Climatic limits of temperate rainforest tree species are explained by xylem embolism resistance among angiosperms but not among conifers

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Summary

- Hydraulic failure explains much of the increased rates of drought-induced tree mortality around the world, underlining the importance of understanding how species distributions are shaped by their vulnerability to embolism. Here we determined which physiological traits explain species climatic limits among temperate rainforest trees in a region where chronic water limitation is uncommon.
- We quantified the variation in stem embolism vulnerability and leaf turgor loss point among 55 temperate rainforest tree species in New Zealand and tested which traits were most strongly related to species climatic limits.
- Leaf turgor loss point and stem P50 (tension at which hydraulic conductance is at 50% of maximum) were uncorrelated. Stem P50 and hydraulic safety margin were the most strongly related physiological traits to climatic limits among angiosperms, but not among conifers. Morphological traits such as wood density and leaf dry matter content did not explain species climatic limits.
- Stem embolism resistance and leaf turgor loss point appear to have evolved independently. Embolism resistance is the most useful predictor of the climatic limits of angiosperm trees. High embolism resistance in the curiously overbuilt New Zealand conifers suggests that their xylem properties may be more closely related to growing slowly under nutrient limitation and to resistance to microbial decomposition.

Introduction

Hydraulic failure explains much of the increased rates of drought-induced tree mortality around the world (van Mantgem *et al.*, 2009; Allen *et al.*, 2010, 2015; Adams *et al.*, 2017; Hammond *et al.*, 2019). Improving our understanding of how species distributions are shaped by their resistance to hydraulic failure will improve forecasts of species responses to environmental change (McDowell *et al.*, 2008; Anderegg *et al.*, 2012). The most drought-resistant species are found in the most arid biomes (Larter *et al.*, 2017) and these regions have been the focus of drought-related research, but temperate and tropical rainforests are not immune to drought (Atkinson & Greenwood, 1972; Innes & Kelly, 1992; Phillips *et al.*, 2009; Choat *et al.*, 2012). Variation in drought resistance among rainforest species has received limited attention, yet drought is predicted to increase with rising global temperatures in biomes that historically have experienced infrequent drought (Allen *et al.*, 2015), and all forest biomes, including wet forests, are vulnerable to hydraulic failure (Choat *et al.*, 2012).

Therefore, determining the traits that best explain drought resistance and species climatic ranges will improve our understanding of temperate rainforest responses to drought.

Trees need water so that their stomata can remain open for CO_2 uptake during photosynthesis, and trees first respond to water limitation by closing their stomata. Water tensions continue to increase within leaves under prolonged dry and hot conditions, but eventually leaves wilt and nearly all the stomata close. Turgor loss point (TLP), also referred to as leaf water potential at turgor loss, indicates the capacity of a plant to maintain cell turgor pressure in leaves during dehydration and has been proposed to be an indicator of stomatal closure (Brodribb *et al.*, 2003; Rodriguez-Dominguez *et al.*, 2016) and species drought tolerance (Bartlett *et al.*, 2012b; Jiang *et al.*, 2018). Plants with lower TLP maintain metabolic function, stomatal conductance and growth at lower soil water contents (Kramer & Boyer, 1995; Blackman *et al.*, 2010).

Tree species exhibit a remarkable range of variation in the water tensions that are tolerable within the stem xylem

(Bartlett *et al.*, 2016; Gleason *et al.*, 2016). The tension at which hydraulic conductance is at 50% of maximum (P50) is a useful indicator of drought resistance (Delzon, 2015). The time it takes for stem xylem conduits to cavitate (i.e. fill with air bubbles) will depend on the rate of soil drying, the vulnerability of the stem xylem to embolism and rates of cuticular transpiration (Blackman *et al.*, 2016). Excessive embolism formation in the xylem ultimately leads to tree death (Urli *et al.*, 2013; Adams *et al.*, 2017; Hammond *et al.*, 2019). A measure of hydraulic safety margin (HSM) can be computed by taking the difference between leaf TLP and stem P50. Species with HSM values close to zero are more vulnerable to drought because embolisms form in their xylem as soon as their leaves lose turgor (Bartlett *et al.*, 2016; Martin-StPaul *et al.*, 2017).

These three physiological traits (leaf TLP, stem P50 and HSM) are linked directly to mechanisms of mortality and could be the best predictors of tree responses to drought and climatic distributions (Larter *et al.*, 2017). One drawback to their widespread application is that they can be difficult to measure. Easy-to-measure morphological traits, such as leaf mass per area (LMA) and wood density, have been shown to vary along climatic gradients (Baltzer *et al.*, 2009; Simpson *et al.*, 2016) and predict drought-induced mortality (Phillips *et al.*, 2009; Greenwood *et al.*, 2017). If morphological traits are correlated with physiological traits then they could be used as surrogate proxies to predict climatic niches of rainforest species.

There is increasing interest in using traits to predict how species will respond to a changing climate. The objective of this paper is to determine which traits are most strongly related to climatic tolerance limits of temperate rainforest tree species in New Zealand. We measured physiological and morphological traits on 55 phylogenetically and functionally diverse tree species and used a national forest inventory to compute climatic limits for each species based on their geographic distributions. We asked the following questions: (1) What is the range of variation in hydraulic traits among these temperate rainforest tree species? (2) What is the relationship between leaf TLP and stem embolism resistance (stem P50) among these species? (3) Are physiological or morphological traits more strongly related to the climatic limits of each species? The answers to these questions have important implications for understanding how temperate rainforest ecosystems will respond to increasing frequencies of hotter droughts under climate change and will inform strategies for managing forest recovery following tree mortality.

Materials and Methods

Study system and phylogeny

This study was carried out in the almost entirely evergreen temperate rainforests of New Zealand, which range from warm temperate to cool temperate forests, recently classified as 'oceanic temperate forests' (McGlone *et al.*, 2016). Elevational and latitudinal gradients and especially west-to-east gradients determined by prevailing westerly winds drive variation in moisture availability across the country. Drought-related tree mortality does occur in New Zealand (Atkinson & Greenwood, 1972; Grant, 1984; Bannister, 1986; Innes & Kelly, 1992), and species differ in their tolerance of dry conditions (Hinds & Reid, 1957; Leathwick & Whitehead, 2001).

We selected 55 phylogenetically and functionally diverse tree species (Fig. 1; Supporting Information Table S1) that spanned a range of climatic zones across both of the main islands. This is the largest compilation of mechanistic physiological trait measurements on native New Zealand tree species; to date, very few studies have quantified drought-related functional traits in the New Zealand flora (Esperón-Rodríguez *et al.*, 2018). We assembled a phylogenetic tree for these species by grafting our species onto a genus-level phylogeny for New Zealand vascular plant species, constructed using chloroplast DNA (cpDNA) *rbcL* (Millar *et al.*, 2017). Grafting was implemented with the *add.species.to.genus* function in the R library PHYTOOLS (Revell, 2012).

Climatic limits

We quantified the climatic limits of each species by summarizing climate variables across a sample of 500 occurrence records taken from vegetation plot data and other observations in the Global Biodiversity Information Facility (GBIF, 2020). Most of our species distribution data relied on an objective grid-based sample of New Zealand's forests and shrublands (Simpson *et al.*, 2016; Holdaway *et al.*, 2017). This sampling network consists of > 1200 permanent 0.04 ha plots evenly spaced across mapped indigenous forests and shrublands on the intersections of an 8 km grid. This unbiased, spatially balanced sample provides the most robust data for quantifying the climate niche of each species. We randomly sampled 500 occurrences of each species from this plot network. If a species occurred on fewer than 500 of these plots, we randomly sampled the required number of occurrences without replacement from GBIF to reach our sample size of 500 for each species.

