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

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Affiliations:

Key-words:

Abstract

To-do: homogeneiser frost vs cold

Introduction

In forests in the northern hemisphere (NH), trees must survive seasonal frost and drought, and compete for resources with other species in order to grow and reproduce, leading to a balancing act between investing in stress tolerance and resistance traits, i.e. the ability to survive extreme climate events, or growth and reproduction (Grime, 1977; Reich, 2014). In particular, fitness costs and benefits of functional traits related to frost and drought resistance can result in trade-offs within the plant, across seasons and throughout the life of the plant, which in turn determine their ability to compete and survive, especially at the margins of their species' distribution (Sanchez-Martinez et al., 2023). Climate also plays a leading role in determining NH tree species distributions, which are limited at the northern margins by frost tolerance and on the southern margin by drought resistance (Richardson & Bond, 1991; Hampe & Petit, 2005; Morin et al., 2007; Choat et al., 2018; Körner, 2021). Climate change has already deeply modified rainfall and temperature patterns in many areas of the world, as well as increased the stochasticity and duration of extreme climate events such as droughts and heatwaves (Masson-Delmotte et al., 2021). It is bringing large-scale tree mortality events following droughts, documented in all forested ecosystems (Allen et al., 2010; Anderegg et al., 2015b). A general warming pattern could also increase vulnerability to sudden autumn and winter cold snaps and spring frosts (Matusick et al., 2014; Greco et al., 2018; Körner, 2021). From boreal to Mediterranean ecosystems, forests are therefore likely to be exposed to more frequent, alternating sudden frost and drought stresses, with compounding effects on productivity and survival (Charrier et al., 2021). Understanding how tree functional traits interact to determine species-specific response to climate extremes is crucial in order be able to predict forest dynamics at local and continental scales (Aubin et al., 2016), from mortality events to range limits and distribution shifts with climate change (Pollock et al., 2012; Stahl et al., 2014; Wiens, 2016).

Plant responses to drought and frost are well documented, with both climatic stresses leading to a reduction in plant performance, and links to plant death (ref). Under severe drought, the pressure in the vascular system drops, causing air-bubbles to spread through the xylem, leading to reduced water flow and hydraulic failure (Tyree & Sperry, 1989). This run-away embolism within xylem conduits is a major driver of plant mortality in forests worldwide (Choat et al., 2012, 2018; Anderegg et al., 2015a; McDowell et al., 2022)(Choat et al., 2012, 2018; Anderegg et al., 2015a; McDowell et al., 2022). Trees deploy adaptations to limit the risk of damaging loss of conductance, linked to the fine anatomy of inter-conduit pits – these changes result in increased embolism resistance, classically termed P_{50} (MPa). Embolism resistance varies widely across species, from around -1 to -19 MPa (Maherali et al., 2004; Choat et al., 2012; Larter et al., 2017)(Maherali et al., 2004; Choat et al., 2012; Larter et al., 2017) and is closely related to survival time during prolonged drought (Brodribb & Cochard, 2009; Urli et al., 2013) (Brodribb & Cochard, 2009; Urli et al., 2013). Across gymnosperms and angiosperms, xylem embolism resistance is a key functional trait directly related to aridity and species distributions (Brodribb & Hill, 1999; Delzon et al., 2010; Larter et al., 2017; Skelton et al., 2021). At the onset of winter, environmental cues trigger woody plants preparations for the coming freezing temperatures by lowering the freezing point of the intracellular compartment, synthesizing anti-freeze proteins, and changing the composition of their cell membranes (Weiser, 1970; Sakai & Larcher, 1987; Charrier et al., 2021). This allows them to tolerate the formation of extra-cellular ice-crystals down to extremely negative temperatures, which induces intensive freeze dehydration (e.g. at temperatures lower than-50°C). After winter hardening, frost-resistant tissues can survive in a

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deep frozen state for several months, in some cases even recovering from the temperature of liquid nitrogen (Sakai & Larcher, 1987). Similar to the osmotic adjustments occurring during drought-response, these processes mobilize internal carbon resources and involve changes in the state of carbon reserves (soluble carbohydrates vs. starch), while concomitantly decreasing bulk water content (Baffoin *et al.*, 2021). While trees' ability to withstand drought without reaching damaging xylem embolism levels and extreme cold temperatures without widespread cellular damage are recognized as critical traits for plant survival, they are seldom studied together, limiting our ability to understand whether these traits show trade-offs or exist together in a stress-tolerance syndrome (ref).

