoin et al., 2021). We collected branches from 5 individual trees
 189 per species. Short stem segments from each individual tree were exposed to maximum negative temperatures
 190 of -15, -25, -35, -50, -80°C, as well as a +5°C control, and an extreme treatment using liquid nitrogen aiming to
 191 reach below -100°C for the most frost hardy species. The temperature dynamic was followed using thermocouples
 192 connected to a CR1000 datalogger (Campbell Scientific LTD, UK). For temperature settings between -15 and -50°C,
 193 we programmed four temperature-controlled chambers to drop by 5 K.h⁻¹ from +5°C to the target temperature, hold
 194 for 1 hour at the target temperature, then return to +5°C at a rate of 5 K.h⁻¹. For the -80°C treatment, samples
 195 were placed in a large thermos container inside an -80°C freezer. Using a thermocouple, we monitored temperature
 196 inside the thermos which reached a minimum of around -70°C within a few hours. Thawing was achieved by placing
 197 the samples at room temperature ensuring gradual thawing over several hours. For the extreme treatment, liquid N₂
 198 was placed at the bottom of an expanded polystyrene box. The samples were then placed on a platform and never in
 199 contact with the liquid N₂. A large temperature gradient existed between samples closest to the liquid, monitored with
 200 5-10 thermocouple sensors placed throughout the box. The average minimum temperature across all thermocouples
 201 was used to estimate minimum temperature, which varied from around -90 to -120°C across all experiments. Each
 202 sample from the different temperature steps are then cut into 1 mm thick slices and placed in 15mL of milliQ ultrapure
 203 water, and agitated overnight at 5°C to release the electrolytes into solution. Electrical conductivity was measured
 204 with a standard electrical conductivity meter (c_1), and then measured a second time (c_2) following autoclaving for 30
 205 mins at 120°C to kill all living cells.

206 The ratio of the two conductivities, REL was calculated as follows:

$$REL = c_1 / c_2 \quad (1)$$

207 Then a four-parameter logistic function was fit using nlme (Pinheiro et al., 2023), with the self-starting function SSfpl
 208 (R Core Team, 2023). This function defines REL as a function of temperature (x), such as:

$$REL = a + (b - a) / (1 + e^{d*(x-c)}) \quad (2)$$

209 where c is the inflection point (i.e., LT_{50}), d is the slope at the inflection point and a and a+c the two asymptotes, the
210 minimum and maximum REL at +5°C and at the lowest temperature, respectively. We fit one curve per species with
211 individual as a random effect. The final database contained data of 593 species, from 94 families.

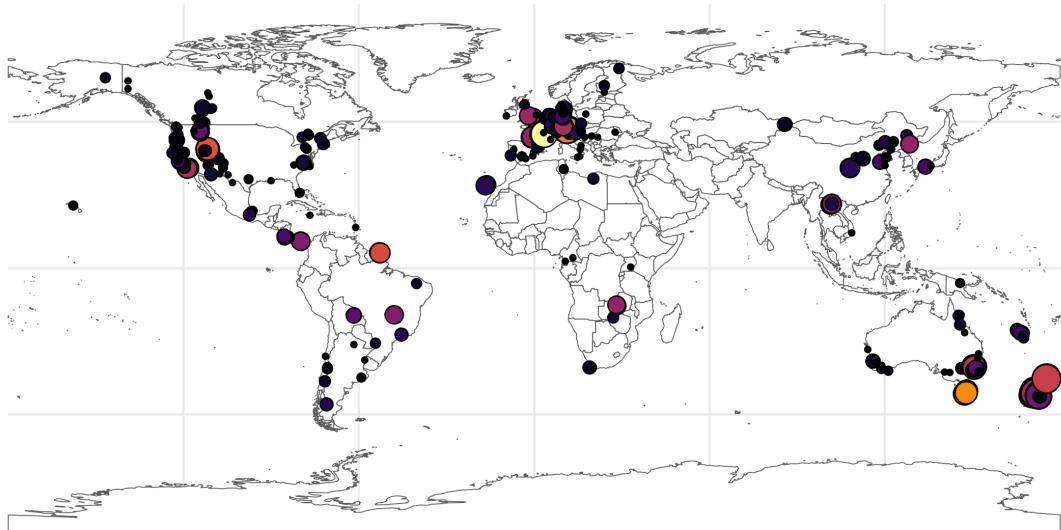
212 **Drought resistance database**

213 We built a large database of embolism resistance, based on previous efforts ([Choat et al., 2012](#); [Hammond et al., 2021](#)),
214 combined with unpublished data ([Larter, 2016](#)) for conifers (124 species), as well as additional measurements
215 for 20 species. The Xylem Functional Traits (XFT) database contains published data of hydraulic vulnerability to
216 drought ([Choat et al., 2012](#)), and updated recently ([Hammond et al., 2021](#)). Since this database included a number of
217 measurement techniques, some of which can induce artifacts that over-estimate vulnerability to embolism ([Cochard
et al., 2010](#); [Wheeler et al., 2013](#); [Torres-Ruiz et al., 2015](#)), we applied strict quality control filters. First, we used
218 the database's curve shape variable to remove vulnerability curves that were not sigmoid in shape, a tell tale sign of
219 the "open-vessel" artifact. We also filtered out many 'r-shaped' curves that were not initially flagged in the database.
220 We kept data for woody species, in stems only, and removed measurements in seedlings, resulting in data for 639
221 species. Finally, to improve coverage of long-vesseled species, we added stem P_{50} data for 25 species from a recent
222 review of non-invasive measurement techniques ([Cardoso et al., 2022](#)), as well as 52 species from a separate
223 curated database (Martin StPaul, pers. comm.). We also added new measurements using the flow-centrifuge
224 technique ([Burlett et al., 2022](#)), focusing on short-vesseled species for which we already had frost resistance data.
225 Overall, the embolism resistance database contained 860 species from 107 families.

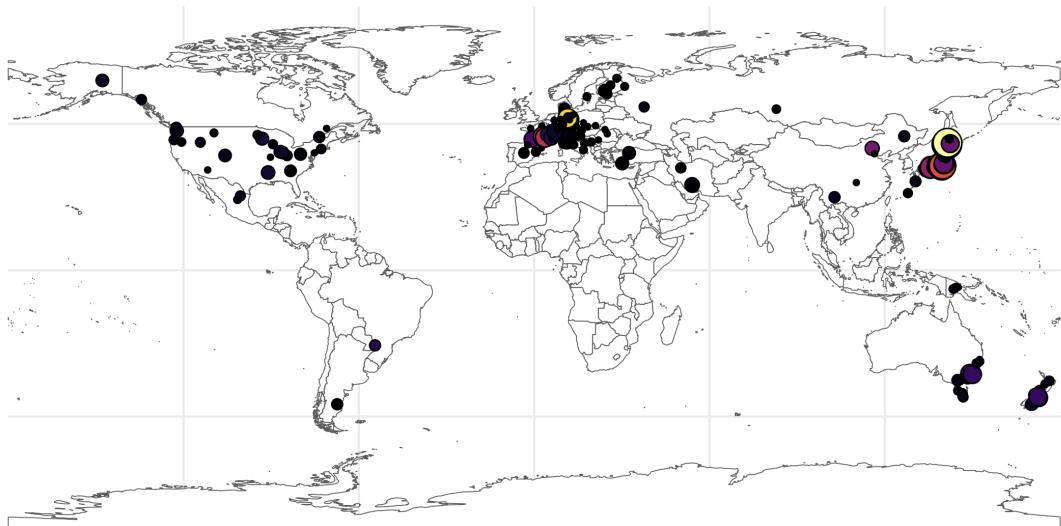
227 **Other traits**

228 To examine the trade-off between species ability to resist stresses and their ability to grow and compete with their
229 neighbors, we obtained the following functional trait data using available published databases: Xylem mean conduit
230 diameter (μm) and xylem specific conductivity (K_s ; $\text{kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-1}$) were taken from physiological studies in the
231 XFT database ([Hammond et al., 2021](#)). We also added xylem conduit diameter data from a recent review of the
232 links between xylem structure and function ([Lens et al., 2022](#)), and conifer K_s from the CaviPlace lab database
233 ([Delzon et al., 2010](#); [Larter, 2016](#)). For wood density (g cm^{-3}), we used the Wood Economics Spectrum database
234 ([Chave et al., 2009](#)), with additional data taken from the XFT and the CaviPlace lab databases. For plant maximum
235 height (m), we obtained maximum height for 111 species from an allometry modeling approach (?). In this database,
236 based on species-specific allometric relationships, maximum height is modeled using measured stem diameter and
237 crown shape data from forestry plots in Europe and North America. We then obtained height data from the Tallo
238 database ([Jucker et al., 2022](#)). After removing outliers (with the "height_outlier" variable), we removed all species
239 with fewer than 100 data points. Because the data is skewed with many small individuals, we ranked the values
240 for each species and took the 10th tallest individual of each species as a measure of species maximum height,
241 resulting in estimates for maximum height for 611 species. These two different estimations of maximum height are

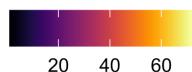
A



B



Number of species



Number of data points



Figure 1. Data distribution of (A) the drought tolerance and (B) frost tolerance databases. Coordinates represent the study site or population of origin of the plants, when that information was available. The color of the points represents the number of different species, and circle size highlights the number of individual data points summarized across all species, for each cell of 1° latitude by 1° longitude.

242 reasonably well correlated, although the Tallo data are generally lower across species ($r^2=***$), with some outliers in
243 gymnosperms, which are much taller according to the modeling approach (**Supplementary figure xx**). We checked
244 these data against information for maximum size from the Gymnosperm Database([Earle, 2024](#)), and found them
245 much closer to the model maximum height than the values derived from Tallo. For these reasons, we chose to use
246 the modeling data when available, and Tallo for the other species. For specific leaf area ($m^2 kg^{-1}$), we used data
247 extracted from TRY ([Kattge et al., 2020](#)), with additional data from the Botanical Information and Ecology Network
248 (BIEN;) using the R package rBIEN ([Maitner et al., 2018](#)).

249 Climate

250 For all species in the physiological traits databases, we obtained climate data across the species range. We
251 downloaded occurrences from GBIF ([GBIF: The Global Biodiversity Information Facility, 2023](#)), and ran error filtering
252 methods available in the rgbif package ([Chamberlain et al., 2023](#)). For species with large numbers of records, we
253 re-sampled the occurrences with random draws, keeping a maximum of 15000 records per species, and keeping
254 a minimum distance of 10km between points ([Aiello-Lammens et al., 2015](#)) to avoid oversampling of highly visited
255 areas of species ranges. From these sets of point coordinates for each species, we extracted climate information
256 from different sources. First, the Worldclim extrapolated climate layers at a resolution of 2.5 minutes ([Fick and](#)
257 [Hijmans, 2017](#)), which we summarized by computing the mean, median and 5th and 95th percentiles for mean
258 annual precipitation (MAP; $mm\ year^{-1}$) and mean annual temperature ($^{\circ}C$). As a better measure of habitat aridity
259 than MAP, we used the aridity index (AI; no unit) from the Global Aridity Index and Potential Evapotranspiration
260 Climate Database v3 ([Zomer, R.J. and Trabucco, 2022](#)). AI in this spatial dataset is based on MAP divided by
261 mean annual potential evapotranspiration, and quantifies the availability of precipitation relative to atmospheric water
262 demand. Finally, to obtain an estimate of the absolute lowest temperature experienced by species, we obtained daily
263 minimum temperature records from the CHELSA dataset ([Karger et al., 2023](#)), using the global daily minimum Near
264 Surface Air Temperature ("tasmin") variable for the period 1980 to 2005. From this series of monthly files over the
265 period, we extracted the minimum value to a raster layer using the raster package in R ([Hijmans, 2025](#)). We then
266 matched this minimum temperature layer to each location from the GBIF occurrence dataset. Then, for each species,
267 we extracted the 5th percentile of minimum temperature from the species GBIF distributions.

268 Statistics

269 To test for an evolutionary trade-off between frost tolerance and drought resistance, we used phylogenetic mixed
270 models.
271 We used a large published seed plant phylogeny ([Smith and Brown, 2018](#)) which we matched to the species of
272 our trait database with R packages ape ([Paradis et al., 2004](#)) and phytools ([Revell, 2012](#)). Our trait dataset had
273 236 species not present in the original tree: we placed them within their genera at a random place using the
274 "add.species.to.genus" function from the phytools package. This resulted in a final phylogeny with 1304 tips. We

275 then pruned tips from the tree to match it with species for which both embolism resistance and frost resistance were
276 in the database, resulting in a matching tree and dataset with 183 species. We also made trees matching each of
277 the embolism resistance dataset (XXX species) and the frost resistance dataset (XXX species). For both traits, we
278 computed phylogenetic signal statistics, using the phylosig function of the phytools package. We calculated both
279 Bloomberg's K ([?](#)) and Pagel's lambda ([Pagel, 1999](#)). These statistic aim to quantify the degree of similarity in
280 traits between closely related species, relative to what one could expect, based on their evolutionary relatedness
281 described by the branch lengths of the phylogenetic tree under a Brownian motion model of trait evolution. Values
282 of K or lambda close to 1 indicate strong phylogenetic signal - closely related species share similar trait values. On
283 the other hand, values of K or lambda close to 0 indicate low phylogenetic signal, with related species less similar
284 than expected under Brownian motion. We used the built in tests to check for significant deviation from 0 for both
285 statistics. For lambda, we test whether lambda was different from 1 using a likelihood ratio test against a Brownian
286 motion model of evolution. We did this using the

287 We used caper ([Orme, 2013](#)) to fit phylogenetic generalized linear models ("pgls") while taking into account
288 non-independence of the data points. We adjusted for the strength of phylogenetic signal using the lambda
289 branch-length transformation parameter ([Pagel, 1999](#)).