We used these occurrence records to quantify the climatic limits of each species that relate most directly to drought. Using existing spatial layers of interpolated climate data (Leathwick *et al.*, 2002; Leathwick *et al.*, 2003) we extracted the mean annual precipitation (MAP, mm), the annual vapor pressure deficit (VPD, kPa), the mean maximum temperature of the warmest month (T_{max}, °C), and the precipitation-to-potential evapotranspiration ratio (P : PET, an index of aridity). Note that these climate measures address only average dryness of a region, and the frequency and intensity of drought is only partly correlated with these measures. Our 500 occurrences sample the full range of each climate variable where each species occurs, but to estimate the climatic limits of each species, we calculated the 5th percentiles of MAP (MAP_5) and P : PET ($P : PET_5$), and the 95th percentiles of T_{max} (T_{max95}) and VPD (VPD_{95}). These climatic range limits were correlated; for example, MAP_5 and VPD_{95} exhibited a strong negative correlation ($r = -0.81$). We sought to
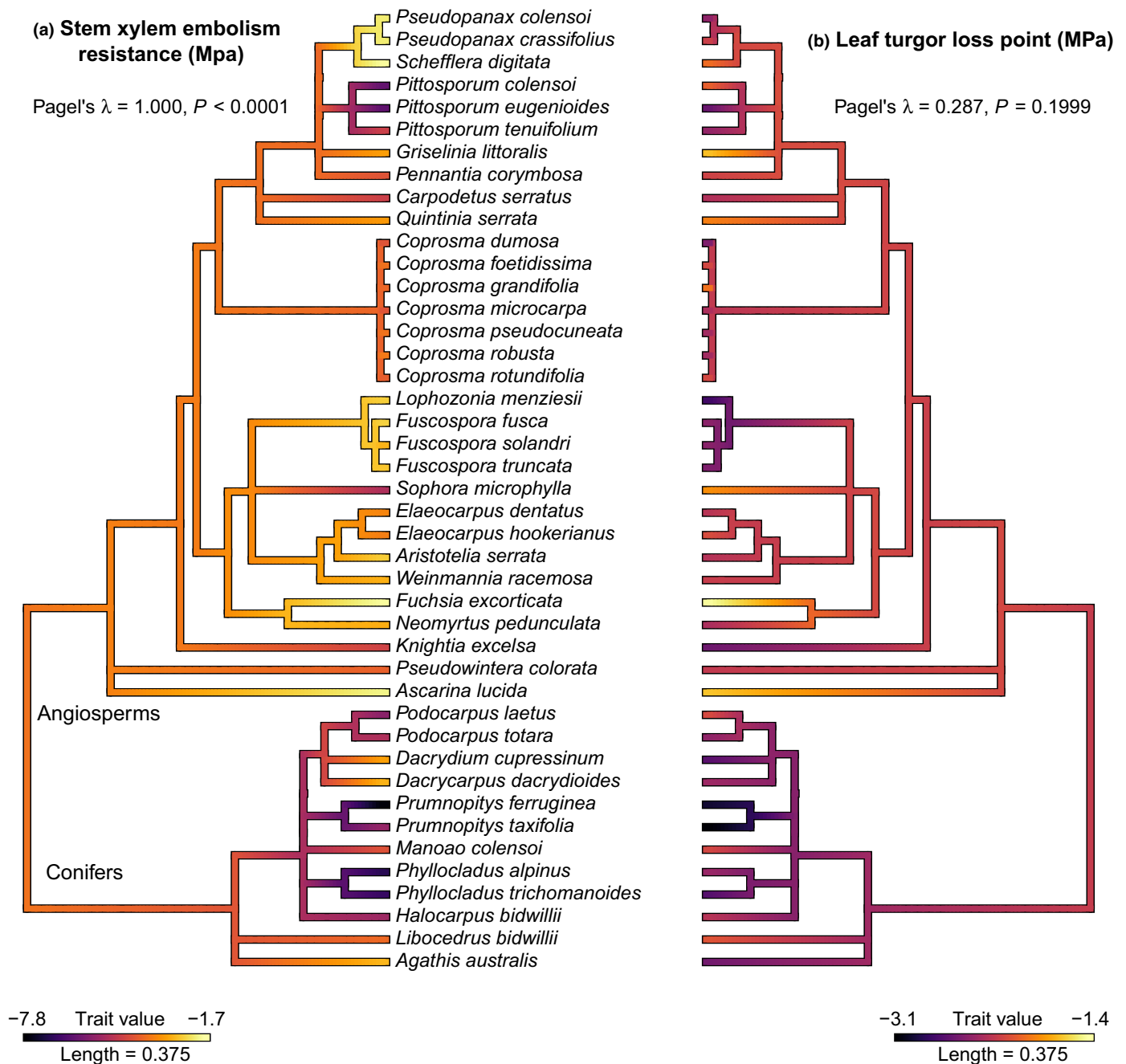
Fig. 1 Phylogenetic relationships among temperate rainforest tree species plotted with trait values of (a) stem embolism resistance (P50, MPa) and (b) leaf turgor loss point (TLP, MPa). Stem P50 exhibited strong phylogenetic signal ($\lambda = 1.000$, $P < 0.0001$) whereas leaf TLP did not ($\lambda = 0.287$, $P = 0.1999$). There were 10 species on which only one of the two traits was measured and therefore could not be included on this phylogeny.

determine whether traits could predict these climatic range limits among species.

Morphological traits

We used mean values of leaf dry matter content ($mg\,g^{-1}$) and wood density (i.e. stem-specific density; $mg\,mm^{-3}$) from existing databases collected between 2002 and 2015 from forests and shrublands throughout New Zealand (Richardson *et al.*, 2004; Mason *et al.*, 2012; Jager *et al.*, 2015; Simpson *et al.*, 2016)

following standard protocols (Pérez-Harguindeguy *et al.*, 2013). We focused on these two traits because wood density and specific leaf area (a trait that is inversely correlated with leaf dry matter content (LDMC)) have been shown to be predictors of drought-induced mortality (Greenwood *et al.*, 2017).

Leaf osmotic potential and turgor loss point

We used a vapor pressure osmometer (Vapro 5600; Wescor Inc., Logan, UT, USA) to measure leaf osmotic potential at full

hydration, then estimated ψ_{tlp} from osmotic potential using the published relationship between the two variables (Bartlett *et al.*, 2012a, 2012b; Maréchaux *et al.*, 2016). Two shoots were cut from separate, healthy, sun-exposed branches of three to six trees per species, immediately wrapped in plastic with damp tissue paper and transported to the laboratory under dark and cool conditions for further processing within 1–3 d. In the laboratory each shoot was recut under water and allowed to rehydrate overnight while standing in water in the dark and covered with a plastic bag. The following day a clean healthy leaf was selected from each shoot and a 4 mm disk was cut from the lamina, avoiding major veins where possible. When sampling small-leaved species (< 4 mm wide) the major veins could not be avoided, and segments of leaves with an area equivalent to a 4 mm disk were cut instead. For conifers with imbricate leaves, 4 mm lengths of the distal ends of shoots were used. Leaf samples were immediately wrapped in aluminum foil and frozen in liquid nitrogen. After removal from the liquid nitrogen, the samples were then punctured repeatedly while thawing with fine forceps before being sealed in the osmometer chamber. Osmolality (mmol kg^{-1}) was recorded after a 10 min equilibration time, then converted to osmotic potential (MPa) by multiplying osmolality by -0.002437 m^3 MPa mol^{-1} following the Van't Hoff relation (Nobel, 2009). Leaf TLP was estimated from leaf osmotic potential using equation 5 from Bartlett *et al.* (2012a). These estimations have since been validated in other systems (Griffin-Nolan *et al.*, 2019; Májeková *et al.*, 2019).