On a wider evolutionary scale, disconnected selective pressures occur across a species range, with selection for cold tolerance in the populations experiencing the harshest winters, whereas drought-tolerance will have higher fitness in populations in dry areas (ref). On the other hand, a trait (or trait combinations) increasing both drought and cold resistance would be highly adaptive in species exposed to both stresses (McCulloh *et al.*, 2023). Even with no direct links between functional traits, indirect relationships can exist, for example through trade-offs with growth and reproduction (refs). These within-species relationships between traits are sometimes revealed at broad evolutionary scales, with links between traits across whole clades. Xylem exposure to strong negative pressure during drought requires building thicker conduit walls relative to lumen area to avoid conduit deformation or collapse (Hacke *et al.*, 2001). This trade-off is thought to drive the link between safety from drought-induced embolism and the efficiency of xylem water transport across species, because of a 4th power relationship between conduit radius and water flow (Gleason *et al.*, 2016; Liu *et al.*, 2021). A higher proportion of conduit cell wall has been hypothesized to result in higher wood density in embolism resistant species (Pittermann *et al.*, 2006; Sperry *et al.*, 2006), but this is not always the case (Gleason *et al.*, 2016; Larter *et al.*, 2017). However, xylem conduit diameter determines the volume of dissolved air in the frozen sap that can form embolisms after a freeze-thaw cycle, leading to a negative trade-off between hydraulic efficiency and freeze-thaw embolism resistance (Davis *et al.*, 1999; Zanne *et al.*, 2014).

From a mechanistic point of view, we can expect synergies or antagonisms between drought-resistance and frost-resistance in woody plants. Firstly, both types of stress induce tissue dehydration, therefore producing similar molecular responses and shared signaling pathways (Beck *et al.*, 2007; Charrier *et al.*, 2021). At the vascular level, both stresses can induce air-bubble formation (drought- and freeze-thaw-induced embolism). Second, from an evolutionary perspective, woody angiosperms are thought to have moved into freezing-environments poleward from the frost-free tropics by co-opting adaptations to drought, such as deciduousness, herbaceousness or more embolism-resistant conduits (Zanne *et al.*, 2014). Conifer physiology allows 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, at least in harsh and nutrient-poor habitats (Augusto *et al.*, 2014).

Therefore, even if not directly linked, we can expect positive correlations between functional traits linked to drought resistance and frost hardinessresistance. In this case, we can hypothesize (1) the absence of a trade-off between drought resistant-resistance and cold resistant-resistance traits, and the existence of therefore some trait-combinations allowing species to be adapted to both extreme cold and extreme drought.

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Commented [7]: I'm wondering if we should include this section in the next two paragraphs where we discuss if we could expect synergies or tradeoff. I ha the feeling that there are two groups of arguments 1. functional tradeoff or synergies due to direct mechanistic link (+ or -) between the meca of stress tolerance of frost and drought and 2. evolutionary process leading to synergy or tradeoff. Maybe we could organise that along these lines?

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On the other hand, costs associated with establishing resistance to either type of stress (for example, increased construction costs of thick walls for an embolism resistant xylem) could limit resources available for resisting the other type of stress. A shared, limited pool of non-structural carbohydrates necessary for drought and cold stress responses could preclude surviving or limit the ability to compete and reproduce in habitats with hot dry summers and harsh winters. In this case, we can hypothesize (2) a trade-off between drought resistance and frost hardinessresistance, with the absence of poly-stress resistance traits combinations (McCulloh *et al.*, 2023). Accordingly, investment in resistance traits (either or both) can limit allocation to growth, resource acquisition and reproduction, which is sometimes called physiological or allocation trade-off (Grime, 1977; Stearns, 1992; Willi & Van Buskirk, 2022). We can therefore further hypothesize (3) a trade-off between stress-resistance traits on the one hand and maximum height, maximum hydraulic conductivity, and wood density.

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Loehle, C. 1998. Height growth rate tradeoffs determ[ine] northern and southern range limits for tree. J. Bioge[ogr.] 25: 735–742.

Materials and methods

Frost resistance database

We obtained frost resistance data from the literature, using search terms 1) "frost", "cold" and 2) "resistance", "tolerance", or "hardiness". We limited our search to trees, shrubs and woody species. Overall, we collected data from around 200 references in tables, supplementary data or directly from figures when necessary using WebPlotDigitizer (Rohatgi, 2022). From these papers, combined with unpublished data (Charrier, pers. comm.), we accumulated a database of around 4000 measurements in over 600 species. We also recovered as much metadata as possible regarding the experimental setup, including the date and location of the study, the age of the plant, which organ/tissue was used, and other parameters of the experiment, such as which technique was used, the rate of temperature change, and the duration of exposure at the lowest temperature.