290 We fit phylogenetic mixed models using the brms package in R (cite). For these models, we used

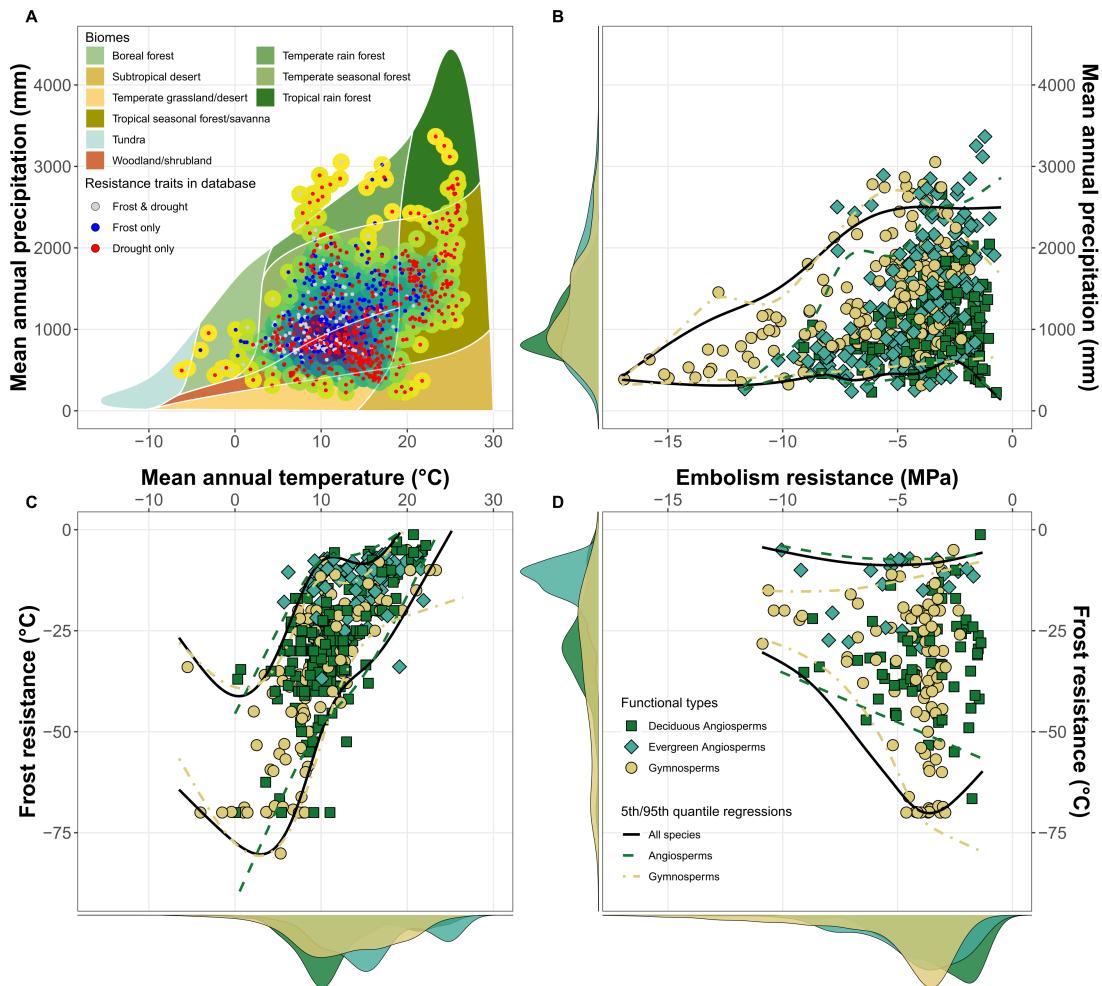


Figure 2. Functional trait trade-off of frost and drought stress resistance and their relationship with the climate ranges of tree species. (A) Mean annual precipitation and temperature of the ranges of each species in the trait database ($n = 1300$). Shaded areas represent the Whittaker biomes (adapted from Ricklefs, 2008). Large dots represent the density of overlapping species on the graph (yellow = low density, darkblue = high density). Small dots show which stress resistance traits are present in the database used in this study. Relationships between (B) embolism resistance (P_{50} in MPa) and mean annual precipitation (mm), and (C) frost resistance and mean annual temperature (°C). (D) Trade-off between embolism resistance and frost resistance. Colors and symbols indicate (dark green squares) deciduous and (blue-green diamonds) evergreen angiosperms and (yellow circles) gymnosperms. Lines in panels B, C, and D show quantile regression models for angiosperms (dashed line, green), gymnosperms (dot-dashed line, yellow) and all species together (solid black line).

291 Results

292 Drought vs. frost resistance trade-off

293 Our trait dataset covered all terrestrial biomes in which trees occur, with mean annual precipitation varying from
 294 around 200 to over 3000 mm per year, and mean annual temperature from -5°C to over 20°C (Figure 2A). The
 295 embolism-resistance dataset covers the complete climatic spectrum, from the coldest to the warmest environments,
 296 and from the wettest to the driest (red and grey dots in Figure 2A). In contrast, the frost resistance trait data
 297 has lower coverage in warmer climates, from subtropical deserts to tropical forests (blue and grey dots in Figure
 298 2A). Overall, most species for which both traits are available occur in temperate biomes in the precipitation range

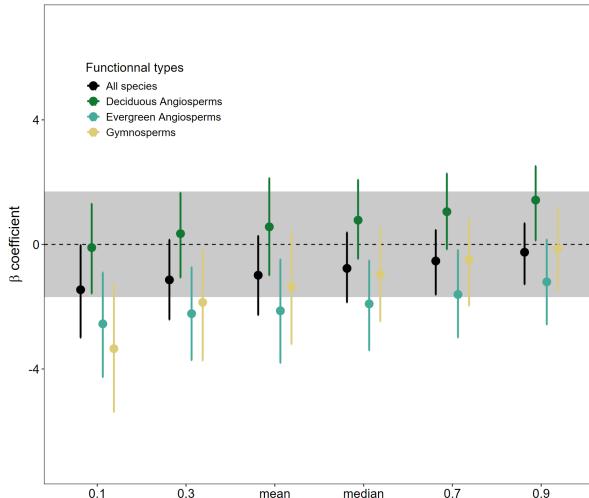


Figure 3. Regression coefficients (median +/- 95% HDI) from phylogenetic Bayesian mixed effects quantile regressions between embolism resistance and frost resistance at different quantiles. The "mean" coefficients are from a non-quantile, i.e. "means-based" regression (see methods), whereas the "median" is for the 0.5 quantile regression. The shaded area represents the Region Of Practical Equivalence, indicating where regression slopes are not significantly different from 0.

299 between 500-2000 mm per year and with mean annual temperatures between +5 and +15°C (woodland/shrubland
 300 and temperate seasonal forests). There is a weak association between embolism resistance and annual rainfall
 301 in our dataset (Figure 2B), as xylem drought-resistance is strongly linked with growing in arid zones. However,
 302 some species with low embolism resistance are still able to grow in low rainfall areas, likely due to deeper rooting
 303 systems or other drought avoidance strategies. Precipitation seasonality of some biomes is not captured with mean
 304 annual precipitation, which explains the occurrence of some moderately resistant species in some wetter areas. The
 305 drought resistance dataset covered a large range of rainfall, from under 300 to over 3000 mm per year. Accordingly,
 306 embolism resistance in these species varied from extremes of close to -19 MPa in some Australian conifers ([Larter et al., 2015](#)) to above -1MPa in some wet tropical species (Figure 2). Gymnosperms and evergreen angiosperms
 308 tend to be more embolism resistant and have a wider range of P_{50} than deciduous angiosperms. We found a strong
 309 link between high embolism-resistance and low rainfall environments, whereas the more vulnerable species are
 310 restricted to wet environments. Species in more mesic environments display a range of embolism resistance, due
 311 to the role of the seasonality of water availability in the level of drought stress plants experience, and other traits
 312 such as rooting depth or stomatal closure dynamics can contribute to drought-tolerance strategies in these species.
 313 These findings are consistent with previous inter-specific analyses across wide taxonomic range (Maherali et al.,
 314 2004; Choat et al., 2012).

315

316 Similar to P_{50} , our dataset covers a broad range of frost hardiness LT_{50} , from around 0°C down to -80°C in the
 317 most resistant species. Evergreen angiosperms tend to be more frost-tender, with higher average LT_{50} , and a lower
 318 slope of the relationship with minimum temperature (Figure XD). Frost hardiness tracked the climate of species, with
 319 the most resistant species in the colder environments (Figure XD). Frost hardiness was around 20°C lower than

320 the minimum temperature experienced over the period 1985-2005 ($y = -20+0.Xx$; $R^2 = , p = xx$; supplementary
321 figure SX). There was no strong correlation between P_{50} and LT_{50} across the mean of the distribution 3. However,
322 drought-resistant species tend to be less frost hardy, and frost-resistant species tend to be vulnerable to drought
323 (Figure 2C). There are notably few species extremely resistant to both stresses, the ones stretching to the limit tend
324 to be shrubs with slow growth like junipers. At lower quantiles of the trait distributions, the regression slopes leave the
325 ROPE, indicating they are no longer equivalent to 0. This shows that extreme resistances are acting as constraints
326 on the evolution of one another, especially in conifers and evergreen angiosperm species 3. As stated previously, we
327 lack frost-tolerance data for many drought-adapted species on the extremes of the P_{50} spectrum, however, notably
328 for embolism resistant conifers, these are known to be extremely vulnerable to frost (e.g. *Callitris*, *Cupressus*).
329 Using a phylogeny, we assessed the evolutionary relationships between these traits. Firstly, both traits show
330 significant phylogenetic signal (K and λ different from 0), but λ is significantly different from 1, and K
331 values are low suggesting low similarities between closely related species.
332 This is confirmed by looking at the mapping of trait evolution, with in general similar trait values across closely
333 related species 4, for example pines for P_{50} and maples for LT_{50} . On the other hand, in some clades there is
334 substantial variation in traits over relative short evolutionary timescales, i.e. *Juniperus* for P_{50} and *Betula* for LT_{50} .
335 Furthermore, independent instances of evolution of extreme resistance to embolism, e.g. *Rosmarinus*, *Juniperus*,
336 and frost hardiness, e.g. *Betula*, *Populus*, shows the remarkable lability of these traits across large evolutionary
337 timescales.

338 Ressource acquisition traits

339 Wood density show significant positive trends with drought resistance. Like many other analyses, we find
340 no relationship between K_{max} and P_{50} – no safety-efficiency trade-off at this evolutionary scale. We did not
341 find a correlation between frost hardiness and conduit diameter in angiosperms, although a significant one in
342 gymnosperms.

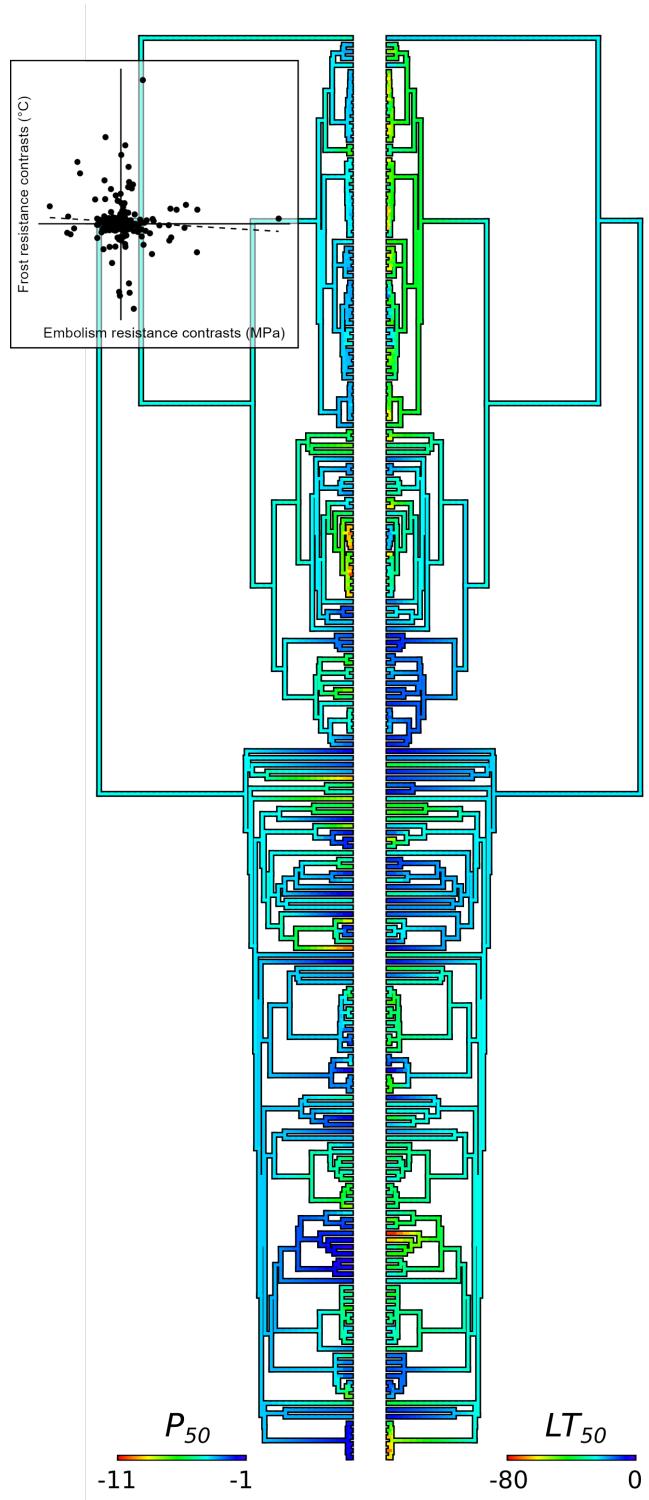


Figure 4. Evolutionary history of P_{50} (left side) and LT_{50} (right side) on a phylogeny of the 210 tree species in the trait database. Trait evolution mapped using maximum likelihood estimation of ancestral states under a Brownian motion model of trait evolution. Insert (top-left) show the lack of evolutionary correlation between the two traits using phylogenetic independent contrasts (PICs).