Xylem vulnerability to embolism

Vulnerability to drought-induced embolism was determined at the Caviplace (University of Bordeaux, Talence, France (http://sylvain-delzon.com/caviplace) with the Cavitron technique (Cochard *et al.*, 2005). We collected branches from five to 10 healthy mature trees per species in 2017 and 2018 from multiple sampling sites on both main islands of New Zealand to quantify the range of both interspecific and intraspecific variation in stem P50. Samples had a standard length of 45 cm. Transpiration losses were prevented by removing the leaves or needles immediately after sampling and wrapping the branches in moist paper to keep them humid and cool during air transport to France. The measurement of embolism resistance occurred within 3 wk of sampling, and storage times of 10 wk have been shown to have no effect on this measurement in *Fagus sylvatica* (Herbette *et al.*, 2010). The bark was removed from conifer branches to prevent resin filling the cavitron reservoirs (Delzon *et al.*, 2010), and all branches were recut with a razor blade, under water, to a standard length of 27 cm.

Samples were infiltrated with a reference ionic solution of 10 mM KCl and 1 mM CaCl$_2$ in deionized ultrapure water. Centrifugal force was used to generate negative pressure into the xylem and induce embolism. This method allows measurement of xylem conductance under negative pressure using the custom software CAVISOFT 4.0 (Univ. Bordeaux, Pessac, France). Initially, the maximum stem conductance (K_{max}, in m^2 MPa^{-1} s^{-1}) was calculated under low xylem pressures. The percentage loss of

conductance (PLC) of the stems was calculated at different xylem pressures (P_i) from -0.8 to -12 MPa with the following equation:

$$PLC = 100 \left(1 - \frac{K}{K_{max}} \right) \qquad \text{Eqn 1}$$

We obtained one vulnerability curve per tree showing the percentage loss of xylem conductance as a function of xylem pressure (Delzon *et al.*, 2010). For each branch, the relationship between PLC and xylem water pressure was fitted with the following sigmoidal equation (Pammenter & Van der Willigen, 1998):

$$PLC = \frac{100}{\left(1 + \exp\left(\frac{S}{25} (P_i - P50) \right) \right)} \qquad \text{Eqn 2}$$

where P50 (MPa) is the xylem pressure inducing a 50% loss of conductivity and S (% MPa^{-1}) is the slope of the vulnerability curve at the inflection point. All sigmoidal functions were significant and fitted with the NLIN procedure in SAS (v.9.4; SAS Institute, Cary, NC, USA). The xylem-specific hydraulic conductivity (K_s, kg m^{-1} MPa^{-1} s^{-1}) was calculated by dividing the hydraulic conductivity measured at low speed by the sapwood area of the sample. Xylem vulnerability curves for each species are illustrated in the Figs S1 and S2. HSM was calculated as the difference between species-level average leaf TLP and stem P50 (Martin-StPaul *et al.*, 2017). Vulnerability curves for each species are given in Figs S1 and S2.

For angiosperm species, some samples per species were used to test the presence of open vessels (Torres-Ruiz *et al.*, 2017) by injecting air into stems at 2 bar at one end. Samples from three species (*Metrosideros umbellata*, *Melicytus ramiflorus* and *Myrsine australis*) had open vessels in 27 cm long samples, provided r-shaped curves and were therefore discarded. We discarded one or two samples from four other species (*Coprosma linariifolia*, *Coprosma pseudocuneata*, *Brachyglottis repanda* and *Griselinia littoralis*) but obtained robust measurements on the remaining samples of these species.

Statistical analyses

To answer our first question, we determined the range of variation in hydraulic traits by comparing the minimum and maximum trait values among the angiosperms and conifers. To determine how much of this variation could be attributed to interspecific vs intraspecific variation we used variance partitioning. We fitted random effects models using the *lme* function in the R package NLME (Pinheiro *et al.*, 2011) where the trait was a function of a global intercept and random intercepts for each species. For the leaf hydraulic trait, two leaf disks were measured per individual, so we included an intercept for individual nested within species. HSM was computed at the species level so we could not estimate intraspecific variation in this trait. We used the varcomp function in the APE R package (Paradis *et al.*, 2004) to decompose the variation between vs within species.

Before addressing our second and third questions, we determined the strength of phylogenetic signals in the traits using Pagel's λ (Freckleton *et al.*, 2002) with the *phylosig* function in the PHYTOOLS R package (Revell, 2012). Given the strength of the phylogenetic signals (see Results), we applied phylogenetic generalized least squares (PGLS) using the *pgls* function in the CAPER R package (Orme *et al.*, 2018) to answer our second and third questions. We used PGLS in all analysis that tested for the strength of covariation among traits (second question) and the strength of association between traits and climatic limits (third question). The PGLS models included traits, phylogenetic group and their interaction as independent predictor variables and species climatic range limits as the response variable. The species climatic range limits represent species distributional responses to climate, and therefore these analyses determine whether traits predict species responses to water limitation.

Data availability

Data and R script are available online in the Landcare Research Datastore (https://doi.org/10.7931/egbd-a914).