These measurements included data from various plant organs (mainly leaves, stems, buds), and using different techniques. Briefly, two methods exist in the literature that both examine samples for damage after exposure to cold temperatures. Firstly, the visual scoring technique (VS) is based on visual examination of multiple tissue samples exposed to different cold temperatures, and LT0 (°C) is recorded as the coldest temperature before the samples show cell damage, usually a visible discoloration of the tissue (Sakai & Larcher, 1987b). The electrolyte leakage (EL) employs a similar cold temperature gradient, and aims to quantify the release of electrolytes from plant cells as they die following exposure to lethal cold temperatures. From the sigmoid response curve of the relationship between the relative electrolyte leakage obtained and the minimum temperature of exposure, we can derive the inflection point called LT50 (°C), i.e. the temperature at which 50% of REL is reached. For more details, please refer to the supplementary materials. These two techniques result in critical temperature thresholds that describe the species frost resistance. Although measured differently, LT0 and LT50 were well correlated across species considering measurements across all organs (R^2=0.34; $p<0.001$; n=110 species; Suppl. Figure X), with LT0 at higher temperatures on average than LT50 for the same species.

Among branches, buds and leaves, we found LT0 and LT50 to be generally comparable (Suppl. Figure X). However, to ensure as much homogeneity as possible while maximizing the number of species in the dataset, we proceeded as follows: within a species, we averaged all data grouping by organ () and by method, resulting in a maximum of six different values per species (branch/bud/leaf by LT0/LT50). We prioritized measurements using the EL technique, which had protocols that are more consistent across studies (notably regarding freezing rate, see below). Branch data was much more common in the database, and we avoided the bias towards conifers (since leaf data was not available for deciduous species) by placing leaf data last. Thus, we selected which value to use based on availability in this order: 1: LT50 in branches, 2: LT50 in buds, 3: LT0 in branches, 4: LT0 in buds, 5: LT50 in leaves, 6: LT0 in leaves.

We removed from all measurements that were not from the middle of winter, so that natural hardening had occurred, and the late-winter de-hardening process had not started. Finally, we also applied a selection criterion based on the age of the plants, selecting only data collected using adult or mature individuals. This mainly excluded experiments on juvenile and/or potted plants, and data source not reporting plant age. Additionally, slow freezing/thawing rates can artificially induce hardening and high rates can change the dynamics of ice-crystal formation (Weiser, 1970; Sakai & Larcher, 1987c). We chose arbitrary cut-offs, removing data with rates below 0.2°C h^{-1} and over 9°C h^{-}

[1]. This resulted in two datasets that were used in the downstream analyses. Although the overall differences between species in both datasets are not notable, in some cases there was a 30°C shift of frost hardiness in the same species between datasets.

We also added measurements for 79 species (suppl. Materials), focusing on adding species from drier areas (temperate and Mediterranean climates), which were underrepresented in frost hardiness studies. We used the EL technique (Zhang & Willison, 1987), modified from the protocol described elsewhere (Baffoin *et al.*, 2021). We collected branches from 5 individual trees per species. Short stem segments from each individual tree were exposed to maximum negative temperatures of -15, -25, -35, -50, -80°C, as well as a +5°C control, and an extreme treatment using liquid nitrogen aiming to reach below -100°C for the most frost hardy species. The temperature dynamic was followed using thermocouples connected to a CR1000 datalogger. For temperature settings between -15 and -50°C, we programmed four temperature-controlled chambers to drop by 5°C per hour from +5°C to the target temperature, hold for 1 hour at the target temperature, then return to +5°C at a rate of 5°C per hour. For the -80°C treatment, samples were placed in a large thermos container inside an -80°C freezer. Using a thermocouple, we monitored temperature inside the thermos which reached a minimum of around -70°C within a few hours. Thawing was achieved by placing the samples at room temperature ensuring gradual thawing over several hours. For the extreme treatment, liquid N_2 was placed at the bottom of an expanded polystyrene box. The samples were then placed on a platform and never in contact with the liquid N_2. A large temperature gradient existed between samples closest to the liquid, monitored with 5-10 thermocouple sensors placed throughout the box. The average minimum temperature across all thermocouples was used to estimate minimum temperature, which varied from around -90 to -120°C across all experiments.