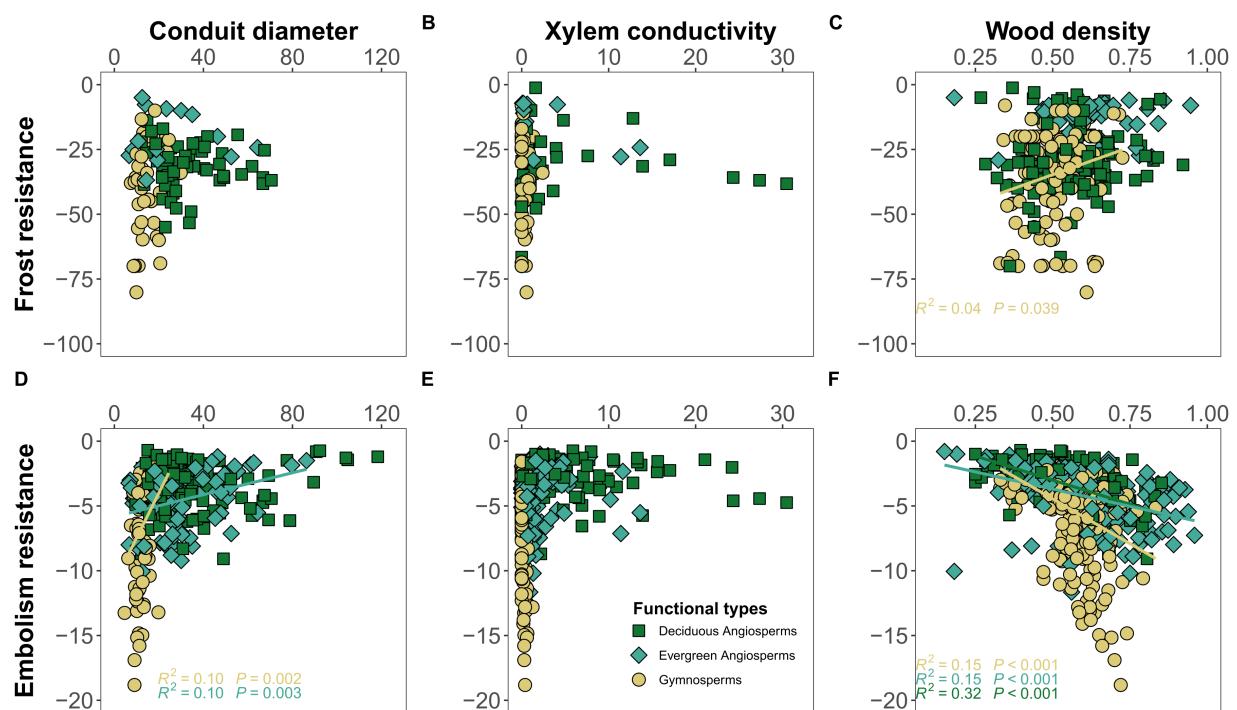


Figure 5. Relationships between xylem functional traits and climate resistance traits. Top panels show frost hardiness, lower panels show embolism resistance, and from left to right (A and D) xylem average conduit diameter (μm), (B and E) xylem specific hydraulic conductivity ($\text{kg MPa}^{-1} \text{m}^{-1} \text{s}^{-1}$) and (C and F) wood density (g cm^3). Colors and symbols show functional groups: deciduous angiosperms (green squares), evergreen angiosperms (blue-green diamonds) and gymnosperms (yellow circles). Significant relationships at $p < 0.01$ are shown in each panel. To improve readability of panels A and C, we do not show *Rhipidocladum racemiflorum*, a tropical bamboo with conduit diameter close to 200 μm .

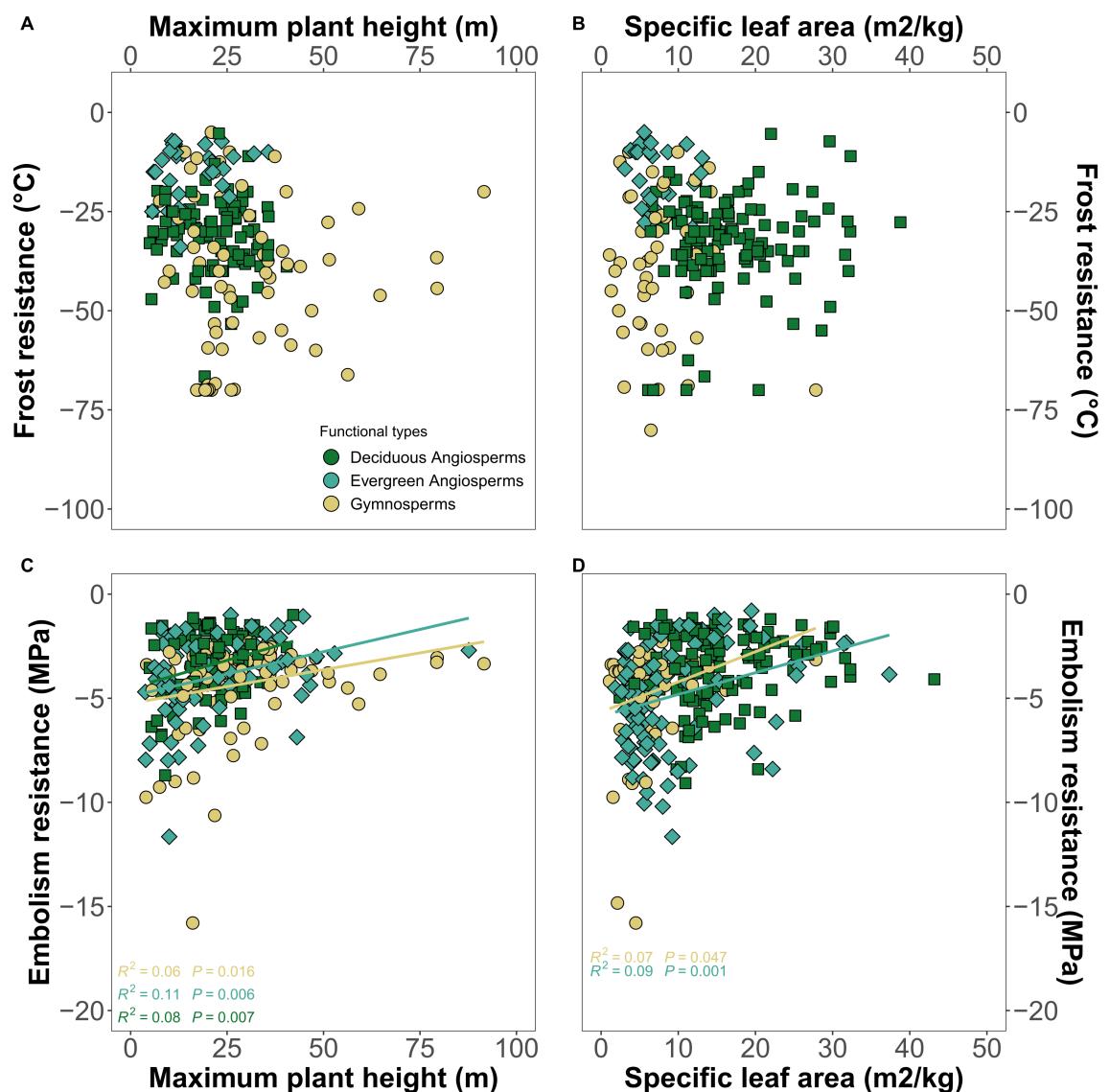


Figure 6. Plant height and specific leaf area are associated with lower drought resistance but no visible cost for frost tolerance.

343 **Discussion**

344 **Main conclusions**

345 We found evidence of a weak trade-off between frost and drought resistance in tree species, based on broad
346 sampling across all forested biomes. We show that woody species that have evolved strong resistance to one type
347 of stress tend to be vulnerable to the other type of stress, and no species have evolved high resistance to both frost
348 and drought stress. On the other hand, many species are relatively vulnerable to both stresses, possibly indicating
349 that when selective pressure for stress resistance is relaxed in mild biomes with no severe summer droughts and
350 extremely cold winters, plants optimize along other axes of fitness. Firstly, we did not find positive correlations
351 between resistance to frost and drought, in spite of similarities in stress response, and hypothesized synergies of a
352 “stress resistance” syndrome (hypothesis 1) ([Puglielli et al., 2023](#)). Second, we did not find evidence for a strong
353 negative evolutionary relationship between frost and drought resistance traits (hypothesis 2), although no species
354 seem to have evolved much resistance to both stresses. We expected to explain this by finding trade-offs between
355 resistance traits and functional traits related to growth and competition (hypothesis 3). However, we did not find any
356 strong evolutionary correlations indicating a significant cost of these traits, either in growth or resource acquisition
357 traits.

358 **Broader implications of results**

359 **Trait trade-offs and life-history strategies**

360 Trait combinations of plants are driven by life-history strategies to optimize resource capture and storage, growth,
361 reproduction and survival in a given environment ([Grime, 2006](#)). The classic CSR framework (Competitors,
362 Stress tolerators, Ruderals) places species on varying stress and disturbance axes, classifying species based
363 on their tolerance to low/high stress and low/high levels of disturbance ([Grime, 1977, 2006](#)). In this framework,
364 stress-tolerating species are typically viewed as slow growing and have typically conservative traits such as small
365 evergreen leaves and low reproductive output. On the opposite end of the stress-resistance spectrum, competitive
366 species tend to favor high growth rate and resource acquisition traits (such as large tender leaves with a short
367 lifespan), which is consistent with other approaches to plant trait optimization frameworks, such as the growth –
368 mortality trade-off ([Russo et al., 2021](#)) or the fast vs. slow plant economics theory ([Reich, 2014](#)). We hypothesized
369 that our results would reflect species strategies and their ranking along the stress tolerance axis, and that species
370 vulnerable to climatic stresses should be optimizing growth or resource acquisition traits. However, we found no
371 significant relationships between resistance traits and growth / competition traits, as represented by the absence
372 of significant trends between stress tolerance and specific leaf area and wood density. High resistance to xylem
373 embolism is associated with smaller conduits (especially in evergreens), and denser wood. However, this does not
374 result in a compromise with low hydraulic efficiency, as vulnerable species have low and high density wood, which is
375 consistent with previous results ([Gleason et al., 2016; Larter et al., 2017](#)). Embolism resistant species do not grow

376 very tall, however there are many short vulnerable species. In evergreen species, embolism resistance seems to be
377 associated with tougher leaves. Rather, we found no impact of frost resistance on conduit size, which goes against
378 the idea that species from cold environments should evolve smaller conduits to avoid freeze-thaw embolisms. We
379 found a slight trend to lower density wood in frost resistant conifers, but the relationship is very weak, and no trend
380 exists in angiosperms.

381 It is admitted than angiosperms tend to be less resistant to drought-induced xylem embolism than gymnosperms,
382 likely because of differences in the inter-conduit pits. The torus of gymnosperms' heterogeneous pit membranes act
383 as a valve that limit the spread of air-bubbles. In angiosperms, the thickness of the membrane limits the spread of
384 air-bubbles, with species with thicker membranes more resistant to embolism. For frost resistance, the distribution of
385 trait values largely overlap, with evergreen angiosperms less resistant than deciduous angiosperms. Gymnosperms
386 show a much flatter distribution, with more extremely resistant species than then angiosperms angiosperms. This is
387 somewhat surprising as the diversity of cell types in angiosperm wood, relative to gymnosperms (composed mostly
388 of tracheids) should favor the adaptation to freezing temperatures.

389 **Filling knowledge gap**

390 To our knowledge, this is the first effort to combine woody plant drought-induced embolism resistance and frost
391 resistance in a global database. For drought resistance, previous work has compiled data from the literature
392 ([Hammond et al., 2021](#); [Choat et al., 2012](#); [Gleason et al., 2016](#); [Sanchez-Martinez et al., 2023](#)), focusing on the
393 evolution of embolism resistance, the vulnerability of tree species to drought and relationships with functional traits
394 linked to the xylem such as wood density and water transport efficiency. Regarding frost resistance, a recent study
395 examined the global distribution of thermal tolerance, combining datasets for extreme hot and cold temperature
396 cellular damage. We took a different approach to that study, applying strict cut-offs for inclusion based on the
397 methodology of the source studies. Overall, our

398 While our effort combines two of the most studied traits related to drought and frost resistance, these traits are
399 not perfect to describe a species' stress resistance. Embolism resistance is but one facet of drought response,
400 our approach could be improved by including more traits such as osmotic potential, turgor loss point, or water-use
401 efficiency in a multivariate framework. We could also work to exclude species that escape the need for embolism
402 resistance, for example by increasing rooting depth ([Laughlin et al., 2023](#)). Additionally, while variation in P_{50} is
403 often small within species ([Lamy et al., 2011](#); [Lobo et al., 2018](#); [Bouche et al., 2016](#); [Alon et al., 2023](#)), there exists
404 variation in some species, withing the plant based on organ age or growth rate differences ([Grossman et al., 2024](#);
405 [Sorek et al., 2022](#); [Johnson and Brodribb, 2023](#)), or across populations ([Stojnić et al., 2018](#); [Schuldt et al., 2015](#);
406 [López et al., 2013](#)). Similarly, frost resistance is a dynamic 'trait', that adjusts based on phenology. Measuring frost
407 resistance at maximum hardness (i.e. in the middle of winter) poses challenges, since plants tend to be sensitive
408 to early frost, i.e. before hardening, or after bud break. Yet, to make comparisons meaningful across species, it
409 is best to compare frost resistance at maximum (i.e. full winter) hardness. Again, there is likely within species

410 variation for this trait, across populations and individuals, but this varies between species (Harbol et al., 2023). In our
411 dataset we found little evidence for this (include supplementary figures). Some species, mostly conifers, are notably
412 difficult to measure accurately, especially in species with extreme resistance. Measuring these species requires
413 the use of liquid N₂, which makes controlling the rate of freezing and thawing of the samples difficult. In others,
414 for example in genera *Larix* and *Picea*, getting accurate measurements of electrolyte leakage from the xylem is
415 challenging, perhaps because there is little living tissue in the samples used, or the presence of resin canals makes
416 quantifying the electrolytes challenging. Finally, freeze-thaw embolism is another axis of frost resistance that could
417 be interesting to compare to other xylem functional traits related to drought and frost. However, we are so far lacking
418 a unified dataset or measurement protocol for this trait.