Results

Trait variation

Stem embolism resistance (stem P50) exhibited a negatively skewed distribution and ranged from −7.7 to −2.7 MPa among 14 conifers and from −7.6 to −1.7 MPa among 41 angiosperms, with an overall mean of −3.8 MPa (Figs 2a, 3a). Leaf TLP was normally distributed and ranged from −3.1 to −2.1 MPa in conifers and from −2.7 to −1.4 MPa in angiosperms, with an overall mean of −2.3 MPa (Figs 2b, 3b). HSM (= TLP − P50) was positively skewed and ranged from 0.1 to 4.8 MPa in conifers
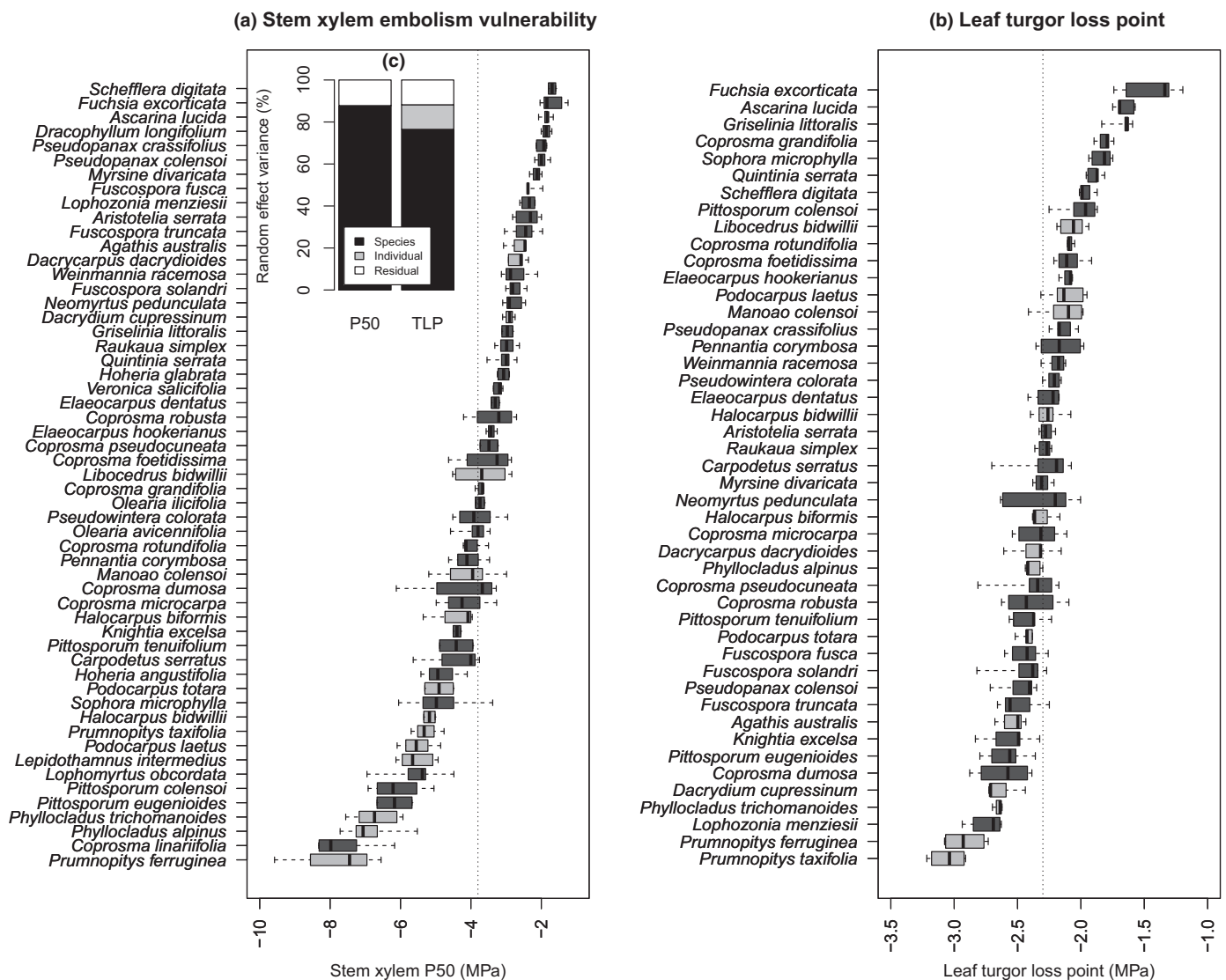
Fig. 2 (a) Stem embolism vulnerability (P50, MPa) and (b) leaf turgor loss point (TLP, MPa) for each species ranked by decreasing mean values. Boxplots illustrate the full range of variation measured within each species. Light grey, conifers; dark grey, angiosperms. (c) Inset illustrating the amount of variation that can be attributed to interspecific differences: > 75% of the variation is between species. The vertical dotted lines denote the grand means.
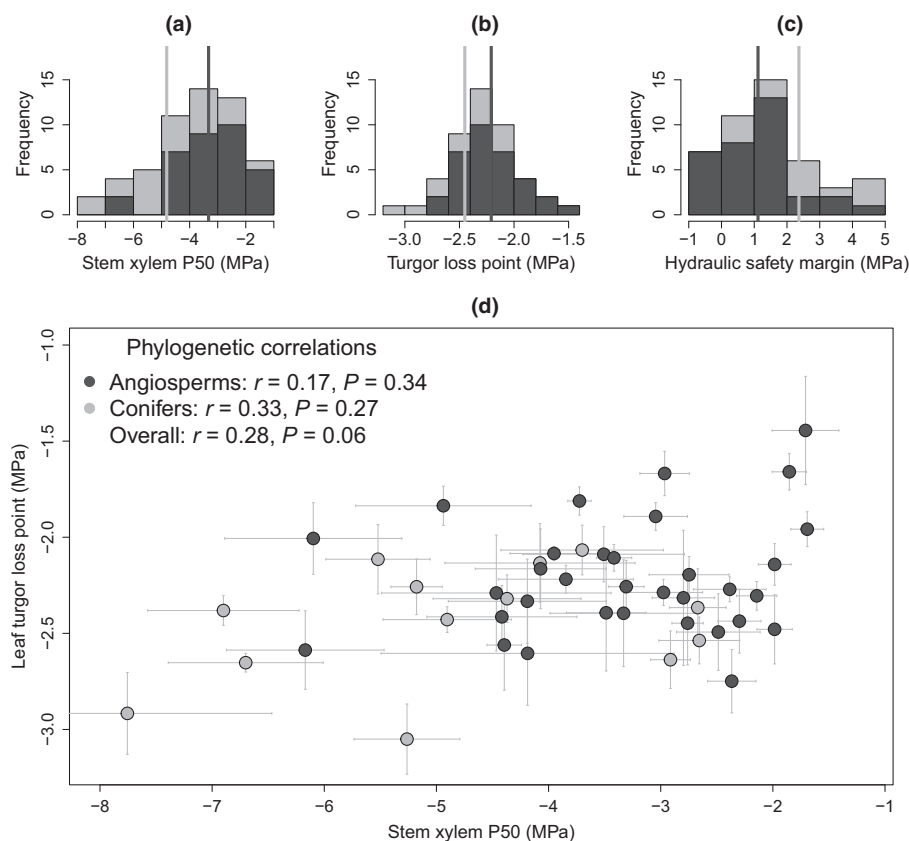
Fig. 3 (a–c) Distributions of physiological traits, and (d) bivariate scatterplot of stem embolism resistance (P50) and leaf turgor loss point (TLP). Vertical lines in (a–c) represent mean values of angiosperms (dark grey) and conifers (light grey). Error bars in (d) represent SD.

and from -0.5 to 4.1 MPa in angiosperms, with an overall mean of 1.5 MPa (Fig. 3c). Conifers exhibited significantly more resistant xylem ($t = -3.2$, df $= 52$, $P = 0.0025$; Fig. 3a) and lower leaf TLP ($t = -2.5$, df $= 44$, $P = 0.0177$; Fig. 3b) than angiosperms. HSM did not differ among conifers and angiosperms ($t = 0.6$, df $= 44$, $P = 0.53$; Fig. 3c).

Most of the variation observed in both P50 and TLP can be attributed to interspecific differences rather than intraspecific differences: 88% of the variation in stem P50 was between species, and 77% of the variation in leaf TLP was between species (inset Fig. 2c). Stem P50 ($\lambda = 1.00$, $P < 0.0001$) and HSM ($\lambda = 0.99$, $P < 0.0001$) exhibited strong phylogenetic signals, whereas leaf TLP did not ($\lambda = 0.28$, $P = 0.1998$) (Fig. 1). All the following regression models include phylogenetic structure to account for evolutionary relatedness among taxa.

Trait covariation

P50 was not significantly correlated with leaf TLP (Fig. 3d), especially when the relationship was assessed within conifers ($P = 0.27$) and within angiosperms ($P = 0.34$) (Fig. 3d). There was a weak relationship when all species were analyzed together ($P = 0.06$), but this may still be influenced by the ancient divergence between conifers and angiosperms even after incorporating the phylogenetic correlation structure.
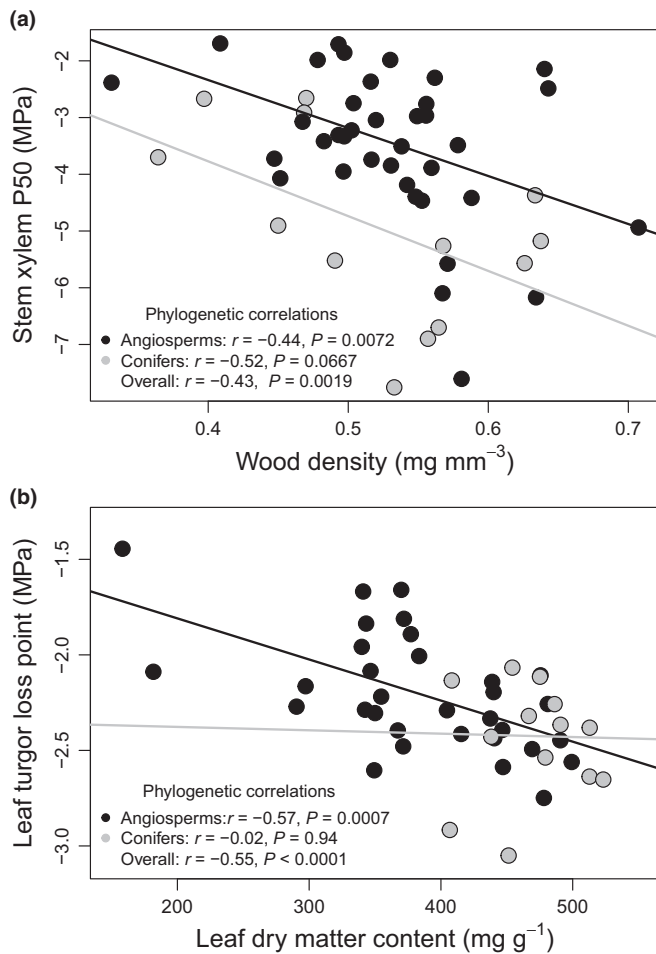
Wood density was negatively correlated with stem P50 among angiosperms, but this relationship was weaker among conifers

(Fig. 4a). LDMC was negatively correlated with leaf TLP among angiosperms, but not among conifers (Fig. 4b).