Each sample from the different temperature steps are then cut-up and placed in 15mL of milliQ ultrapure water, and agitated overnight to release the electrolytes into solution. Electrical conductivity was measured with a standard electrical conductivity meter (c_1), and then measured a second time (c_2) following autoclaving for 30 mins at 120°C to kill all living cells.

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

$$REL = \frac{c_1}{c_2}$$

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

$$REL = a + \frac{b - a}{1 + e^{d \times (x-c)}}$$

where c is the inflection point (i.e., LT50), d is the slope at the inflection point and the two asymptotes, the maximum and minimum of REL at low and high temperatures respectively. We fit one curve per species with individual as a random effect.

The final database contained data 593 species, from 94 families.

Drought resistance database

We built a large database of embolism resistance, based on previous efforts (Hammond *et al.*, 2021), combined with unpublished data (Delzon, pers. comm.) for conifers (124 species), as well as additional measurements for 20 species. The Xylem Functional Traits (XFT) database contains published data of hydraulic vulnerability to drought, collected first in 2012 (Choat *et al.*, 2012) and updated recently. Since this database included a number of 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 the database's curve shape variable to remove vulnerability curves that were not sigmoid in shape. Then we computed the mean embolism resistance by method for each species to identify wide variations in embolism resistance across methods within species. This allowed us to filter out several 'r-shaped' curves that were not initially flagged in the database. We kept data for woody species, in stems only, and removed measurements in seedlings, resulting in data for 639 species. Finally, to improve coverage of long-vesseled species, we added stem P_{50} data for 25 species from a recent review of non-invasive measurement techniques (Cardoso *et al.*, 2022), as well as 52 species from a separate curated database (Martin StPaul, pers. comm.). Overall, the embolism resistance database contained 860 species from 107 families.
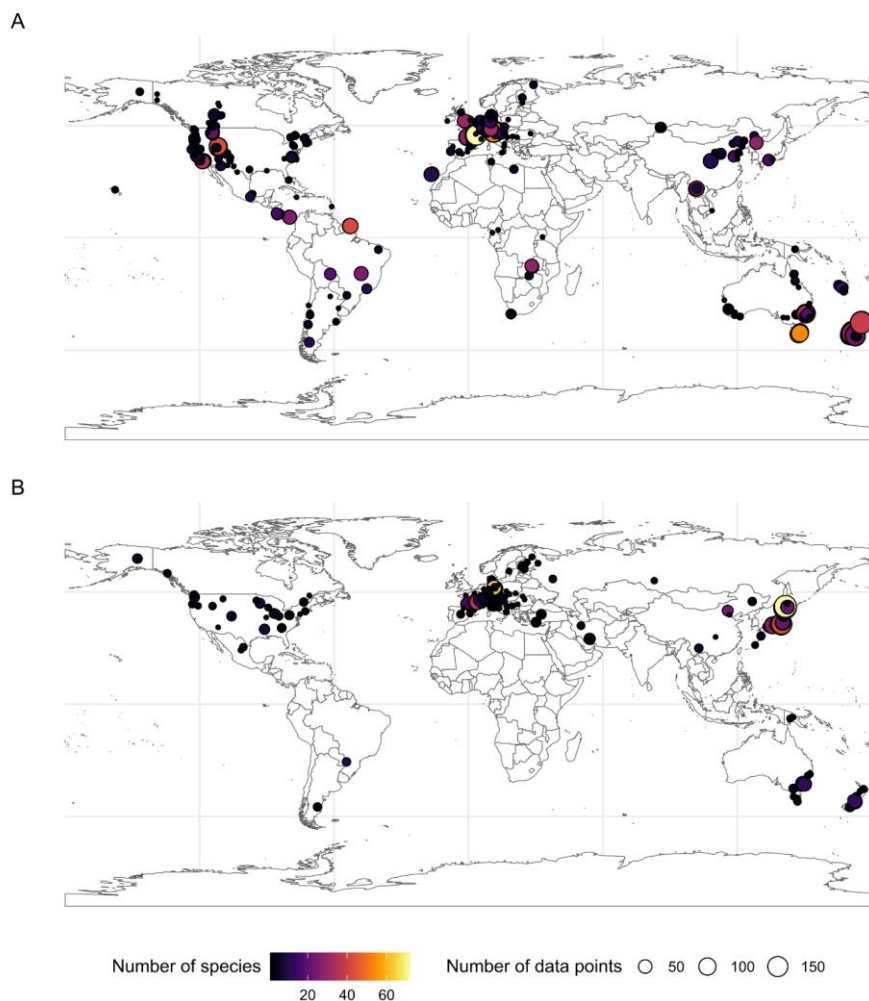
A

B

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.