419 **Conclusion**

420 We found a weak evolutionary trade-off between drought and frost resistance traits across a broad species level
421 database, covering all forested biomes. While there are a number vulnerable species to both stresses, other have
422 developed high resistance to either drought or extreme cold temperature. However, no species are able to be
423 extremely resistant to both stresses simultaneously. Using quantile regressions we show evolutionary constraints
424 increases the slope of the trade-off relationship when one trait value is at extreme parts of the distribution. These
425 constraints are released for moderate and low trait values, indicating other factors could be acting as constraints on
426 resistance traits, such as limits on plant height, or wood density for drought resistant. However, we haven't identified
427 a limiting trade-off for frost resistance based on the traits studied here, offering avenues for future research.

428 **Bibliography**

- 429 Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., and Anderson, R. P. (2015). spThin: an R package for spatial
430 thinning of species occurrence records for use in ecological niche models. *Ecography*, 38(5):541–545. doi: 10.1111/ecog.
431 01132. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/ecog.01132>.
- 432 Alderotti, F., Bussotti, F., Brunetti, C., Ferrini, F., Gori, A., and Pollastrini, M. (2024). Linking patterns of forest dieback to triggering
433 climatic and weather events: an overview on Mediterranean forests. *IFOREST*, 17:309–316. doi: 10.3832/ifor4545-017.
434 Accepted: 2024-10-10T16:25:24Z.
- 435 Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears,
436 D. D., Hogg, E. T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W.,
437 Semerci, A., and Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate
438 change risks for forests. *Forest Ecology and Management*, 259(4):660–684. doi: 10.1016/j.foreco.2009.09.001.
- 439 Alon, A., Cohen, S., Burlett, R., Hochberg, U., Lukyanov, V., Rog, I., Klein, T., Cochard, H., Delzon, S., and David-Schwartz,
440 R. (2023). Acclimation limits for embolism resistance and osmotic adjustment accompany the geographical dry edge of
441 Mediterranean species. *Functional Ecology*, 37(5):1421–1435. doi: 10.1111/1365-2435.14289. Publisher: John Wiley &
442 Sons, Ltd.
- 443 Anderegg, W. R. L., Schwalm, C., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., Ogle, K., Shaw, J. D., Shevliakova, E.,
444 Williams, A. P., Wolf, A., Ziaco, E., and Pacala, S. (2015). Pervasive drought legacies in forest ecosystems and their
445 implications for carbon cycle models. *Science*, 349(6247):528–532. doi: 10.1126/science.aab1833. arXiv: 1011.1669v3
446 ISBN: 9780874216561.
- 447 Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., and Jansen, S. (2016). Meta-analysis reveals
448 that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the
449 National Academy of Sciences*, 113(18):5024–5029. doi: 10.1073/pnas.1525678113. Publisher: Proceedings of the National
450 Academy of Sciences.
- 451 Anisko, T. and Lindstrom, O. M. (1995). Applying the Richards function in freezing tolerance determination with electrolyte and
452 phenolic leakage techniques. *Physiologia Plantarum*, 95(2):281–287. doi: 10.1111/j.1399-3054.1995.tb00839.x. _eprint:
453 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1399-3054.1995.tb00839.x>.
- 454 Aubin, I., Munson, A., Cardou, F., Burton, P., Isabel, N., Pedlar, J., Paquette, A., Taylor, A., Delagrange, S., Kebli, H., Messier,
455 C., Shipley, B., Valladares, F., Kattge, J., Boisvert-Marsh, L., and McKenney, D. (2016). Traits to stay, traits to move: a review
456 of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. *Environmental
457 Reviews*, 24(2):164–186. doi: 10.1139/er-2015-0072. Publisher: NRC Research Press.
- 458 Augusto, L., Davies, T. J., Delzon, S., and De Schrijver, A. (2014). The enigma of the rise of angiosperms: can we untie the knot?
459 *Ecology Letters*, 17(10):1326–38. doi: 10.1111/ele.12323.
- 460 Baffoin, R., Charrier, G., Bouchardon, A.-E., Bonhomme, M., Améglio, T., and Lacointe, A. (2021). Seasonal changes in
461 carbohydrates and water content predict dynamics of frost hardiness in various temperate tree species. *Tree Physiology*, 41
462 (9):1583–1600. doi: 10.1093/treephys/tpab033.
- 463 Bansal, S., Harrington, C. A., and St. Clair, J. B. (2016). Tolerance to multiple climate stressors: a case study of
464 Douglas-fir drought and cold hardiness. *Ecology and Evolution*, 6(7):2074–2083. doi: 10.1002/ece3.2007. _eprint:
465 <https://onlinelibrary.wiley.com/doi/pdf/10.1002/ece3.2007>.
- 466 Baranger, A., Cordonnier, T., Charrier, G., Delzon, S., Larter, M., Martin-StPaul, N. K., and Kunstler, G. (2024). Living on the
467 edge – physiological tolerance to frost and drought explains range limits of 35 European tree species. *Ecography*, n/a(n/a):
468 e07528. doi: 10.1111/ecog.07528. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/ecog.07528>.

- 469 Beck, E. H., Fettig, S., Knake, C., Hartig, K., and Bhattacharai, T. (2007). Specific and unspecific responses of plants to cold and
470 drought stress. *Journal of Biosciences*, 32(3):501–510. doi: 10.1007/s12038-007-0049-5.
- 471 Blumstein, M., Gersony, J., Martínez-Vilalta, J., and Sala, A. (2023). Global variation in nonstructural carbohydrate
472 stores in response to climate. *Global Change Biology*, 29(7):1854–1869. doi: 10.1111/gcb.16573. _eprint:
473 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.16573>.
- 474 Bond, W. J. (1989). The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biological
475 Journal of the Linnean Society*, 36(3):227–249. doi: 10.1111/j.1095-8312.1989.tb00492.x.
- 476 Bond, W. J. and Midgley, J. J. (2001). Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution*,
477 16(1):45–51. doi: 10.1016/S0169-5347(00)02033-4. Publisher: Elsevier.
- 478 Bouche, P. S., Larter, M., Domec, J.-C., Burlett, R., Gasson, P., Jansen, S., and Delzon, S. (2014). A broad survey of hydraulic
479 and mechanical safety in the xylem of conifers. *Journal of Experimental Botany*, 65(15):4419–4431. doi: 10.1093/jxb/eru218.
- 480 Bouche, P. S., Jansen, S., Sabalera, J. C., Cochard, H., Burlett, R., and Delzon, S. (2016). Low intra-tree variability in resistance
481 to embolism in four Pinaceae species. *Annals of Forest Science*, (May). doi: 10.1007/s13595-016-0553-6.
- 482 Brodribb, T. and Hill, R. S. (1999). The importance of xylem constraints in the distribution of
483 conifer species. *New Phytologist*, 143(2):365–372. doi: 10.1046/j.1469-8137.1999.00446.x. _eprint:
484 <https://onlinelibrary.wiley.com/doi/pdf/10.1046/j.1469-8137.1999.00446.x>.
- 485 Brodribb, T. J. and Cochard, H. (2009). Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant
486 Physiology*, 149(1):575–84. doi: 10.1104/pp.108.129783.
- 487 Burlett, R., Parise, C., Capdeville, G., Cochard, H., Lamarque, L. J., King, A., and Delzon, S. (2022). Measuring xylem
488 hydraulic vulnerability for long-vessel species: an improved methodology with the flow centrifugation technique. *Annals of
489 Forest Science*, 79(1):5. doi: 10.1186/s13595-022-01124-0.
- 490 Camarerero, J. J., Colangelo, M., Valeriano, C., and Pizarro, M. (2023). Reversible Impacts of a Cold Spell on Forest Cover, Tree
491 Growth and Carbohydrates in Mediterranean Pine and Oak Forests. *Forests*, 14(4):678. doi: 10.3390/f14040678. Number: 4
492 Publisher: Multidisciplinary Digital Publishing Institute.
- 493 Cardoso, A. A., Kane, C. N., Rimer, I. M., McAdam, S. A. M., Cardoso, A. A., Kane, C. N., Rimer, I. M., and McAdam, S. A. M.
494 (2022). Seeing is believing: what visualising bubbles in the xylem has revealed about plant hydraulic function. *Functional Plant
495 Biology*, 49(9):759–772. doi: 10.1071/FP21326. Publisher: CSIRO PUBLISHING.
- 496 Chamberlain, S., Oldoni, D., Barve, V., Desmet, P., Geffert, L., Mcglinn, D., Ram, K., rOpenSci (<https://ropensci.org/>), Waller [aut,
497 J., and cre. rg bif: Interface to the Global Biodiversity Information Facility API, (2023). URL <https://cran.r-project.org/web/packages/rgbif/index.html>.
- 498 Charra-Vaskou, K., Charrier, G., Wortemann, R., Beikircher, B., Cochard, H., Ameglio, T., and Mayr, S. (2012). Drought and frost
499 resistance of trees: a comparison of four species at different sites and altitudes. *Annals of Forest Science*, 69(3):325–333. doi:
500 10.1007/s13595-011-0160-5. Number: 3 Publisher: BioMed Central.
- 502 Charrier, G. and Améglio, T. (2011). The timing of leaf fall affects cold acclimation by interactions with air temperature through
503 water and carbohydrate contents. *Environmental and Experimental Botany*, 72(3):351–357. doi: 10.1016/j.envexpbot.2010.
504 12.019.
- 505 Charrier, G., Charra-Vaskou, K., Kasuga, J., Cochard, H., Mayr, S., and Améglio, T. (2014). Freeze-Thaw Stress: Effects of
506 Temperature on Hydraulic Conductivity and Ultrasonic Activity in Ten Woody Angiosperms. *Plant Physiology*, 164(2):992–998.
507 doi: 10.1104/pp.113.228403.
- 508 Charrier, G., Martin-StPaul, N., Damesin, C., Delpierre, N., Hänninen, H., Torres-Ruiz, J. M., and Davi, H. (2021). Interaction of
509 drought and frost in tree ecophysiology: rethinking the timing of risks. *Annals of Forest Science*, 78(2):1–15. doi: 10.1007/
510 s13595-021-01052-5. Number: 2 Publisher: BioMed Central.