Traits and climatic limits

Hydraulic traits were superior predictors of species climatic limits compared to morphological traits, but there were considerable differences between conifers and angiosperms (Table 1; Figs 5, 6, S3, S4). Stem P50 and HSM values were the best predictors of climatic limits among angiosperm tree species. These relationships were not driven by the species with the highest rainfall quantile (i.e. the angiosperm *Ascarina lucida*) because the relationships remained significant after removing this species. Leaf TLP was the best predictor of climatic limits in conifers, but this relationship was driven by one species with the lowest leaf TLP (i.e. the conifer *Prumnopitys taxifolia*) (Table 1; Fig. 5). Wood density was correlated with the lower limit of MAP among angiosperms, but this wood density effect was not important if P50 was already in the model ($P = 0.16$). LDMC was not correlated with any climatic distributional limits.

Mean annual precipitation Stem P50 was positively correlated with MAP_5 (the 5th quantile of species MAP distributional ranges) (Table 1), where species with the most negative P50 values were associated with the lowest precipitation. This pattern was strongest within angiosperms (Fig. 5a) and was not detected in conifers (Fig. 5b; Table 1). Leaf TLP was unrelated to MAP (Fig. 5c,d; Table 1). HSM was negatively correlated with MAP_5,

Fig. 4 Relationships between (a) stem embolism resistance and wood density and (b) leaf turgor loss point and leaf dry matter content among angiosperms (dark grey) and conifers (light grey).

where species with the most highest safety margins were associated with the lowest precipitation (Table 1). This pattern was strongest within angiosperms (Fig. 5e) but was not detected in conifers (Fig. 5f). Wood density was negatively correlated with MAP_5 among angiosperms but not among conifers (Fig. 5g), and LDMC was uncorrelated with MAP_5 in either taxonomic group (Table 1; Fig. 5i,j).

Vapor pressure deficit Stem P50 was negatively correlated with VPD_{95} (the 95th quantile of species VPD distributional ranges) (Table 1), where species with the most negative P50 values were associated with the highest VPD_{95}. This pattern was strongest within angiosperms (Fig. 6a) and was not detected in conifers (Fig. 6b; Table 1). By contrast, leaf TLP was negatively correlated with VPD_{95} among conifer species (Fig. 6d), where conifer species with the most negative TLP were associated with the highest VPD_{95}. However, this relationship was no longer significant if *Prumnopitys taxifolia*, the species with very high VPD_{95} and very low TLP, was removed from the analysis. This pattern was not detected in angiosperms (Fig. 6c) or when all species were pooled together (Table 1). HSM was positively correlated with VPD_{95}, where species with the most negative HSM values

were associated with the highest VPD_{95} (Table 1). This pattern was strongest within angiosperms (Fig. 6e) but was not detected in conifers (Fig. 6f). Wood density and LDMC were uncorrelated with VPD_{95} (Table 1; Fig. 6g–j).

Maximum temperature Stem P50 was uncorrelated with T_{max95} (the 95th quantile of species maximum temperature distributional ranges) (Table 1; Fig. S3A,B). Leaf TLP in conifers was negatively correlated with T_{max95} (Fig. S3D), where species with the most negative TLP were associated with the highest temperatures. This relationship was still significant if *Prumnopitys taxifolia* was removed from the analysis. This pattern was not detected in angiosperms (Fig. S3C). HSM was weakly positively correlated with T_{max95} (Fig. S3E), where species with the most negative HSM values were associated with the highest temperatures; this pattern was not detected in conifers (Fig. S3F). Wood density and LDMC were uncorrelated with T_{max95} (Table 1; Fig. S3G–J).

Precipitation-to-potential evapotranspiration ratio Stem P50 was positively correlated with $P : PET_5$ (the 5th quantile of species precipitation-to-potential evapotranspiration (P : PET) ratio distributional ranges) (Table 1), where species with the most negative P50 values were associated with low $P : PET_5$. This pattern was strongest within angiosperms (Fig. S4A) and was not detected in conifers (Fig. S4B; Table 1). Leaf TLP was uncorrelated with $P : PET_5$ (Table 1). HSM was negatively correlated with $P : PET_5$, where species with the most positive HSM values were associated with the lowest $P : PET_5$ (Table 1). This pattern was strongest within angiosperms (Fig. S4E) but was not detected in conifers (Fig. S4F). Wood density and LDMC were uncorrelated with $P : PET_5$ (Table 1; Fig. S4G–J).

Discussion

Determining the traits that best explain drought resistance and species climatic ranges can inform more generalized predictions of forest ecosystem responses to drier conditions. Our results demonstrate five key points. (1) Stem embolism resistance is not strongly coupled with leaf turgor loss point, suggesting that these traits may have evolved independently and are under different selection pressures. (2) Stem embolism resistance exhibits strong interspecific variation and is the best predictor of angiosperm species climatic tolerance limits within this temperate rainforest flora. (3) Mechanistic physiological traits directly related to water use are superior predictors of species climatic tolerance than commonly measured morphological traits such as wood density and LDMC. (4) Drought resistance has clearly evolved within the New Zealand tree flora and several species are poised to increase in relative abundance under increasing frequency and duration of drought. (5) Stem P50 in the New Zealand conifers does not correspond well with climatic limits or observations of where these species occur along moisture gradients in the field, suggesting that the xylem properties in these conifers may be exaptive and related to growing slowly under nutrient limitation and the need for resistance to microbial decomposition.

Table 1 Phylogenetic analysis of covariance in which each climatic factor is modeled as a function of a single trait, a binary group factor distinguishing angiosperms and conifers, and an interaction term between the trait and phylogenetic group.