Other traits:

Here, paragraph explaining how we look at the position of species on the slow-fast life-history plant life history strategy spectrum. Basically leaf mass / area, wood density, Kmax.

We have nothing for reproduction (seed mass? Mastiff?).

Climate

For all species in the physiological traits databases, we obtained climate data across the species range. We downloaded occurrences from GBIF (GBIF: The Global Biodiversity Information Facility, 2023), and ran basic filtering methods available in the rgbif package (Chamberlain *et al.*, 2023). For species with large ranges were-sampled the occurrences keeping 15000 records. We then kept a minimum distance of 10km between points (Aiello-Lammens *et al.*, 2015) to avoid oversampling in an accessible narrow area of the species range.

From these sets of point coordinates for each species, we extracted climate information from different sources. First, the Worldclim extrapolated climate layers at a resolution of 2.5 minutes (Fick & Hijmans, 2017), which we summarized by computing the mean, median and 5th and 95th percentiles. We also used the Aridity Index from the Global Aridity Index and Potential Evapotranspiration Climate Database v3 (Zomer, R.J. & Trabucco, 2022).

Finally, because a single extreme cold event can better in extreme selective pressure, to better understand the relationship between frost hardiness and climate, we obtained "absolute" minimum temperature records from the CHELSA dataset. Briefly, from the global daily minimum Near Surface Air Temperature ("tasmin"), for the period 1980 to 2005. From this large time series, we extracted the minimum for each location at 300-arcsec resolution.

Phylogeny

We used a large published seed plant phylogeny (Smith & Brown, 2018) to include evolutionary relationships in our analyses. We used R packages ape (Paradis *et al.*, 2004) and phytools (Revell, 2012) to match the trait data to the tips of the phylogeny. Our trait dataset included 236 species not in the tree, which we placed within their genera at a random place using add.species.to.genus from the phytools package. This resulted in a final phylogeny with 1304 tips. When pruned down to species in both trait databases, the resulting tree had 210 tips (see Figure xx).

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

Results

Figure 2. Functional trait trade-off of frost and drought stress resistance and their relationship with~~Functional trait distribution of~~ the climate ranges ~~drought resistance and frost hardiness~~ of tree species ~~and related climate space~~. 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 in the database used in this study. Links between climate and functional traits: B. ~~The top left and bottom right panels show the relationships of drought and frost resistance functional traits in relation to the climatic niche of each species for (A)~~ embolism resistance (P$_{50}$ in MPa) and mean annual precipitation ~~of the species ranges~~ (mm).and (~~DC~~) frost ~~hardiness~~ resistance and mean annual temperature (both in °C). D. Trade-off between embolism resistance and frost resistance. Colors and symbols indicate (~~purple~~dark green squares) deciduous and (blue-green diamonds) evergreen angiosperms and (~~green~~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).

Our trait dataset covered all terrestrial biomes in which trees occur, with mean annual precipitation varying from around 200 to over 3000 mm per year, and mean annual temperature from -5°C to over 20°C (Figure 2A). The embolism-resistance dataset covers the complete climatic spectrum, from the coldest to the warmest environments, and from the wettest to the driest (red and grey dots in <mark>Figure 2A</mark>). In contrast, the frost resistance trait data has lower coverage in warmer climates, from

subtropical deserts to tropical forests (blue and grey dots in Figure 2A). Overall, most species for which both traits are available occur in temperate biomes in the precipitation range between 500-2000 mm per year and with mean annual temperatures between +5 and +15°C (woodland/shrubland and temperate seasonal forests).

There is a weak association between embolism resistance and annual rainfall in our dataset (Figure 2B), as xylem drought-resistance is strongly linked with growing in arid zones. However, some species with low embolism resistance are still able to grow in low rainfall areas, likely due to deeper rooting systems or other drought resistance strategies. Precipitation seasonality of some biomes is not captured with mean annual precipitation, which explains the occurrence of some moderately resistant species in some wetter areas.