- 511 Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, A. E. (2009). Towards a worldwide
512 wood economics spectrum. *Ecology Letters*, 12(4):351–366. doi: 10.1111/j.1461-0248.2009.01285.x. _eprint:
513 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1461-0248.2009.01285.x>.
- 514 Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G.,
515 Jacobsen, A. L., Lens, F., Maherli, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J.,
516 Pratt, R. B., Sperry, J. S., Westoby, M., Wright, I. J., and Zanne, A. E. (2012). Global convergence in the vulnerability of forests
517 to drought. *Nature*, 491(7426):752–5. doi: 10.1038/nature11688.
- 518 Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., and Medlyn, B. E. (2018). Triggers of tree mortality under
519 drought. *Nature*, 558(7711):531–539. doi: 10.1038/s41586-018-0240-x.
- 520 Christensen-Dalsgaard, K. K. and Tyree, M. T. (2013). Does freezing and dynamic flexing of frozen branches impact the cavitation
521 resistance of *Malus domestica* and the *Populus* clone Walker? *Oecologia*, 173(3):665–674. doi: 10.1007/s00442-013-2656-1.
- 522 Cochard, H., Herbette, S., Barigah, T., Badel, E., Ennajeh, M., and Vilagrosa, A. (2010). Does sample length influence the
523 shape of xylem embolism vulnerability curves? A test with the Cavitron spinning technique. *Plant, Cell and Environment*, 33
524 (9):1543–1552. doi: 10.1111/j.1365-3040.2010.02163.x. Num Pages: 10 Place: Hoboken Publisher: Wiley Web of Science
525 ID: WOS:000280661300009.
- 526 D'Andrea, E., Rezaie, N., Prislan, P., Gričar, J., Collalti, A., Muhr, J., and Matteucci, G. (2020). Frost and drought: Effects
527 of extreme weather events on stem carbon dynamics in a Mediterranean beech forest. *Plant, Cell & Environment*, 43(10):
528 2365–2379. doi: 10.1111/pce.13858. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/pce.13858>.
- 529 Davis, S. D., Sperry, J. S., and Hacke, U. G. (1999). The relationship between xylem conduit diameter and
530 cavitation caused by freezing. *American Journal of Botany*, 86(10):1367–1372. doi: 10.2307/2656919. _eprint:
531 <https://onlinelibrary.wiley.com/doi/pdf/10.2307/2656919>.
- 532 Delzon, S., Douthe, C., Sala, A., and Cochard, H. (2010). Mechanism of water-stress induced cavitation in conifers: Bordered pit
533 structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell and Environment*, 33(12):2101–2111. doi:
534 10.1111/j.1365-3040.2010.02208.x.
- 535 Dexter, S. T., Tottingham, W. E., and Gruber, L. F. (1932). Investigations of the Hardiness of Plants By Measurement of Electrical
536 Conductivity1. *Plant Physiology*, 7(1):63–78. doi: 10.1104/pp.7.1.63.
- 537 D'Andrea, E., Scartazza, A., Battistelli, A., Collalti, A., Proietti, S., Rezaie, N., Matteucci, G., and Moscatello, S. (2021).
538 Unravelling resilience mechanisms in forests: role of non-structural carbohydrates in responding to extreme weather events.
539 *Tree Physiology*, 41(10):1808–1818. doi: 10.1093/treephys/tpab044.
- 540 Earle, C. J. The Gymnosperm Database, (2024). URL <https://conifers.org/>.
- 541 Fernández-Pérez, L., Villar-Salvador, P., Martínez-Vilalta, J., Toca, A., and Zavala, M. A. (2018). Distribution of pines in the
542 Iberian Peninsula agrees with species differences in foliage frost tolerance, not with vulnerability to freezing-induced xylem
543 embolism. *Tree Physiology*, 38(4):507–516. doi: 10.1093/treephys/tpx171.
- 544 Fick, S. and Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International
545 Journal of Climatology*.
- 546 Francescantonio, D. d., Villagra, M., Goldstein, G., and Campanello, P. I. (2020). Drought and frost resistance vary between
547 evergreen and deciduous Atlantic Forest canopy trees. *Functional Plant Biology*, 47(9):779–791. doi: 10.1071/FP19282.
548 Publisher: CSIRO PUBLISHING.
- 549 GBIF: The Global Biodiversity Information Facility. What is GBIF?, (2023). URL <https://www.gbif.org/what-is-gbif>.
- 550 Gleason, S. M., Westoby, M., Jansen, S., Choat, B., Hacke, U. G., Pratt, R. B., Bhaskar, R., Brodribb, T. J., Bucci, S. J., Mayr,
551 S., McCulloch, K. A., Mencuccini, M., Mitchell, P. J., Morris, H., Nardini, A., Pittermann, J., Plavcov, L., Schreiber, S. G., Sperry,
552 J. S., Wright, I. J., and Zanne, A. E. (2016). Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across

- 553 the world's woody plant species. *New Phytologist*, 209:123–36. doi: 10.1111/nph.13646.
- 554 Greco, S., Infusino, M., De Donato, C., Coluzzi, R., Imbrenda, V., Lanfredi, M., Simoniello, T., and Scalercio, S. (2018). Late Spring
555 Frost in Mediterranean Beech Forests: Extended Crown Dieback and Short-Term Effects on Moth Communities. *Forests*, 9(7):
556 388. doi: 10.3390/f9070388. Number: 7 Publisher: Multidisciplinary Digital Publishing Institute.
- 557 Grime, J. P. (1977). Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and
558 Evolutionary Theory. *The American Naturalist*, 111(982).
- 559 Grime, J. P. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. John Wiley & Sons, (2006). ISBN
560 978-0-470-85040-4. Google-Books-ID: k4dOEAAAQBAJ.
- 561 Grossman, J. J., Coe, H. B., Fey, O., Fraser, N., Salaam, M., Semper, C., and Williamson, C. G. (2024). Temperate woody species
562 across the angiosperm phylogeny acquire tolerance to water deficit stress during the growing season. *New Phytologist*, 242
563 (5):1981–1995. doi: 10.1111/nph.19692. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.19692>.
- 564 Hacke, U. G. and Sperry, J. S. (2001). Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and
565 Systematics*, 4(2):97–115. doi: 10.1078/1433-8319-00017.
- 566 Hammond, W., Choat, B., Johnson, D., Ali Ahmed, M., Anderegg, L., Barigah, T. S., Barros, F., Bartlett, M., Bauerle, T., Beikircher,
567 B., Bittencourt, P., Blackman, C., Brodribb, T., Brum, M., Cano, J., Cardoso, A., Chen, Y., Carmesin, C., Cochard, H., Cao, K.,
568 Dayer, S., Delzon, S., Domec, J.-C., Duan, H., Gambetta, G., Ganthalier, A., Gauthey, A., Gleason, S., Gorai, M., Guan, X., Hao,
569 G.-Y., Heuret, P., Hochberg, U., Johnson, K., Kaack, L., Lamarque, L., Larter, M., Laughlin, D., Lens, F., Levionnois, S., Li, X.,
570 Liu, H., Lopez Rodriguez, R., Losso, A., Mantova, M., Martinez-Vilalta, J., Mayr, S., McAdam, S., Mehltreter, K., Mencuccini, M.,
571 Mocko, K., Morris, H., Nadal-Sala, D., Nardini, A., Oliveira, R., Pereira, L., Peters, J., Petruzzellis, F., Pittermann, J., Poyatos,
572 R., Rosner, S., Rowland, L., Ruehr, N., Sack, L., Sanchez-Martinez, P., Schuldt, B., Scoffoni, C., Skelton, R., Smith-Martin, C.,
573 Steppe, K., Sterck, F., Thonglim, A., Torres-Ruiz, J., Trabi, C., Tyree, M., Vargas, G., Wu, M., Yang, D., Zhang, Y., Zhu, S., and
574 Jansen, S. (2021). The global vulnerability of plant xylem. 2021:B31F–07. Conference Name: AGU Fall Meeting Abstracts
575 ADS Bibcode: 2021AGUFM.B31F..07H.
- 576 Hampe, A. and Petit, R. J. (2005). Conserving biodiversity under climate change: the rear edge matters: Rear edges and climate
577 change. *Ecology Letters*, 8(5):461–467. doi: 10.1111/j.1461-0248.2005.00739.x.
- 578 Harbol, S. C., Long, R. W., and Medeiros, J. S. (2023). Juniperus virginiana sourced from colder climates maintain higher ratios
579 of soluble sugars to starch during cold acclimation. *Tree Physiology*, page tpad115. doi: 10.1093/treephys/tpad115.
- 580 Hijmans, R. J. raster: Geographic Data Analysis and Modeling, (2025). URL <https://r-spatial.org/raster>.
- 581 Johnson, K. M. and Brodribb, T. J. (2023). Evidence for a trade-off between growth rate and xylem cavitation resistance in Callitris
582 rhomboidea. *Tree Physiology*, 43(7):1055–1065. doi: 10.1093/treephys/tpad037.
- 583 Jucker, T., Fischer, F. J., Chave, J., Coomes, D. A., Caspersen, J., Ali, A., Loubota Panzou, G. J., Feldpausch, T. R., Falster, D.,
584 Usoltsev, V. A., Adu-Bredu, S., Alves, L. F., Aminpour, M., Angoboy, I. B., Anten, N. P. R., Antin, C., Askari, Y., Muñoz, R.,
585 Ayyappan, N., Balvanera, P., Banin, L., Barbier, N., Battles, J. J., Beeckman, H., Bocko, Y. E., Bond-Lamberty, B., Bongers, F.,
586 Bowers, S., Brade, T., van Breugel, M., Chantrain, A., Chaudhary, R., Dai, J., Dalponte, M., Dimobe, K., Domec, J.-C., Doucet,
587 J.-L., Duursma, R. A., Enríquez, M., van Ewijk, K. Y., Farfán-Ríos, W., Fayolle, A., Forni, E., Forrester, D. I., Gilani, H., Godlee,
588 J. L., Gourlet-Fleury, S., Haeni, M., Hall, J. S., He, J.-K., Hemp, A., Hernández-Stefanoni, J. L., Higgins, S. I., Holdaway,
589 R. J., Hussain, K., Hutley, L. B., Ichie, T., Iida, Y., Jiang, H.-s., Joshi, P. R., Kaboli, H., Larsary, M. K., Kenzo, T., Kloepoppel,
590 B. D., Kohyama, T., Kunwar, S., Kuyah, S., Kvasnica, J., Lin, S., Lines, E. R., Liu, H., Lorimer, C., Loumeto, J.-J., Malhi, Y.,
591 Marshall, P. L., Mattsson, E., Matula, R., Meave, J. A., Mensah, S., Mi, X., Momo, S., Moncrieff, G. R., Mora, F., Nissanka,
592 S. P., O'Hara, K. L., Pearce, S., Pelissier, R., Peri, P. L., Ploton, P., Poorter, L., Pour, M. J., Pourbabaei, H., Dupuy-Rada, J. M.,
593 Ribeiro, S. C., Ryan, C., Sanaei, A., Sanger, J., Schlund, M., Sellan, G., Shenkin, A., Sonké, B., Sterck, F. J., Svátek, M.,
594 Takagi, K., Trugman, A. T., Ullah, F., Vadeboncoeur, M. A., Valipour, A., Vanderwel, M. C., Vovides, A. G., Wang, W., Wang,

- 595 L.-Q., Wirth, C., Woods, M., Xiang, W., Ximenes, F. d. A., Xu, Y., Yamada, T., and Zavala, M. A. (2022). Tallo: A global tree
596 allometry and crown architecture database. *Global Change Biology*, 28(17):5254–5268. doi: 10.1111/gcb.16302. _eprint:
597 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.16302>.
- 598 Karger, D. N., Lange, S., Hari, C., Reyer, C. P., Conrad, O., Zimmermann, N. E., and Frieler, K. (2023). CHELSA-W5E5:
599 Daily 1 km meteorological forcing data for climate impact studies. *Earth System Science Data*, 15(6):2445–2464. Publisher:
600 Copernicus Publications Göttingen, Germany.
- 601 Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi,
602 M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H.,
603 Amiaud, B., Ammer, C., Amoroso, M. M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D. M. G., Ashman, T.-L.,
604 Asmara, D. H., Asner, G. P., Aspinwall, M., Atkin, O., Aubin, I., Bastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker,
605 W. J., Bakker, J. P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D. R., Baruch, Z., Bastianelli,
606 D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry,
607 G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M. L., Berenguer, E., Bergamin, R., Bergmann, J.,
608 Bergmann Carlucci, M., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A. D., Blackman, C., Blanco, C., Blonder,
609 B., Blumenthal, D., Bocanegra-González, K. T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W.,
610 Bond-Lamberty, B., Boom, A., Boonman, C. C. F., Bordin, K., Boughton, E. H., Boukili, V., Bowman, D. M. J. S., Bravo, S.,
611 Brendel, M. R., Broadley, M. R., Brown, K. A., Bruelheide, H., Brunnich, F., Bruun, H. H., Bruy, D., Buchanan, S. W., Bucher,
612 S. F., Buchmann, N., Buitenhof, R., Bunker, D. E., Bürger, J., Burrascano, S., Burslem, D. F. R. P., Butterfield, B. J., Byun, C.,
613 Marques, M., Scalon, M. C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J. J., Campany, C., Campetella,
614 G., Campos, J. A., Cano-Arboleda, L., Canullo, R., Carbognani, M., Carvalho, F., Casanoves, F., Castagnayrol, B., Catford,
615 J. A., Cavender-Bares, J., Cerabolini, B. E. L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F. S., Chelli, S., Chen,
616 S.-C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.-S., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C. G., Conti,
617 L., Coomes, D., Cornelissen, J. H. C., Cornwell, W. K., Corona, P., Coyea, M., Craine, J., Craven, D., Cromsigt, J. P. G. M.,
618 Csecserits, A., Cufar, K., Cuntz, M., da Silva, A. C., Dahlin, K. M., Dainese, M., Dalke, I., Dalle Fratte, M., Dang-Le, A. T.,
619 Danihelka, J., Dannoura, M., Dawson, S., de Beer, A. J., De Frutos, A., De Long, J. R., Dechant, B., Delagrange, S., Delpierre,
620 N., Derroire, G., Dias, A. S., Diaz-Toribio, M. H., Dimitrakopoulos, P. G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong,
621 N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A.,
622 Eckstein, R. L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M. B., Erfmeier, A., Esquivel-Muelbert, A., Esser,
623 G., Estiarte, M., Domingues, T. F., Fagan, W. F., Fagúndez, J., Falster, D. S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng,
624 Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T. J., Flynn, D. F. B., Fontana, V.,
625 Forey, E., Forgiarini, C., François, L., Frangipani, M., Frank, D., Frenette-Dussault, C., Freschet, G. T., Fry, E. L., Fyllas, N. M.,
626 Mazzochini, G. G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido,
627 J. L., de Gasper, A. L., Gea-Izquierdo, G., Gibson, D., Gillison, A. N., Giroldo, A., Glasenhardt, M.-C., Gleason, S., Gliesch, M.,
628 Goldberg, E., Göldel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J. L., González-Melo, A., González-Robles, A., Graae, B. J.,
629 Granda, E., Graves, S., Green, W. A., Gregor, T., Gross, N., Guerin, G. R., Günther, A., Gutiérrez, A. G., Haddock, L., Haines,
630 A., Hall, J., Hambuckers, A., Han, W., Harrison, S. P., Hattingh, W., Hawes, J. E., He, T., He, P., Heberling, J. M., Helm, A.,
631 Hempel, S., Hentschel, J., Hérault, B., Hereş, A.-M., Herz, K., Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A. L., Hirons,
632 A., Hock, M., Hogan, J. A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K. A., Ichie, T., Igić, B.,
633 Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C. M., Izquierdo, J., Jackson, R. B., Jackson, B., Jactel, H.,
634 Jagodzinski, A. M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J. R. P., Jiang, G.-F., Johansen, J. L., Johnson,
635 D., Jokela, E. J., Joly, C. A., Jordan, G. J., Joseph, G. S., Junaedi, D., Junker, R. R., Justes, E., Kabzems, R., Kane, J., Kaplan,
636 Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M. I., Kinlock, N. L., Kissling,