Climate limit	Trait	Intercept	Trait	Phylo group	Trait × Phylo group	R^2
Precipitation, 5th quantile	P50	1674.15***	123.222***	−330.56	−127.07*	0.237
	TLP	1905.897***	267.191	171.461	32.847	0.086
	HMS	1375.844***	−108.042*	−49.671	117.291 (.)	0.156
	WD	2040.804***	−1514.556*	−843.551	1747.686 (.)	0.139
	LDMC	1465.191***	−0.272	910.327	−1.898	0.024
VPD, 95th quantile	P50	0.492***	−0.041***	0.119	0.045*	0.256
	TLP	0.564***	−0.030	−0.471 (.)	−0.175	0.140
	HMS	0.588***	0.039**	0.033	−0.050*	0.184
	WD	0.439***	0.369	0.203	−0.450	0.077
	LDMC	0.654***	0.000	−0.264	0.000	0.040
Maximum temperature, 95th quantile	P50	21.656***	−0.195	1.496	0.286	0.066
	TLP	23.476***	0.438	−6.101*	−2.641*	0.139
	HSM	22.196***	0.28 (.)	0.959	−0.441 (.)	0.100
	WD	21.92***	0.807	3.517	−5.953	0.067
	LDMC	22.571***	−0.001	−1.974	0.005	0.033
P : PET, 5th quantile	P50	40.422***	3.011**	−12.499	−3.703*	0.181
	TLP	32.652	−0.573	35.94	16.64	0.035
	HSM	32.67***	−2.831**	−4.399	3.797*	0.167
	WD	45.94***	−30.121	−32.742 (.)	63.568 (.)	0.087
	LDMC	33.812***	−0.009	25.61	−0.051	0.028

P50, stem embolism resistance; TLP, leaf turgor loss point; HSM, hydraulic safety margin; WD, wood density; LDMC, leaf dry matter content; VPD, vapor pressure deficit; P : PET, precipitation-to-potential evapotranspiration ratio.
These results support the illustration of correlations in Figs 5 and 6.
***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; (.), $P < 0.1$.

Our results suggest that stem P50 and leaf TLP appear to have evolved independently based on two lines of evidence: the traits exhibit contrasting phylogenetic signal, and their phylogenetic correlation (PGLS) is weak. Stem P50 exhibited strong phylogenetic signal, indicating a high degree of similarity among closely related species. However, leaf TLP exhibited no phylogenetic signal, suggesting that these traits evolved independently. The lack of strong covariation observed between stem P50 and leaf TLP is perhaps not surprising given the limited global range of variation in leaf TLP (Martin-StPaul et al., 2017). Multiple combinations of these traits may reflect a diversity of drought strategies. If leaf TLP is an indicator of drought resistance (Bartlett et al., 2012b), then one would expect that selection on drought tolerance traits would favor species with low TLP and low stem P50. However, if leaf TLP is a metric of stomatal closure, then the most drought-tolerant species could be those that close stomates early in a drought (i.e. high TLP) and also exhibit resistant xylem (i.e. low stem P50). This combination of high leaf TLP and low stem P50 would theoretically yield the highest HSM (Martin-StPaul et al., 2017). For example, three species exhibit low stem P50 but high leaf TLP in our study (the conifer *Podocarpus laetus* and the angiosperms *Pittosporum colensoi* and *Sophora microphylla*; Fig. 2), and therefore exhibit high HSM values. By contrast, six other species exhibit low TLP but high stem P50 (the conifer *Agathis australis* and the angiosperms *Fuscospora fusca*, *Lophozonia menziesii*, *Fuscospora truncata*, *Fuscospora solandri* (all Nothofagaceae) and *Pseudopanax colensoi*; Fig. 2), and therefore exhibit HSM values close to zero. These latter species are intolerant to drought because embolisms form in their xylem as soon as their leaves lose turgor (Bartlett et al., 2016; Martin-StPaul et al.,

2017). However, it is difficult to generalize because species responses will depend on the type of drought, defined by the intensity and duration of water limitation (Mitchell et al., 2013).

Selection on leaf TLP and stem P50 is not strongly constrained along a single axis of covariation and this lack of integration indicates that natural selection does not act on both traits simultaneously. Different environmental factors may be responsible for driving variation in each trait. For example, herbivore selection pressure could induce physical defenses in leaves (e.g. a thicker cuticle) that improves moisture retention in the leaf during drought, even if the species grows in a mesic habitat. However, our conclusion that these traits are independent is based on interspecific differences in average trait values. Intraspecific variation in both of these traits was relatively low in our study, but other studies have demonstrated notable intraspecific variation in stem P50 (Love et al., 2019) and osmotic adjustments to leaf TLP (Meinzer et al., 2014; Maréchaux et al., 2017; Nolan et al., 2017; Johnson et al., 2018). Future tests of this relationship should account for both interspecific differences and intraspecific variation to gain a multiscale perspective on the strength of integration between stem P50 and leaf TLP.

Stem P50 and HSM were the best predictors of climatic limits across the angiosperms. All else being equal, given two traits that are measured on the same scale (stem P50 and leaf TLP), the likelihood of detecting relationships with climatic range limits would be higher for the variable with greatest variation. Stem P50 exhibited nearly four-fold greater variation than leaf TLP, and was also the superior predictor of climatic limits among angiosperms. Given that the climate measures only reflect the average dryness of a region, P50 may perform even better as a predictor of species
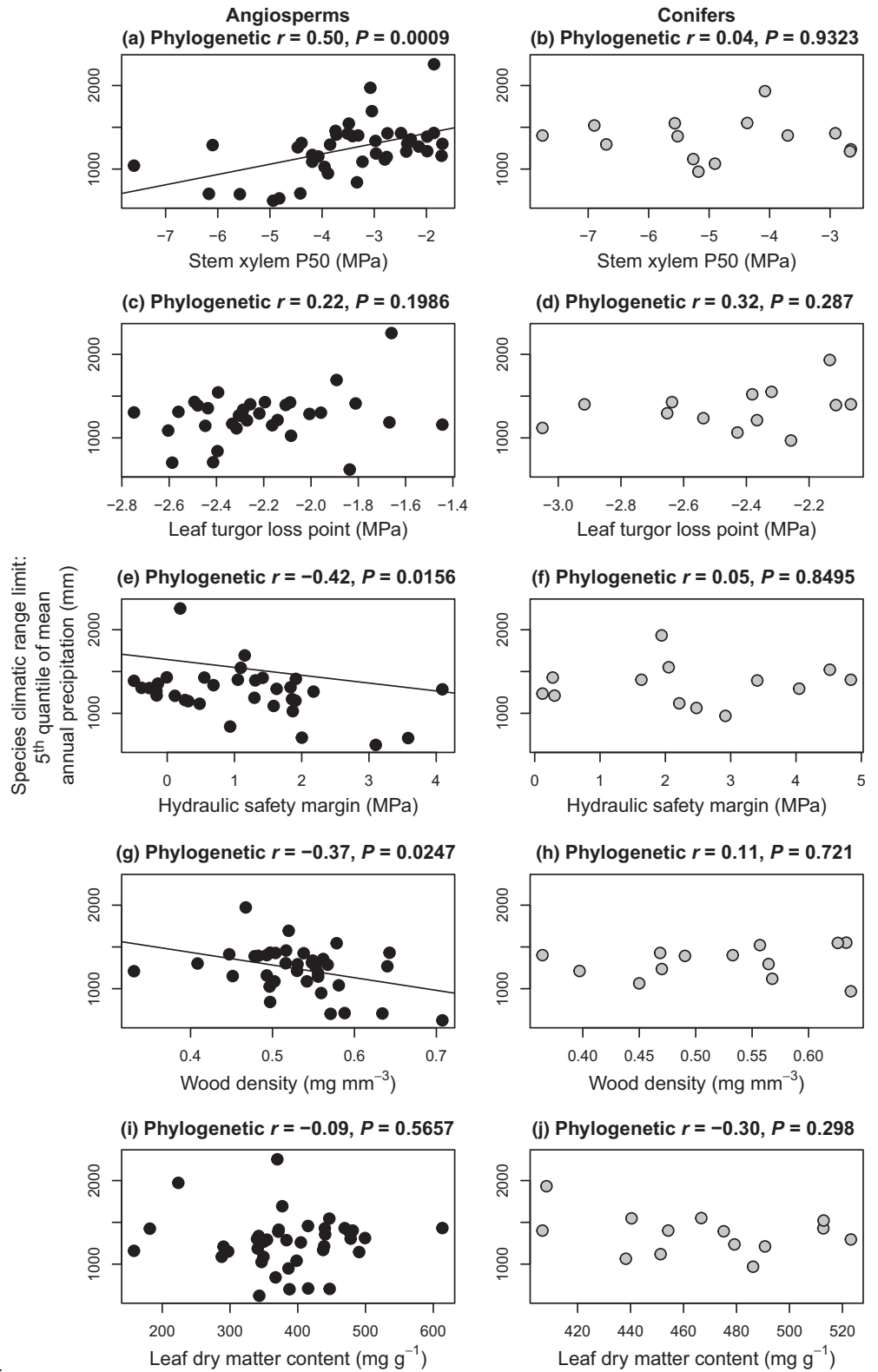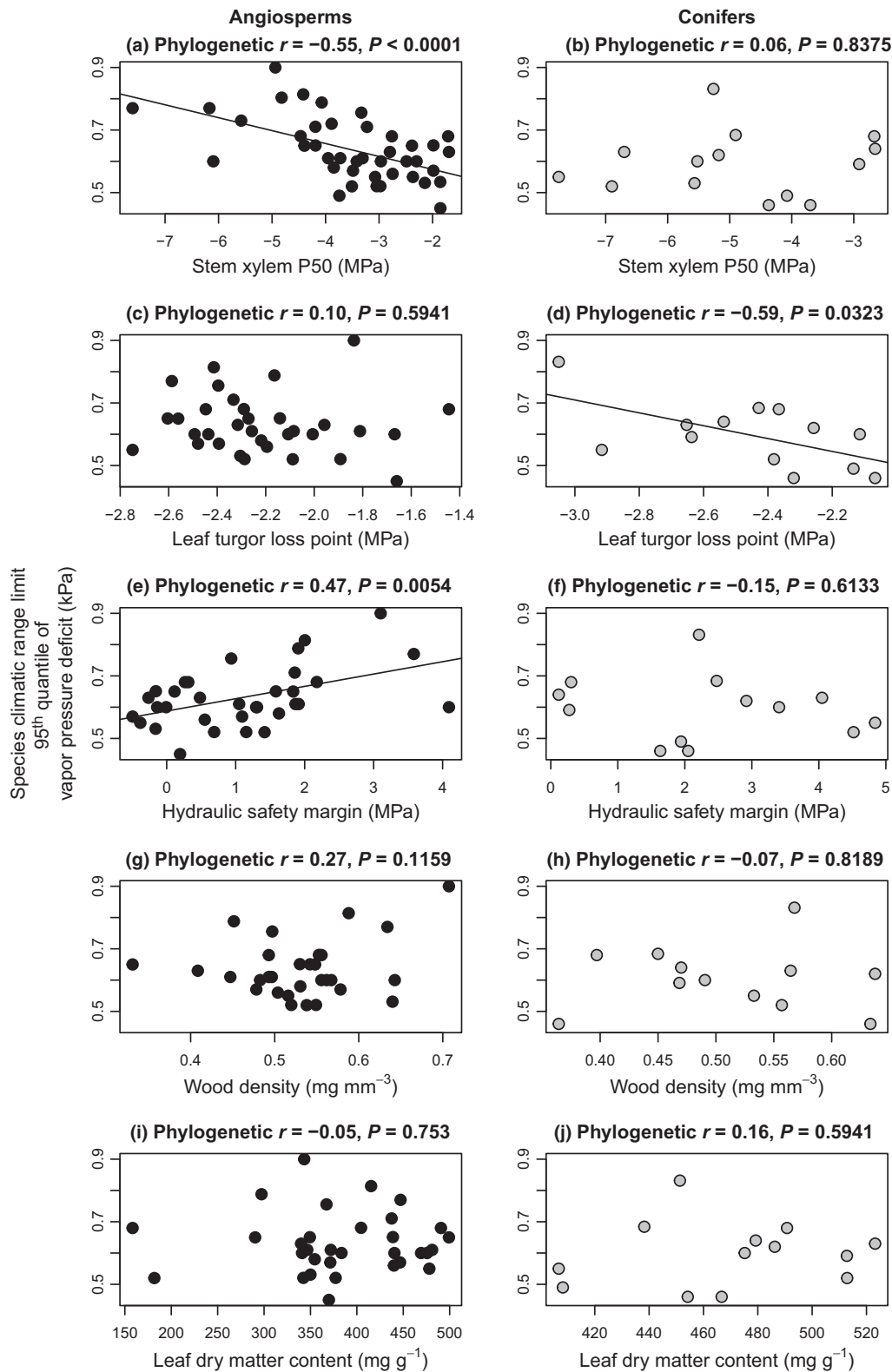
Fig. 5 Relationships between species lower distributional limit of mean annual precipitation (MAP, mm, 5th quantile) for each species and stem xylem P50 (a, b), leaf turgor loss point (c, d), hydraulic safety margin (e, f), wood density (g, h) and leaf dry matter content (i, j). Data for angiosperms are shown in the left column using black circles and data for conifers are shown in the right column using grey circles.

range limits if local drought measures such as soil water potential could be used instead. Stem P50 consistently exhibits strong relationships with climatic niches of trees (Larter *et al.*, 2017), but Farrell, Szota, & Arndt (2017) urged caution in using leaf TLP to predict vulnerability to drought. We measured leaf TLP on rehydrated samples from the field and so implicitly treat leaf TLP as a fixed trait. However, the capacity to adjust leaf TLP either osmotically or elastically has been observed to be an important trait (Meinzer *et al.*, 2014; Maréchaux *et al.*, 2017; Nolan *et al.*, 2017; Johnson *et al.*, 2018). Future work should evaluate the

Fig. 6 Relationships between species upper distributional limit of vapor pressure deficit (95th quantile, kPa) for each species and stem xylem P50 (a, b), leaf turgor loss point (c, d), hydraulic safety margin (e, f), wood density (g, h) and leaf dry matter content (i, j). Data for angiosperms are shown in the left column using black circles and data for conifers are shown in the right column using grey circles.

relationship between species-level leaf TLP measured on rehy-drated samples and species-level ability to adjust leaf TLP across a phylogeneticaly diverse group of species. If leaf TLP

corresponds to the osmotic potentials that induce full stomatal closure (Martin-StPaul *et al.*, 2017), this means that despite being able to assimilate carbon longer by keeping stomates open

longer under drought, the risk of hydraulic failure will be higher for species with lower TLP.

Hydraulic safety margin has been proposed to explain differences in drought resistance among species because it integrates the lag between water loss from leaves to embolism formation in xylem. Species with HSM values close to zero operate in an unsafe domain because embolisms form in their xylem as soon as transpiration stops and their leaves lose turgor (Bartlett *et al.*, 2016; Martin-StPaul *et al.*, 2017). Hydraulic safety margin was nearly as good of a predictor of climatic limits, but this trait is almost entirely determined by stem P50 rather than leaf TLP (Fig. S5). Estimation of HSM is dependent on the assumption that embolism resistance of the stem and leaf xylem are comparable within species, because xylem P50 was measured on stems whereas TLP was measured on leaves. The Hydraulic Segmentation Hypothesis proposes that the xylem of leaves should be more vulnerable than stems (Zimmermann, 1983), but recent evidence suggests that the degree of segmentation may be species-specific, and higher in drought deciduous species (Skelton *et al.*, 2017, 2019). The safety margin may therefore be overestimated for more drought-tolerant species, but a better understanding of this trait will require further investigation of the coordination of embolism resistance in leaves and stems across species.

Easy-to-measure morphological traits, such as wood density and LDMC, were not reliable indicators of drought resistance. While it is true that, across both angiosperms and conifers, species with dense wood exhibited greater stem embolism resistance (Hacke *et al.*, 2001) and species with higher LDMC exhibited more negative leaf TLP, these morphological traits were poor predictors of the climatic limits of species. Wood density was the only morphological trait that exhibited any relationship with species climatic limits, and only with MAP. Our results provide further evidence that we cannot rely on commonly measured morphological traits to develop generalizable predictions of species responses to drought; rather we must quantify mechanistic physiological traits, especially stem P50 (Larter *et al.*, 2017). This suggests that global models for predicting drought-induced mortality (Greenwood *et al.*, 2017) could be improved by replacing morphological traits with physiological traits when they become available at the global scale. It remains an open question, however, about which traits explain conifer distributions in New Zealand (discussed in detail below).

We observed wide variation in drought resistance among these temperate evergreen rainforest tree species. Several trees in this temperate rainforest flora exhibited high levels of drought resistance. *Prumnopitys ferruginea*, a conifer in the Podocarpaceae, exhibited the lowest stem P50 of −7.7 MPa. The angiosperm *Coprosma linariifolia* was a close second with a stem P50 of −7.6 MPa. These values of P50 are considered to confer high drought resistance (Maherali *et al.*, 2004; Choat *et al.*, 2012), but they are moderate compared to the observed global minimum stem P50 of −18.8 MPa (Larter *et al.*, 2017). *Prumnopitys taxifolia* exhibited the lowest average leaf TLP of −3.1 MPa, which is closer to the observed global minimum leaf TLP of −4.0 MPa (Martin-StPaul *et al.*, 2017). Many species exhibited resistant xylem (e.g. the conifers *Phyllocladus trichomanoides*,

Prumnopitys taxifolia and *Podocarpus totara*, and the angiosperms *Pittosporum eugenioides* and *Pittosporum tenuifolium*), which agrees with local observations that these species occur predominantly on dry sites (Hinds & Reid, 1957; Leathwick & Whitehead, 2001). Four species exhibited vulnerable xylem and will probably suffer under more frequent hotter drought, including the angiosperms *Schefflera digitata*, *Fuchsia excorticata*, *Ascarina lucida* and *Pseuodopanax crassifolius* (Fig. 2). However, these species can persist in moist microhabitats such as shaded gully environments (Wardle, 1967; Martin & Ogden, 2005).

This is the largest study to date to examine drought tolerance traits and environmental distributions among the ancient conifers of New Zealand, yet their physiological traits remain puzzling. The conifers as a whole are skewed towards the low end of stem P50 values. These conifers are known for being 'overbuilt' (Pittermann *et al.*, 2006b), that is, they construct narrow tracheids that are highly resistant to embolism formation yet often grow in wet environments. For example, *Lepidothamnus intermedius* and *Manoao colensoi* exhibited resistant xylem (−5.6 and −4.1 MPa, respectively) but often grow in areas that receive > 4000 mm of annual precipitation and in nutrient-poor, waterlogged soil (Hinds & Reid, 1957; Leathwick & Whitehead, 2001; Gaxiola *et al.*, 2010; Coomes & Bellingham, 2011). Most notably, *Prumnopitys ferruginea* exhibited the most resistant xylem in the study (−7.7 MPa), yet is only found in mesic forests that only rarely experience water deficits (Hinds & Reid, 1957; Leathwick & Whitehead, 2001). The fact that we have now established a significant relationship between stem P50 and climate in the angiosperms makes the lack of association among conifers even more puzzling as it rules out any peculiarity of the New Zealand oceanic climate (McGlone *et al.*, 2016). Rather than resisting drought, these conifer species may exhibit other drought strategies such as drought avoidance (Brodribb, 2011; Brodribb *et al.*, 2014; Delzon, 2015). For example, *Agathis australis* exhibits the most vulnerable xylem (− 2.7 MPa) among the conifers and is known to be sensitive to drought as a seedling (Bieleski, 1959), yet its ability to survive in drought as a large canopy tree has been attributed to having large sapwood area and deeper roots, high stomatal regulation, and an ability to shed leaves (Macinnis-Ng & Schwendenmann, 2015; Macinnis-Ng *et al.*, 2016).

The three conifer species with the most vulnerable xylem are either intolerant of seasonal drought (e.g. *Dacrydium cupressinum*), grow in dry regions almost exclusively in wet soil of swamps, floodplains and river terraces (e.g. *Dacrycarpus dacrydioides*), or resist drought through their volume and stomatal regulation (e.g. *Agathis australis*). These three species are among the fastest growing conifers and are among the few native conifers considered for commercial timber operations.

The conifers with resistant xylem grow in both the wettest and the driest climates, yet they all grow slowly. It has been hypothesized that the New Zealand conifers have evolved for slow, persistent growth to outlast and overtop the faster growing angiosperms (Coomes *et al.*, 2005). It has also been suggested that the evolution of conservative xylem in the New Zealand conifers has been in response to other drivers, such as nutrient limitation (Pittermann *et al.*, 2006b). Slow growth and reduced

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whole-plant photosynthesis may put less demand on the soil nutrient pool so species can persist on infertile soil (Cary & Pittermann, 2018). We speculate that slow-growing conifers have exaptively obtained drought resistance not as a direct adaptation to infertile soil, but as a consequence of their slow growth and long-lived survival strategy. Southern hemisphere conifers are known for their small tracheids (Pittermann *et al.*, 2006a) that are associated with slow growth rates and denser wood, which may also enhance their resistance to microbial decomposition in rainy environments (Boddy, 2001). Experimental nutrient additions reduced wood density and increased vulnerability to stem embolism in hybrid poplar saplings (Hacke *et al.*, 2010), but other studies have shown that reduced wood density in response to increased nutrient availability does not necessarily lead to higher vulnerability (Bucci *et al.*, 2006; Lamy *et al.*, 2012; Goldstein *et al.*, 2013). Future work should quantify embolism resistance in other more cavitation-prone organs (leaves and roots) to determine whether these can shed additional light on these curious conifers. Despite the lack of correlation between xylem resistance and climatic limitations among the New Zealand conifers, their resistant xylem may equip them to resist future drought.

We could question our methodological assumption that our leaf osmotic potential measurements were good predictors of leaf TLP, especially given the variation among phylogenetic groups. We used Bartlett's model to predict leaf TLP from leaf osmotic potential, with the assumption that the elastic modulus contributes little to this relationship (Bartlett *et al.*, 2012a). However, we note that elastic modulus has been shown to differ between temperate conifers and angiosperms (Bartlett *et al.*, 2012b), possibly suggesting that this assumption leads to an incorrect estimate of leaf turgor loss in our system. Future studies will need to consider elastic modulus and other aspects of leaf structure and water relations when comparing leaf turgor across two very different phylogenetic groups.

Our metric of climatic limitation is derived from current species distributional ranges, and therefore reflects the realized climatic niche of a species, not their fundamental climatic niches. Future work to improve our understanding of which physiological traits best predict population response to drought could link these physiological traits to individual and population vital rates such as growth and survival during drought events (Russo *et al.*, 2010; Laughlin & Messier, 2015). Determining the traits that best predict population vital rates along climatic gradients across multiple phylogenetic groups will further advance our understanding of community and ecosystem responses to global change.

Author contributions

DCL, SD, MJC, PJB, MSM and SJR planned and designed the research. DCL, SD, SJR and MJC performed experiments, conducted field work and analysed the data. DCL led the writing of the manuscript.

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Supporting Information

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

Fig. S1 Xylem vulnerability curves for conifer species of New Zealand.

Fig. S2 Xylem vulnerability curves for angiosperm species of New Zealand.

Fig. S3 Relationships between maximum temperature limits and traits.

Fig. S4 Relationships between minimum precipitation-to-potential evapotranspiration limits and traits.

Fig. S5 Hydraulic safety margin is determined almost solely by variation in xylem P50 rather than leaf turgor loss point.

Table S1 Species mean trait values used in the analysis.

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