The drought resistance dataset covered a ~~huge~~ large range of rainfall, from under 300 to over 3000 mm per year. Accordingly, 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 XA). Gymnosperms and evergreen angiosperms tend to be more embolism resistant and have a wider range of P_{50} than deciduous angiosperms. We found a strong link between high embolism-resistance and low rainfall environments, whereas the more vulnerable species are restricted to wet environments. Species in more mesic environments display a range of embolism resistance, due to the role of the seasonality of water availability in the level of drought stress plants experience, and other traits such as rooting depth or stomatal closure dynamics can contribute to drought-tolerance strategies in these species. These findings are consistent with previous inter-specific analyses across wide taxonomic range (Maherali $et~al.$, 2004; Choat $et~al.$, 2012).

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 most resistant species. Evergeen angiosperms tend to be more frost-tender, with higher average LT_{50}, and a lower slope of the relationship with minimum temperature (Figure XD). Frost hardiness tracked the climate of species, with the most resistant species in the colder environments (Figure XD). Frost hardiness was around 20°C lower than the minimum temperature experienced over the period 1985-2005 (y = -20+0.Xx; R2 = , p = xx; supplementary figure SX).

~~Species in the dataset covered across all terrestrial biomes in which trees occur, with mean annual precipitation around 200 to over 3000 mm per year, and mean annual temperature from -5°C to over 20°C (Figure XB). The embolism-resistance dataset covers the whole climatic spectrum, from the coldest to the warmest environments, and from the wettest to the driest (green and black dots in Figure XB). In contrast, the frost hardiness data has deficits on the warm end of the "tree" climate niche, notably in the driest and wettest biomes (woodland/shrubland and tropical forests). Although frost likely doesn't occur much in these ecosystems, a trade-off between cold temperature tolerance and xylem resistance to embolism could exist.~~

There was no strong correlation between P_{50} and LT_{50} confirming our first hypothesis. However, drought-resistant species tend to be less frost hardy, and frost-resistant species tend to be vulnerable to drought (Figure XC). There are notably few species extremely resistant to both stresses, the ones stretching to the limit tend to be shrubs with slow growth like junipers. As stated previously, we lack frost-tolerance data for many drought-adapted species on the extremes of the P50 spectrum, however, notably for embolism resistant conifers, these are known to be extremely vulnerable to frost (e.g. Callitris, Cupressus).

Phylogenetic relationship.

Using a phylogeny, we assessed the evolutionary relationships between these traits. Firstly, both traits show significant phylogenetic signal (K and lambda different from 0), but lambda is significantly different from 1, and K values are low suggesting low similarities between closely related species.

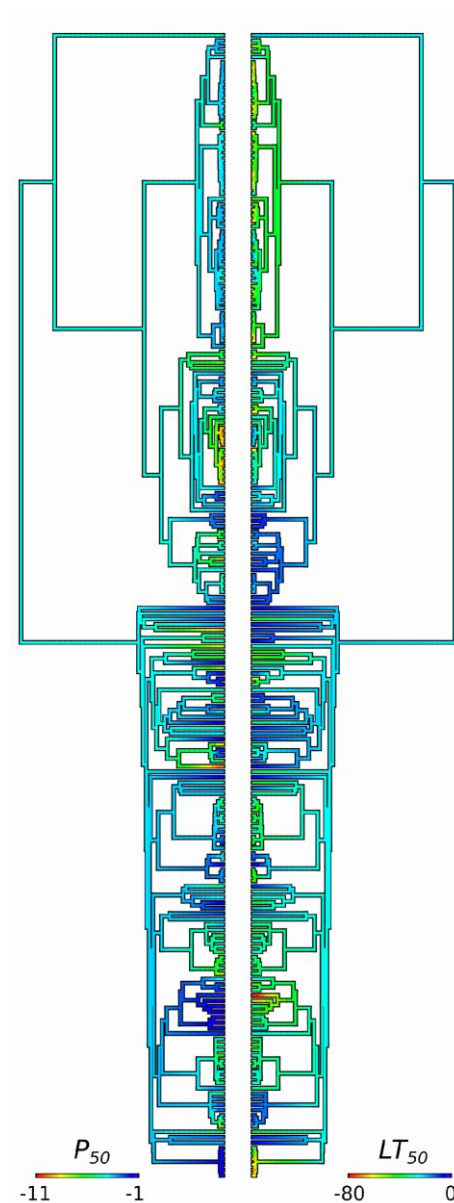*Figure 3: Mirror matching phylogenetic tree of 210 species with P_{50} (left side) and LT_{50} (right side) mapped using maximum likelihood estimation of ancestral states under a Brownian motion model of trait evolution.*

This is confirmed by looking at the mapping of trait evolution, with in general similar trait values across closely related species (Figure xx), for example pines for P50 and maples for LT50. On the

other hand, in some clades there is substantial variation in traits over relative short evolutionary timescales, i.e. Juniperus for P50 and Betula for LT50. Furthermore, independent instances of evolution of extreme resistance to embolism, e.g. Rosmarinus, Juniperus, and frost hardiness, e.g. Betula, Populus, shows the remarkable lability of these traits across large evolutionary timescales.