W. D., Kitajima, K., Kitzberger, T., Kjøller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloepel, B., Klotz, S., Knops, J., M. H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N. J. B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J.-P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D. J., Laughlin, D., Le Bagousse-Pinguet, Y., le Maire, G., le Roux, P. C., le Roux, E., Lee, T., Lens, F., Lewis, S. L., Lhotsky, B., Li, Y., Li, X., Lichstein, J. W., Liebergesell, M., Lim, J. Y., Lin, Y.-S., Linares, J. C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusià, J., Lohbeck, M., López-García, A., Lopez-Gonzalez, G., Lososová, Z., Louault, F., Lukács, B. A., Lukeš, P., Luo, Y., Lussu, M., Ma, S., Maciel Rabelo Pereira, C., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A. C. M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markestijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K., Mason, N., Massad, T. J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M. L., McCulloh, K., McFadden, I. R., McGill, B. J., McPartland, M. Y., Medeiros, J. S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F. P. L., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J., Michaletz, S. T., Michelaki, C., Migalina, S., Milla, R., Miller, J. E. D., Minden, V., Ming, R., Mokany, K., Moles, A. T., Molnár V, A., Molofsky, J., Molz, M., Montgomery, R. A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A. S., Mori, S., Morris, D., Morrison, J., Mucina, L., Mueller, S., Muir, C. D., Müller, S. C., Munoz, F., Myers-Smith, I. H., Myster, R. W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A. S., Neuschulz, E. L., Ni, J., Niedrist, G., Nieto, J., Niinemets, U., Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A., Network, T. N., Nystruen, K. O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., Öllerer, K., Olson, M. E., Onipchenko, V., Onoda, Y., Onstein, R. E., Ordonez, J. C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G. E., Ozinga, W. A., Pahl, A. T., Paine, C. E. T., Pakeman, R. J., Papageorgiou, A. C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J. G., Peco, B., Penuelas, J., Perea, A., Peri, P. L., Petisco-Souza, A. C., Petraglia, A., Petritan, A. M., Phillips, O. L., Pierce, S., Pillar, V. D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A. S., Power, S. A., Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C. A., Reich, P. B., Reichstein, M., Reid, D. E. B., Réjou-Méchain, M., de Dios, V. R., Ribeiro, S., Richardson, S., Riibak, K., Rillig, M. C., Riviera, F., Robert, E. M. R., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A. V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J. A., Rosenfield, M. F., Rossi, C., Roy, D. B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S. B., Rusch, G. M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A. C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J. V., Schowanek, S. D., Schrader, J., Schrodt, F., Schuldt, B., Schurr, F., Selaya Garvizu, G., Semchenko, M., Seymour, C., Sfair, J. C., Sharpe, J. M., Sheppard, C. S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T. A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N. G., Sodhi, D., Soltis, P., Soltis, D., Somers, B., Sonnier, G., Sørensen, M. V., Sosinski Jr, E. E., Soudzilovskaia, N. A., Souza, A. F., Spasojevic, M., Sperandii, M. G., Stan, A. B., Stegen, J., Steinbauer, K., Stephan, J. G., Sterck, F., Stojanovic, D. B., Strydom, T., Suarez, M. L., Svenning, J.-C., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau, S., Tavsanoglu, C., te Beest, M., Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P. E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M. G., Tng, D. Y. P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J. M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J. L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadéboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., van Bodegom, P. M., van Breugel, M., Van Cleemput, E., van de Weg, M., van der Merwe, S., van der Plas, F., van der Sande, M. T., van Kleunen, M., Van Meerbeek, K., Vanderwel, M., Vanselow, K. A., Vårhammar, A., Varone, L., Vasquez Valderrama, M. Y., Vassilev, K., Vellend, M., Veneklaas, E. J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacis, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A. P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J. T., Wei, L., Weigelt, P., Weiher, E., Wells, A. W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P. J., Whitten, M., Williams, M., Winkler, D. E., Winter, K., Womack,

- 679 C., Wright, I. J., Wright, S. J., Wright, J., Pinho, B. X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B.,
680 Zanini, K. J., Zanne, A. E., Zelený, D., Zhao, Y.-P., Zheng, J., Zheng, J., Ziemińska, K., Zirbel, C. R., Zizka, G., Zo-Bi, I. C.,
681 Zotz, G., and Wirth, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, 26
682 (1):119–188. doi: 10.1111/gcb.14904. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.14904>.
- 683 Kovaleski, A. P. and Grossman, J. J. (2021). Standardization of electrolyte leakage data and a novel liquid nitrogen control
684 improve measurements of cold hardiness in woody tissue. *Plant Methods*, 17(1):53. doi: 10.1186/s13007-021-00755-0.
- 685 Körner, C. (2021). The cold range limit of trees. *Trends in Ecology & Evolution*, 36(11):979–989. doi: 10.1016/j.tree.2021.06.011.
- 686 Laanisto, L. and Niinemets, U. (2015). Polytolerance to abiotic stresses: how universal is the shade–drought tolerance
687 trade-off in woody species? *Global Ecology and Biogeography*, 24(5):571–580. doi: 10.1111/geb.12288. _eprint:
688 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/geb.12288>.
- 689 Lamy, J.-B., Bouffier, L., Burlett, R., Plomion, C., Cochard, H., and Delzon, S. (2011). Uniform Selection as a Primary Force
690 Reducing Population Genetic Differentiation of Cavitation Resistance across a Species Range. *PLoS ONE*, 6(8):e23476. doi:
691 10.1371/journal.pone.0023476.
- 692 Lancaster, L. T. and Humphreys, A. M. (2020). Global variation in the thermal tolerances of plants. *Proceedings of the National
693 Academy of Sciences*, 117(24):13580–13587. doi: 10.1073/pnas.1918162117. Publisher: Proceedings of the National
694 Academy of Sciences.
- 695 Larter, M. *Evolution de la résistance à la cavitation chez les conifères The evolution of cavitation resistance in conifers*. PhD
696 thesis, Universite de Bordeaux, (2016).
- 697 Larter, M., Brodribb, J., Timothy, Pfautsch, S., Burlett, R., Cochard, H., and Delzon, S. (2015). Extreme aridity pushes trees to
698 their physical limits. *Plant Physiology*, 168(July):pp.00223.2015. doi: 10.1104/pp.15.00223.
- 699 Larter, M., Pfautsch, S., Domec, J. C., Trueba, S., Nagalingum, N., and Delzon, S. (2017). Aridity drove the evolution of extreme
700 embolism resistance and the radiation of conifer genus *Callitris*. *New Phytologist*, 215(1):97–112. doi: 10.1111/nph.14545.
- 701 Laughlin, D. C., Siefert, A., Fleri, J. R., Tumber-Dávila, S. J., Hammond, W. M., Sabatini, F. M., Damasceno, G., Aubin, I.,
702 Field, R., Hatim, M. Z., Jansen, S., Lenoir, J., Lens, F., McCarthy, J. K., Niinemets, U., Phillips, O. L., Attorre, F., Bergeron,
703 Y., Bruun, H. H., Byun, C., Čuštorevska, R., Dengler, J., De Sanctis, M., Dolezal, J., Jiménez-Alfaro, B., Hérault, B.,
704 Homeier, J., Kattge, J., Meir, P., Mencuccini, M., Noroozi, J., Nowak, A., Peñuelas, J., Schmidt, M., Skvorc, Z., Sultana,
705 F., Ugarte, R. M., and Bruelheide, H. (2023). Rooting depth and xylem vulnerability are independent woody plant traits
706 jointly selected by aridity, seasonality, and water table depth. *New Phytologist*, n/a(n/a). doi: 10.1111/nph.19276. _eprint:
707 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.19276>.
- 708 Lens, F., Gleason, S. M., Bortolami, G., Brodersen, C., Delzon, S., and Jansen, S. (2022). Functional xylem characteristics
709 associated with drought-induced embolism in angiosperms. *New Phytologist*, 236(6):2019–2036. doi: 10.1111/nph.18447.
710 _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.18447>.
- 711 Lobo, A., Torres-Ruiz, J. M., Burlett, R., Lemaire, C., Parise, C., Francioni, C., Truffaut, L., Tomášková, I., Hansen, J. K., Kjær,
712 E. D., Kremer, A., and Delzon, S. (2018). Assessing inter- and intraspecific variability of xylem vulnerability to embolism in
713 oaks. *Forest Ecology and Management*, 424:53–61. doi: 10.1016/j.foreco.2018.04.031.
- 714 López, R., López de Heredia, U., Collada, C., Cano, F. J., Emerson, B. C., Cochard, H., and Gil, L. (2013). Vulnerability to
715 cavitation, hydraulic efficiency, growth and survival in an insular pine (*Pinus canariensis*). *Annals of Botany*, 111(6):1167–79.
716 doi: 10.1093/aob/mct084.
- 717 Maherali, H., Pockman, W. T., and Jackson, R. B. (2004). Adaptive variation in the vulnerability of woody plants to xylem cavitation.
718 *Ecology*, 85(8):2184–2199. doi: 10.1890/02-0538.
- 719 Maitner, B. S., Boyle, B., Casler, N., Condit, R., Donoghue II, J., Durán, S. M., Guaderrama, D., Hinchliff, C. E., Jørgensen, P. M.,
720 Kraft, N. J., McGill, B., Merow, C., Morueta-Holme, N., Peet, R. K., Sandel, B., Schildhauer, M., Smith, S. A., Svensson, J.-C.,

- 721 Thiers, B., Violle, C., Wiser, S., and Enquist, B. J. (2018). The bien r package: A tool to access the Botanical Information
722 and Ecology Network (BIEN) database. *Methods in Ecology and Evolution*, 9(2):373–379. doi: 10.1111/2041-210X.12861.
723 _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/2041-210X.12861>.
- 724 Mantova, M., Cochard, H., Burlett, R., Delzon, S., King, A., Rodriguez-Dominguez, C. M., Ahmed, M. A., Trueba, S., and
725 Torres-Ruiz, J. M. (2023). On the path from xylem hydraulic failure to downstream cell death. *New Phytologist*, 237(3):
726 793–806. doi: 10.1111/nph.18578. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.18578>.
- 727 Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M. I.,
728 Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R., Maycock, T. K., Waterfield, T., Yelekçi, O., Yu, R., and Zhou, B., editors.
729 *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the
730 Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY,
731 USA, (2021). doi: 10.1017/9781009157896.
- 732 Matusick, G., Ruthrof, K. X., Brouwers, N. C., and Hardy, G. S. (2014). Topography influences the distribution of autumn frost
733 damage on trees in a Mediterranean-type Eucalyptus forest. *Trees*, 28(5):1449–1462. doi: 10.1007/s00468-014-1048-4.
- 734 Mayr, S., Hacke, U., Schmid, P., Schwienbacher, F., and Gruber, A. (2006). Frost Drought in Conifers at the Alpine Timberline:
735 Xylem Dysfunction and Adaptations. *Ecology*, 87(12):3175–3185. doi: 10.1890/0012-9658(2006)87[3175:FDICAT]2.0.CO;
736 2. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1890/0012-9658%282006%2987%5B3175%3AFDICAT%5D2.0.CO%3B2>.
- 737 McCulloh, K. A., Augustine, S. P., Goke, A., Jordan, R., Krieg, C. P., O'Keefe, K., and Smith, D. D. (2023). At least it is a dry
738 cold: the global distribution of freeze–thaw and drought stress and the traits that may impart poly-tolerance in conifers. *Tree
739 Physiology*, 43(1):1–15. doi: 10.1093/treephys/tpac102.
- 740 McDowell, N. G. (2011). Mechanisms Linking Drought, Hydraulics, Carbon Metabolism, and Vegetation Mortality. *Plant
741 Physiology*, 155(3):1051–1059. doi: 10.1104/pp.110.170704.
- 742 McDowell, N. G., Beerling, D. J., Breshears, D. D., Fisher, R. A., Raffa, K. F., and Stitt, M. (2011). The interdependence of
743 mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution*, 26(10):523–532. doi: 10.1016/j.
744 tree.2011.06.003.
- 745 McDowell, N. G., Sapes, G., Pivovaroff, A., Adams, H. D., Allen, C. D., Anderegg, W. R. L., Arend, M., Breshears, D. D., Brodribb,
746 T., Choat, B., Cochard, H., De Cáceres, M., De Kauwe, M. G., Grossiord, C., Hammond, W. M., Hartmann, H., Hoch, G.,
747 Kahmen, A., Klein, T., Mackay, D. S., Mantova, M., Martínez-Vilalta, J., Medlyn, B. E., Mencuccini, M., Nardini, A., Oliveira,
748 R. S., Sala, A., Tissue, D. T., Torres-Ruiz, J. M., Trowbridge, A. M., Trugman, A. T., Wiley, E., and Xu, C. (2022). Mechanisms
749 of woody-plant mortality under rising drought, CO₂ and vapour pressure deficit. *Nature Reviews Earth & Environment*, 3(5):
750 294–308. doi: 10.1038/s43017-022-00272-1. Publisher: Nature Publishing Group.
- 751 Medeiros, J. S. and Pockman, W. T. (2011). Drought increases freezing tolerance of both leaves and xylem
752 of Larrea tridentata. *Plant, Cell & Environment*, 34(1):43–51. doi: 10.1111/j.1365-3040.2010.02224.x. _eprint:
753 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1365-3040.2010.02224.x>.
- 754 Morris, H., Plavcová, L., Cvecko, P., Fichtler, E., Gillingham, M. A. F., Martínez-Cabrera, H. I., McGinn, D. J.,
755 Wheeler, E., Zheng, J., Ziemińska, K., and Jansen, S. (2016). A global analysis of parenchyma tissue fractions
756 in secondary xylem of seed plants. *New Phytologist*, 209(4):1553–1565. doi: 10.1111/nph.13737. _eprint:
757 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.13737>.
- 758 Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M., and Gibon, Y. (2011). Water deficits uncouple growth from
759 photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *Journal of Experimental
760 Botany*, 62(6):1715–1729. doi: 10.1093/jxb/erq438.
- 761 Orme, D. (2013). The caper package : comparative analysis of phylogenetics and evolution in R. *R package version 0.5, 2*,
762 pages 1–36. doi: 1.

- 763 Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401(6756):877–84. doi: 10.1038/44766.
- 764 Paradis, E., Claude, J., and Strimmer, K. (2004). APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics*,
765 20(2):289–90. doi: 10.1093/bioinformatics/btg412.
- 766 Pescador, D. S., Sierra-Almeida, A., Torres, P. J., and Escudero, A. (2016). Summer Freezing Resistance: A Critical Filter for
767 Plant Community Assemblies in Mediterranean High Mountains. *Frontiers in Plant Science*, 7. doi: 10.3389/fpls.2016.00194.
768 Publisher: Frontiers.
- 769 Pinheiro, J., Bates, D., and Team, R. C. nlme: Linear and Nonlinear Mixed Effects Models, (2023). URL <https://cran.r-project.org/web/packages/nlme/index.html>.
- 770 Pittermann, J. and Sperry, J. (2003). Tracheid diameter is the key trait determining the extent of freezing-induced embolism in
771 conifers. *Tree Physiology*, 23(13):907–914. doi: 10.1093/treephys/23.13.907.
- 772 Pittermann, J., Sperry, J. S., Wheeler, J. K., Hacke, U. G., and Sikkema, E. H. (2006). Mechanical reinforcement of tracheids
773 compromises the hydraulic efficiency of conifer xylem. *Plant, Cell and Environment*, 29(8):1618–28. doi: 10.1111/j.1365-
774 3040.2006.01539.x. ISBN: 0140-7791.
- 775 Pollock, L. J., Morris, W. K., and Vesk, P. A. (2012). The role of functional traits in species distributions
776 revealed through a hierarchical model. *Ecography*, 35(8):716–725. doi: 10.1111/j.1600-0587.2011.07085.x. _eprint:
777 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1600-0587.2011.07085.x>.
- 778 Preston, J. C. and Sandve, S. R. (2013). Adaptation to seasonality and the winter freeze. *Frontiers in Plant Science*, 4. doi:
779 10.3389/fpls.2013.00167. Publisher: Frontiers.
- 780 Puglielli, G., Hutchings, M. J., and Laanisto, L. (2021). The triangular space of abiotic stress tolerance in woody
781 species: a unified trade-off model. *New Phytologist*, 229(3):1354–1362. doi: 10.1111/nph.16952. _eprint:
782 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/nph.16952>.
- 783 Puglielli, G., Laanisto, L., Gori, A., and Cardoso, A. A. (2023). Woody plant adaptations to multiple abiotic stressors: Where are
784 we? *Flora*, 299:152221. doi: 10.1016/j.flora.2023.152221.
- 785 R Core Team. R: A Language and Environment for Statistical Computing, (2023). URL <https://www.r-project.org/>.
- 786 Reich, P. B. (2014). The world-wide ‘fast-slow’ plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2):275–301.
787 doi: 10.1111/1365-2745.12211. ISBN: 2806.
- 788 Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and
789 Evolution*, 3(2):217–223. doi: 10.1111/j.2041-210X.2011.00169.x. ISBN: 2041-210X.
- 790 Richardson, D. M. and Bond, W. J. (1991). Determinants of Plant Distribution: Evidence from Pine Invasions. *The American
791 Naturalist*, 137(5):639–668. doi: 10.1086/285186. Publisher: The University of Chicago Press.
- 792 Rohatgi, A. WebPlotDigitizer, (2022). URL <https://automeris.io/WebPlotDigitizer>.
- 793 Rueda, M., Godoy, O., and Hawkins, B. A. (2017). Spatial and evolutionary parallelism between shade and drought tolerance
794 explains the distributions of conifers in the conterminous United States. *Global Ecology and Biogeography*, 26(1):31–42. doi:
795 10.1111/geb.12511. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/geb.12511>.
- 796 Russo, S. E., McMahon, S. M., Detto, M., Ledder, G., Wright, S. J., Condit, R. S., Davies, S. J., Ashton, P. S., Bunyavejchewin, S.,
797 Chang-Yang, C.-H., Ediriweera, S., Ewango, C. E. N., Fletcher, C., Foster, R. B., Gunatilleke, C. V. S., Gunatilleke, I. A. U. N.,
798 Hart, T., Hsieh, C.-F., Hubbell, S. P., Itoh, A., Kassim, A. R., Leong, Y. T., Lin, Y. C., Makana, J.-R., Mohamad, M. B., Ong,
799 P., Sugiyama, A., Sun, I.-F., Tan, S., Thompson, J., Yamakura, T., Yap, S. L., and Zimmerman, J. K. (2021). The interspecific
800 growth–mortality trade-off is not a general framework for tropical forest community structure. *Nature Ecology & Evolution*, 5(2):
801 174–183. doi: 10.1038/s41559-020-01340-9. Number: 2 Publisher: Nature Publishing Group.
- 802 Sakai, A. and Larcher, W. Cold Acclimation in Plants. In Sakai, A. and Larcher, W., editors, *Frost Survival of Plants: Responses
803 and Adaptation to Freezing Stress*, pages 97–137. Springer, Berlin, Heidelberg, (1987). ISBN 978-3-642-71745-1. doi: 10.

- 805 1007/978-3-642-71745-1_5. URL https://doi.org/10.1007/978-3-642-71745-1_5.
- 806 Sakai, A. and Larcher, W. The Freezing Process in Plants. In Sakai, A. and Larcher, W., editors, *Frost Survival of Plants: Responses and Adaptation to Freezing Stress*, Ecological Studies, pages 21–38. Springer, Berlin, Heidelberg, (1987). ISBN 978-3-642-71745-1. doi: 10.1007/978-3-642-71745-1_2. URL https://doi.org/10.1007/978-3-642-71745-1_2.
- 807 Sakai, A. and Larcher, W. Freezing Injuries in Plants. In Sakai, A. and Larcher, W., editors, *Frost Survival of Plants: Responses and Adaptation to Freezing Stress*, Ecological Studies, pages 39–58. Springer, Berlin, Heidelberg, (1987). ISBN 978-3-642-71745-1. doi: 10.1007/978-3-642-71745-1_3. URL https://doi.org/10.1007/978-3-642-71745-1_3.
- 808 Sakai, A. and Yoshida, S. (1968). The role of sugar and related compounds in variations of freezing resistance. *Cryobiology*, 5 (3):160–174. doi: 10.1016/S0011-2240(68)80161-0.
- 809 Sanchez-Martinez, P., Mencuccini, M., García-Valdés, R., Hammond, W. M., Serra-Diaz, J. M., Guo, W.-Y., Segovia, R. A., Dexter, K. G., Svenning, J.-C., Allen, C., and Martínez-Vilalta, J. (2023). Increased hydraulic risk in assemblages of woody plant species predicts spatial patterns of drought-induced mortality. *Nature Ecology & Evolution*, pages 1–13. doi: 10.1038/s41559-023-02180-z. Publisher: Nature Publishing Group.
- 810 Schuldt, B., Knutzen, F., Delzon, S., Jansen, S., Müller-Haubold, H., Burlett, R., Clough, Y., and Leuschner, C. (2015). How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction? *New Phytologist*. doi: 10.1111/nph.13798.
- 811 Sierra-Almeida, A., Reyes-Bahamonde, C., and Cavieres, L. A. (2016). Drought increases the freezing resistance of high-elevation plants of the Central Chilean Andes. *Oecologia*, 181(4):1011–1023. doi: 10.1007/s00442-016-3622-5.
- 812 Skelton, R. P., Anderegg, L. D. L., Diaz, J., Kling, M. M., Papper, P., Lamarque, L. J., Delzon, S., Dawson, T. E., and Ackerly, D. D. (2021). Evolutionary relationships between drought-related traits and climate shape large hydraulic safety margins in western North American oaks. *Proceedings of the National Academy of Sciences*, 118(10):e2008987118. doi: 10.1073/pnas.2008987118. Publisher: Proceedings of the National Academy of Sciences.
- 813 Smith, S. A. and Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105 (3):302–314. doi: 10.1002/ajb2.1019. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1002/ajb2.1019>.
- 814 Sorek, Y., Greenstein, S., and Hochberg, U. (2022). Seasonal adjustment of leaf embolism resistance and its importance for hydraulic safety in deciduous trees. *Physiologia Plantarum*, 174(5):e13785. doi: 10.1111/ppl.13785. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/ppl.13785>.
- 815 Sperry, J. S. and Sullivan, J. E. M. (1992). Xylem Embolism in Response to Freeze-Thaw Cycles and Water Stress in Ring-Porous, Diffuse-Porous, and Conifer Species. *Plant Physiology*, 100(2):605–613. Publisher: American Society of Plant Biologists (ASPB).
- 816 Sperry, J. S. and Tyree, M. T. (1988). Mechanism of Water Stress-Induced Xylem Embolism. *Plant Physiology*, 88(3):581–587. doi: 10.1104/pp.88.3.581.
- 817 Sperry, J. S., Hacke, U. G., and Pittermann, J. (2006). Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany*, 93(10):1490–500.
- 818 Stahl, U., Reu, B., and Wirth, C. (2014). Predicting species' range limits from functional traits for the tree flora of North America. *Proceedings of the National Academy of Sciences*, 111(38):13739–13744. doi: 10.1073/pnas.1300673111.
- 819 Stearns, S. C. *The evolution of life histories*, volume 249. Oxford University Press, Oxford, (1992). URL https://scholar.google.com/scholar_lookup?title=The+evolution+of+life+histories&publication_year=1992&.
- 820 Stojnić, S., Suchocka, M., Benito-Garzón, M., Torres-Ruiz, J. M., Cochard, H., Bolte, A., Cocozza, C., Cvjetković, B., de Luis, M., Martinez-Vilalta, J., Ræbeld, A., Tognetti, R., and Delzon, S. (2018). Variation in xylem vulnerability to embolism in European beech from geographically marginal populations. *Tree Physiology*, 38(2):173–185. doi: 10.1093/treephys/tpx128.
- 821 Stolsmo, S. P., Lindberg, C. L., Ween, R. E., Schat, L., Preston, J. C., Humphreys, A. M., and Fjellheim, S. (2024). Evolution of

- 847 drought and frost responses in cool season grasses (Pooideae): was drought tolerance a precursor to frost tolerance? *Journal*
848 *of Experimental Botany*, 75(20):6405–6422. doi: 10.1093/jxb/erae316.
- 849 Sumner, E. E., Williamson, V. G., Gleadow, R. M., Wevill, T., and Venn, S. E. (2022). Acclimation to water stress improves
850 tolerance to heat and freezing in a common alpine grass. *Oecologia*, 199(4):831–843. doi: 10.1007/s00442-022-05245-1.
- 851 Torres-Ruiz, J. M., Jansen, S., Choat, B., McElrone, A. J., Cochard, H., Brodribb, T. J., Badel, E., Burlett, R., Bouche, P. S.,
852 Brodersen, C. R., Li, S., Morris, H., and Delzon, S. (2015). Direct X-Ray Microtomography Observation Confirms the Induction
853 of Embolism upon Xylem Cutting under Tension. *Plant Physiology*, 167(1):40–43. doi: 10.1104/pp.114.249706.
- 854 Torres-Ruiz, J. M., Cochard, H., Mencuccini, M., Delzon, S., and Badel, E. (2016). Direct observation and modelling of embolism
855 spread between xylem conduits: a case study in Scots pine. *Plant, Cell & Environment*, 39(12):2774–2785. doi: 10.1111/pce.
856 12840. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/pce.12840>.
- 857 Trueba, S., Muñoz, N. G., Burlett, R., Lamarque, L. J., Gibon, Y., Gimeno, T. E., Kaisermann, A., Benard, C., Lemaire, C.,
858 Torres-Ruiz, J. M., Wingate, L., and Delzon, S. (2024). The rates of starch depletion and hydraulic failure both play a role in
859 drought-induced seedling mortality. *Annals of Forest Science*, 81(1):27. doi: 10.1186/s13595-024-01246-7.
- 860 Tyree, M. T. and Sperry, J. S. (1989). Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Biology*, 40(1):
861 19–36. Publisher: Annual Reviews 4139 El Camino Way, PO Box 10139, Palo Alto, CA 94303-0139, USA.
- 862 Tyree, M. T. and Zimmermann, M. H. *Xylem Structure and the Ascent of Sap*. Springer Science & Business Media, (2002). ISBN
863 3-540-43354-6. URL <https://books.google.com/books?hl=en&lr=&id=AhVON2aHJMCC&pgis=1>.
- 864 Urli, M., Porté, A. J., Cochard, H., Guengant, Y., Burlett, R., and Delzon, S. (2013). Xylem embolism threshold for catastrophic
865 hydraulic failure in angiosperm trees. *Tree Physiology*, 33(7):672–83. doi: 10.1093/treephys/tpt030.
- 866 Vanoni, M., Bugmann, H., Nötzli, M., and Bigler, C. (2016). Drought and frost contribute to abrupt growth decreases before tree
867 mortality in nine temperate tree species. *Forest Ecology and Management*, 382:51–63. doi: 10.1016/j.foreco.2016.10.001.
- 868 Visakorpi, K., Manzanedo, R. D., Görlich, A. S., Schiendorfer, K., Altermatt Bieger, A., Gates, E., and Hille Ris Lambers, J. (2024).
869 Leaf-level resistance to frost, drought and heat covaries across European temperate tree seedlings. *Journal of Ecology*, 112
870 (3):559–574. doi: 10.1111/1365-2745.14254. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/1365-2745.14254>.
- 871 Vitasse, Y., Bottero, A., Cailleret, M., Bigler, C., Fonti, P., Gessler, A., Lévesque, M., Rohner, B., Weber, P., Rigling,
872 A., and Wohlgemuth, T. (2019). Contrasting resistance and resilience to extreme drought and late spring frost in
873 five major European tree species. *Global Change Biology*, 25(11):3781–3792. doi: 10.1111/gcb.14803. _eprint:
874 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.14803>.
- 875 Volaire, F., Barkaoui, K., Grémillet, D., Charrier, G., Dangles, O., Lamarque, L. J., Martin-StPaul, N., and Chuine, I. (2022). Is
876 a seasonally reduced growth potential a convergent strategy to survive drought and frost in plants? *Annals of Botany*, page
877 mcac153. doi: 10.1093/aob/mcac153.
- 878 Weiser, C. J. (1970). Cold Resistance and Injury in Woody Plants: Knowledge of hardy plant adaptations to freezing stress may
879 help us to reduce winter damage. *Science*, 169(3952):1269–1278. doi: 10.1126/science.169.3952.1269.
- 880 Wheeler, J. K., Huggett, B. A., Tofte, A. N., Rockwell, F. E., and Holbrook, N. M. (2013). Cutting xylem under tension or
881 supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. *Plant, Cell and Environment*,
882 36(11):1938–1949. doi: 10.1111/pce.12139.
- 883 Wiens, J. J. (2016). Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. *PLOS Biology*,
884 14(12):e2001104. doi: 10.1371/journal.pbio.2001104. Publisher: Public Library of Science.
- 885 Willi, Y. and Van Buskirk, J. (2022). A review on trade-offs at the warm and cold ends of geographical distributions. *Philosophical
Transactions of the Royal Society B: Biological Sciences*, 377(1848):20210022. doi: 10.1098/rstb.2021.0022.
- 886 Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. a., FitzJohn, R. G., McGlinn, D. J., O'Meara, B. C.,
887 Moles, A. T., Reich, P. B., Royer, D. L., Soltis, D. E., Stevens, P. F., Westoby, M., Wright, I. J., Aarssen, L., Bertin, R. I.,

- 889 Calaminus, A., Govaerts, R., Hemmings, F., Leishman, M. R., Oleksyn, J., Soltis, P. S., Swenson, N. G., Warman, L., and
890 Beaulieu, J. M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506(7486):89–92. doi:
891 10.1038/nature12872. ISBN: 0028-0836.
- 892 Zhang, F., Liu, Y.-W., Qin, J., Jansen, S., Zhu, S.-D., and Cao, K.-F. (2024). Xylem embolism induced by freeze–thaw and drought
893 are influenced by different anatomical traits in subtropical montane evergreen angiosperm trees. *Physiologia Plantarum*, 176
894 (5):e14567. doi: 10.1111/ppl.14567. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/ppl.14567>.
- 895 Zhang, H., Zhao, Y., and Zhu, J.-K. (2020). Thriving under Stress: How Plants Balance Growth and the Stress Response.
896 *Developmental Cell*, 55(5):529–543. doi: 10.1016/j.devcel.2020.10.012. Publisher: Elsevier.
- 897 Zhang, M. I. N. and Willison, J. H. M. (1987). An improved conductivity method for the measurement of frost hardiness. *Canadian
898 Journal of Botany*, 65(4):710–715. doi: 10.1139/b87-095. Publisher: NRC Research Press.
- 899 Zomer, R.J. and Trabucco, A. Global Aridity Index and Potential Evapotranspiration Climate Database v3, (2022). URL
900 [https://csidotinfo.wordpress.com/2019/01/24/global-aridity-index-and-potential-evapotranspiration-
901 climate-database-v3/](https://csidotinfo.wordpress.com/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v3/).

902 **Supplementary Information**

903 List of Supplementary figures:

904

905 Fig. S1. Comparison of frost tolerance methods: visual scoring (LT0) vs. Electrolyte leakage (LT50).

906 Fig. S2. Comparison of frost tolerance data across the different organs in the database, classified as bud, branch
907 and leaf for both Lt0 (A,C,E) and LT50 (B,D,F).

908 Fig. S3. Comparison of two datasets of frost tolerance, cleaned vs. non-cleaned.

909 Fig. S4. Comparison of the different methods from the embolism resistance database.

910

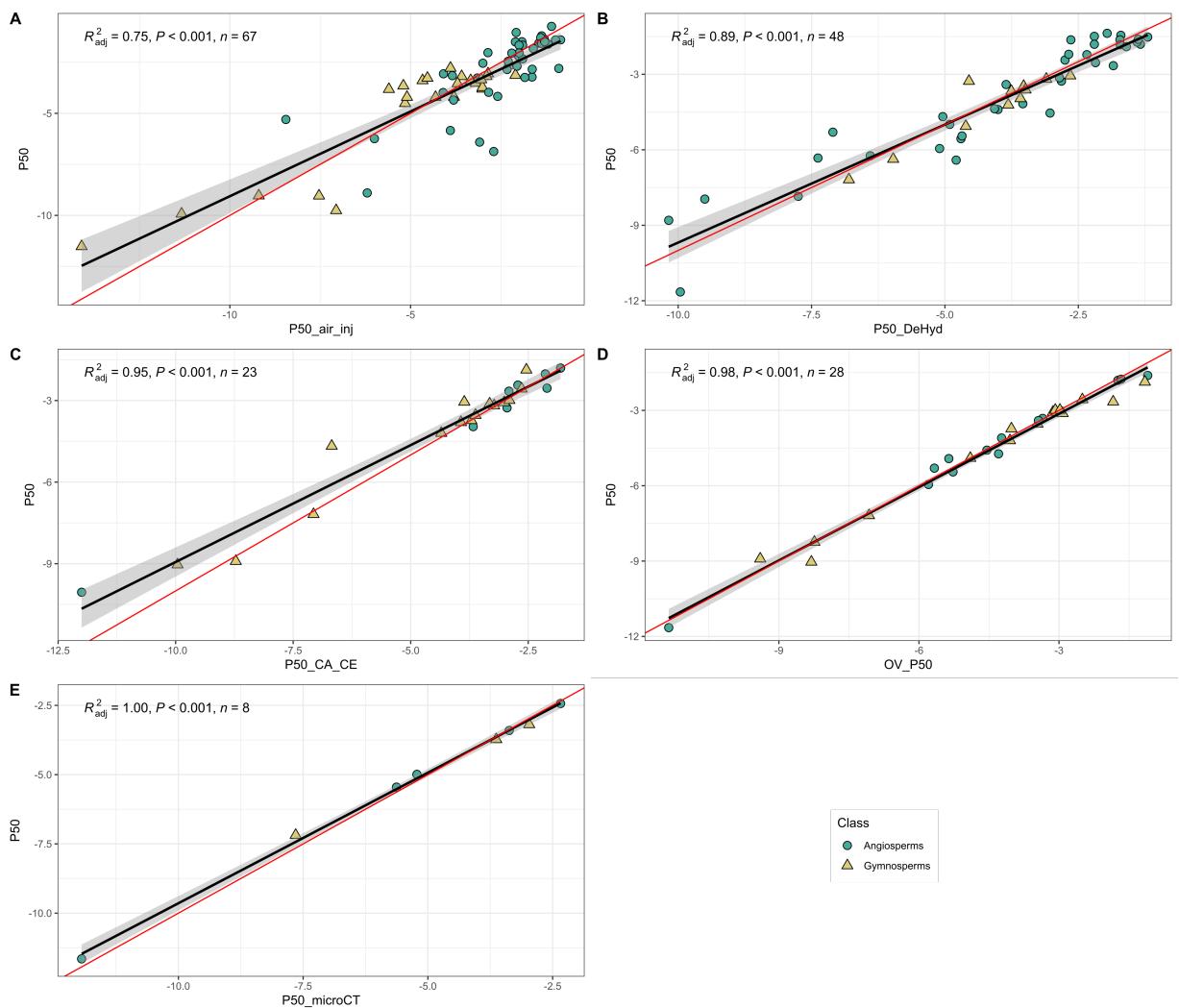


Figure 1. Comparison of frost tolerance methods: visual scoring (LT0) vs. Electrolyte leakage (LT50). Data shows points for the 110 species with data for both methods. Lines and shaded area show the linear model and 95% confidence interval, with the corresponding adjusted R-squared, p-value and number of points. Yellow triangles are for gymnosperm species and green dots for Angiosperms. Red line is the 1:1 line.

911 **Figure S3 Comparison of two datasets of frost tolerance, cleaned vs. non-cleaned.** Lines and shaded area
 912 show the linear model and 95% confidence interval, with the corresponding adjusted R-squared, p-value and number
 913 of points. Yellow triangles are for gymnosperm species and green dots for Angiosperms. Red line is the 1:1 line.
 914 **Figure S4 Comparison of the different methods from the embolism resistance database.**
 915 **Figure S5 traits vs climate**

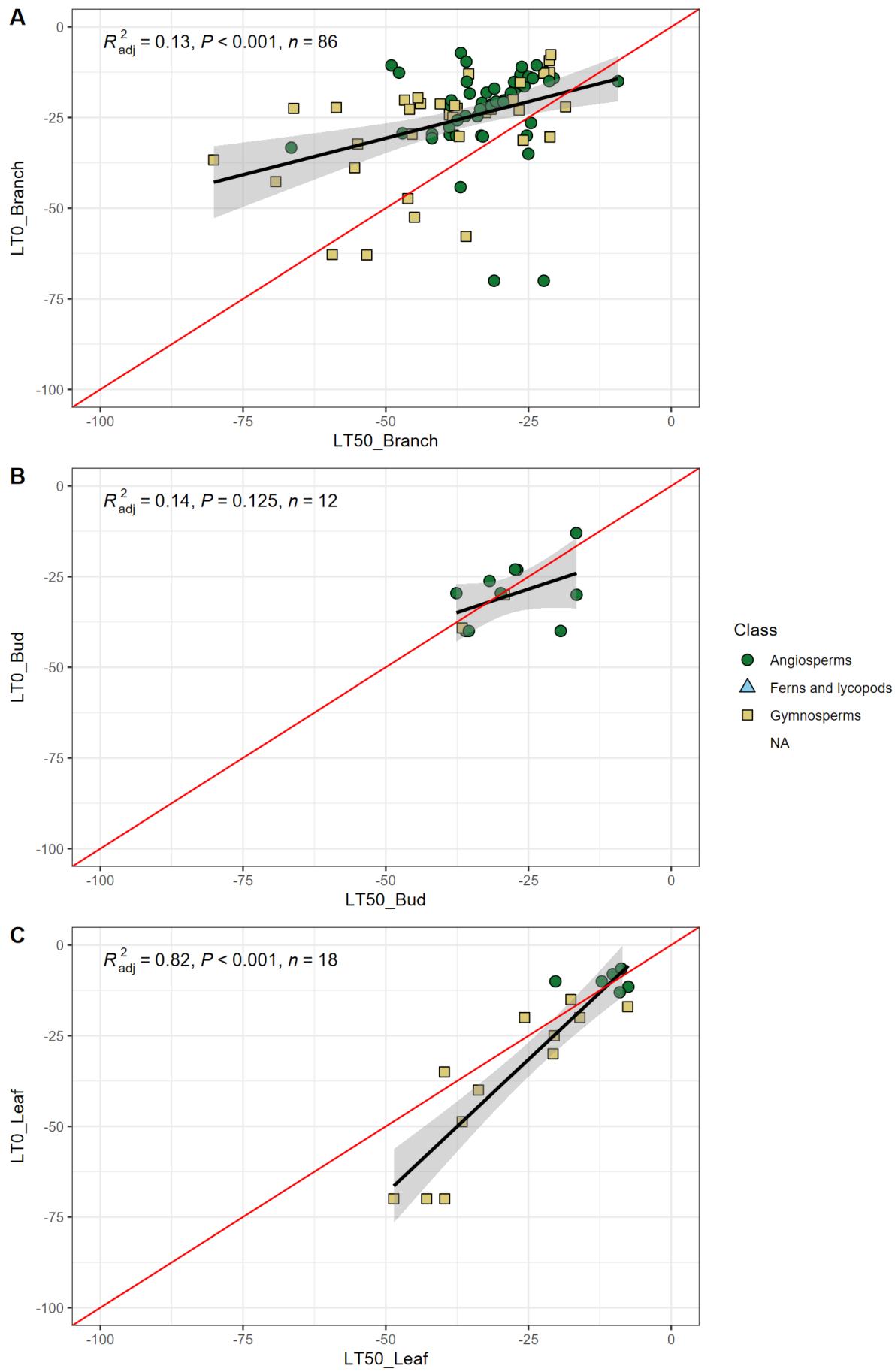


Figure S2

Figure 2. Comparison of frost tolerance data across the different organs in the database, classified as bud, branch and leaf for both LT0 (A,C,E) and LT50 (B,D,F). In each panel, lines and shaded area show the linear model and 95% confidence interval, with the corresponding adjusted R^2 -value, p-value and number of points. Yellow triangles are for gymnosperm species and green dots for Angiosperm species. Red line is the 1:1 line.