Using both phylogenetic least-squares (PGLS) and phylogenetic independent contrasts (PICs) we found no correlation between these traits, suggesting there is no evolutionary trade-off between embolism resistance and drough resistance (supplementary figure xx).

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> **Commented [34]:** if here you are referring to the correlation between LT50 and P50, I would start by saying taht you don't find simple relation (with phylo correction or not) but that you find evidence a constra on the limit of a maximum resistance with quantile regression
>
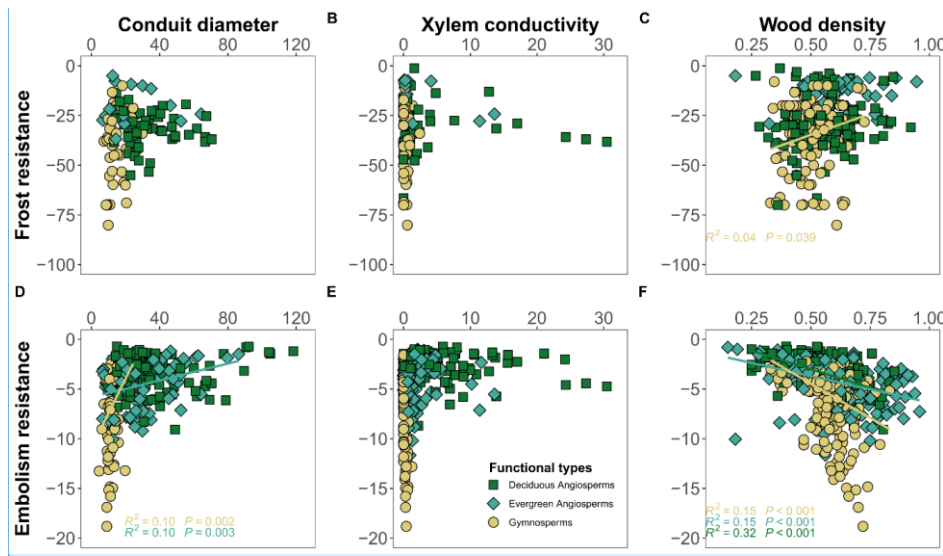> **Commented [35]:** we don't see the label A and D

Figure 4: Relationships between xylem investment 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 (kg MPa^{-1} m^{-1} 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.

Wood density show significant trends with higher wood density in drought resistant species. Like many other analyses, we find no relationship between Kmax and P50 – no safety-efficiency trade-off at this evolutionary scale. Surprisingly, we didn't find a correlation between frost hardiness and conduit diameter in angiosperms, although a significant one in gymnosperms.

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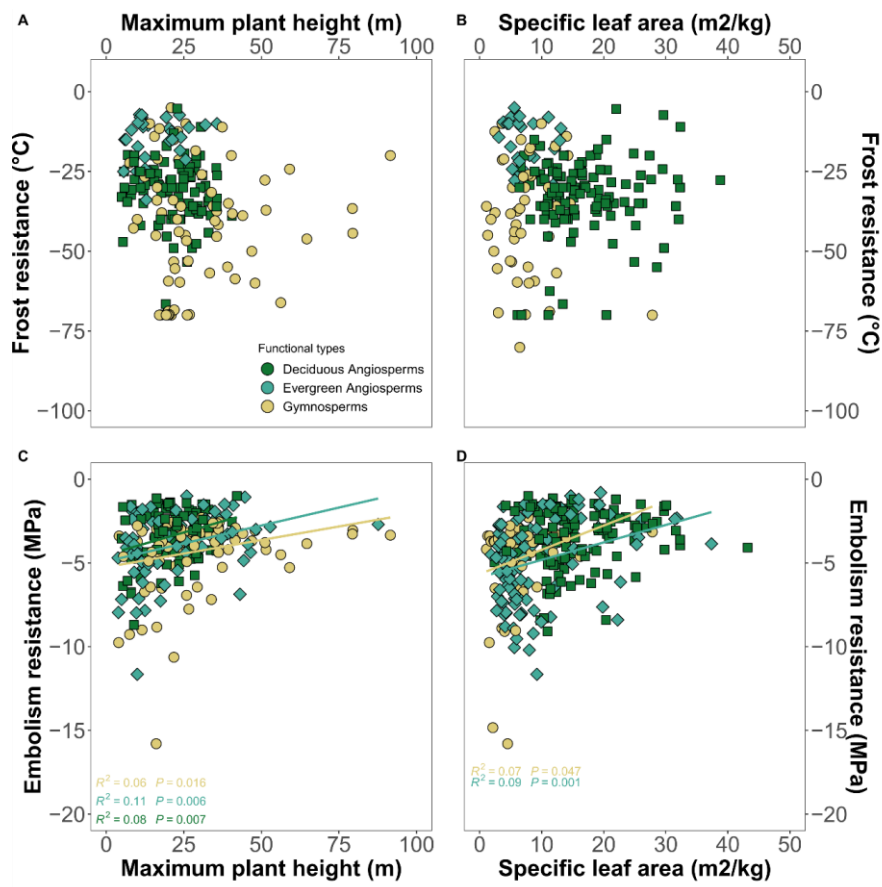
Ressource acquisition traits:

Figure 5: Plant height and specific leaf area are associated with lower drought resistance but no visible cost for frost tolerance. 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.

Discussion

1. Main conclusions:

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

2. Trait trade-offs and life-history strategies

Trait combinations of plants are driven by life-history strategies to optimize resource capture and storage, growth, reproduction and survival in a given environment (Grime, 2006). The classic CSR framework (Competitors, Stress tolerators, Ruderals) places species on varying stress and disturbance axes, classifying species based on their tolerance to low/high stress and low/high levels of disturbance (Grime, 1977, 2006). In this framework, stress-tolerating species are typically viewed as slow growing and have typically conservative traits such as small evergreen leaves and low reproductive output. On the opposite end of the stress-resistance spectrum, competitive species tend to favor high growth rate and resource acquisition traits (such as large tender leaves with a short lifespan), which is consistent with other approaches to plant trait optimization frameworks, such as the growth – mortality trade-off (Russo *et al.*, 2021) or the fast vs. slow plant economics theory (Reich, 2014). We hypothesized that our results would reflect species strategies and their ranking along the stress tolerance axis, and that species vulnerable to climatic stresses should be optimizing growth or resource acquisition traits. However, we found no significant relationships between resistance traits and growth / competition traits, as represented by the absence of significant trends between stress tolerance and specific leaf area and wood density.

High resistance to xylem embolism is associated with smaller conduits (especially in evergreens), and denser wood. However, this doesn't result in a compromise with low hydraulic efficiency, as vulnerable species have low and high density wood, which is consistent with previous results (Gleason *et al.*, 2016). Embolism resistant species do not grow very tall, however there are many short vulnerable species. In evergreen species, embolism resistance seems to be associated with tougher leaves.

Rather, we found no impact of frost resistance on conduit size, which goes against the idea that species from cold environments should evolve smaller conduits to avoid freeze-thaw embolisms. We found a slight trend to lower density wood in frost resistant conifers, but the relationship is very weak, and no trend exists in angiosperms.

Commented [38]: I think we need to say something the discussion about the new data base with both tra this a an important achievement. But there is also limitation to discus abut the data teh type of traits ...

Commented [39]: Here I think this should be discuss in regard to the threshold in conduit size not a simple linear regression

Problems using few functional traits to describe range of plant adaptation strategies (fast vs slow (Reich, 2014).

growth vs. mortality trade-off (Russo *et al.*, 2021), CSR theory (Grime, 1977, 2006), fast vs slow (Reich, 2014).

Problems with P50 to capture "drought resistance" – maybe including other traits would change the picture slightly, with drought resistant trees in cold areas showing more of a stress tolerance / slow growth syndrome. Rooting depth (Laughlin *et al.*, 2023), organ age differences (Grossman 2024, Sorek et al 2022

Oftentimes the net effect of a functional trait on fitness is unknown (Siefert & Laughlin, 2023), and trade-offs are identified by comparing traits of interest across species, population or individuals.

Areas where trees grow in dry+cold areas (with low competition) that we don't have in the database?

Discussion of how these traits can help predict range limits and effects of climate change

With climate change bringing combinations of drier summers in many regions of the NH, as well as warmer winters modifying phenological timings increasing the risk of late frosts impacting early budburst for example. How do species cope with combined stresses alternating in time?

Can trees be both drought and cold resistant? é

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Supplementary materials

Figures

Tables

Methods

LT50: