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Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species

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Summary

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- The evolution of lignified xylem allowed for the efficient transport of water under tension, but also exposed the vascular network to the risk of gas emboli and the spread of gas between xylem conduits, thus impeding sap transport to the leaves. A well-known hypothesis proposes that the safety of xylem (its ability to resist embolism formation and spread) should trade off against xylem efficiency (its capacity to transport water).
- We tested this safety–efficiency hypothesis in branch xylem across 335 angiosperm and 89 gymnosperm species. Safety was considered at three levels: the xylem water potentials where 12%, 50% and 88% of maximal conductivity are lost.
- Although correlations between safety and efficiency were weak ($r^2 < 0.086$), no species had high efficiency and high safety, supporting the idea for a safety–efficiency tradeoff. However, many species had low efficiency and low safety. Species with low efficiency and low safety were weakly associated ($r^2 < 0.02$ in most cases) with higher wood density, lower leaf- to sapwood-area and shorter stature.
- There appears to be no persuasive explanation for the considerable number of species with both low efficiency and low safety. These species represent a real challenge for understanding the evolution of xylem.

*These authors contributed equally to this work.

Introduction

Plants require water to maintain stomatal conductance and CO₂ uptake during photosynthesis. Although the biological requirements for water are well understood, the risks and tradeoffs associated with water transport are less clear. Ever since the cohesion–tension theory was proposed (Dixon, 1914), the risks of transporting water in a metastable state (under large tension) have been appreciated. The most serious danger involves the expansion of small gas bubbles (embolism) within the transpiration stream and the subsequent spread of this gas across interconduit pits (hereafter abbreviated ‘pit’) (Tyree *et al.*, 1994). If most of the conduits within the xylem become filled with gas, transport of water becomes limited until new conduits are produced or conduits are refilled (Hacke & Sperry, 2001), although the frequency and conditions of refilling remain unresolved (Cochard & Delzon, 2013; Rockwell *et al.*, 2014; Trifilò *et al.*, 2014). Because plants benefit from a water transport system that is both efficient and also safe from embolism, variation in both efficiency and safety are expected to reflect ecological and evolutionary differences among species (Sperry, 2003; Baas *et al.*, 2004).

Here, we use the most common definition of hydraulic efficiency (hereafter ‘efficiency’) as the rate of water transport through a given area and length of sapwood, across a given pressure gradient – the xylem-specific hydraulic conductivity (K_S). We define hydraulic safety (hereafter ‘safety’) as the xylem water potential at which a meaningful percentage of maximum efficiency is lost (P_X), likely resulting from embolism. We investigated a range of safety definitions, including the loss of 12, 50 and 88% of maximum efficiency (i.e. P_{12} , P_{50} , P_{88}) (as defined by Domec & Gartner, 2001), but focus on P_{50} because this is the most commonly used index of embolism resistance in the literature. P_{50} usually represents the steepest part of the vulnerability curve (Choat *et al.*, 2012), where small changes in xylem tension result in large changes in conductivity.

What are the discernible benefits of efficiency and safety?

At a given pressure gradient, higher efficiency can deliver higher potential transpiration and potential photosynthesis per unit xylem cross-section area, or else can deliver the same water supply while requiring less xylem cross-section area. Supporting the first possibility, efficiency has been reported as being correlated with higher leaf-level photosynthesis in angiosperms (Brodribb & Feild, 2000; Santiago *et al.*, 2004; Nardini & Salleo, 2005; Choat *et al.*, 2011), gymnosperms (Brodribb & Feild, 2000; Hubbard *et al.*, 2001), and across pteridophytes, gymnosperms and angiosperms (Mencuccini, 2003; Brodribb *et al.*, 2005). Efficiency has also been linked with faster growth and greater leaf- to xylem-area ratio – that is, leafier stems across angiosperm species (Tyree *et al.*, 1998; Sack *et al.*, 2003; Poorter *et al.*, 2010; Gleason *et al.*, 2012). Alternatively, higher efficiency could also permit lower xylem construction and maintenance costs per unit transpiration. For example, efficient xylem may require less xylem tissue for a given amount of leaf-area (thinner stems). It is possible that differences among habitats, life histories and plant life forms

might be associated with different safety–efficiency optimization strategies (Hacke *et al.*, 2010; Pratt *et al.*, 2010, 2012; Markesteijn *et al.*, 2011; Plavcová *et al.*, 2011; Plavcová & Hacke, 2012); however, even within these habitats and life forms, higher efficiency should allow for less xylem cross-section area or a lower fraction of sapwood in stems.

Perhaps a less obvious benefit of greater efficiency is that it should result in less negative xylem water potentials (i.e. avoid harmful *tension*) at a given rate of transpiration, as made evident in the Whitehead–Jarvis water transport model (Whitehead *et al.*, 1984). In this way, efficient xylem may reduce the risk that damaging water potentials will occur in the first place, particularly in habitats where soil water potentials and vapour pressure deficit are high (wet soils, dry atmosphere) (Gleason *et al.*, 2013).

Greater safety allows plants to operate at higher xylem tension (more negative water potential) and with fewer gas obstructions within xylem conduits at a given tension. Benefits of greater safety might allow plants to reduce root mass (shallower root penetration), operate in soils with lower matric potential, or transpire through longer periods of the day or the year. Species that must tolerate low xylem water potentials often exhibit markedly negative P_{50} values (Brodribb & Hill, 1999; Choat, 2013; Uri *et al.*, 2013), although some arid-land plants routinely appear to tolerate significant losses of conductivity (Jacobsen *et al.*, 2008; Hacke *et al.*, 2009; Miranda *et al.*, 2010). These safety levels have evolved many times independently in angiosperms (Maherali *et al.*, 2004; Sperry *et al.*, 2007; Hacke *et al.*, 2009), and there is evidence for convergent evolution of safety in gymnosperms as well (Pittermann *et al.*, 2012).

Should natural selection optimize efficiency and safety?

Advantages of possessing efficient as well as safe xylem are self-evident, but the reasons why these traits should trade off against one another are less clear. The tradeoff proposes that xylem efficiency and safety are both direct outcomes of the characteristics of the pit membranes and the nature of the connections within the xylem conduit network. For pits and pit membranes, the thickness, the size of pit membrane-pores (Lens *et al.*, 2011, 2013) and the number of interconduit pits per vessel (Hargrave *et al.*, 1994) are likely determinants of both safety and efficiency. A dominant hypothesis linking efficiency and safety in angiosperms suggests that wider conduits (and therefore more efficient conduits) tend to have more interconduit pits, more pit membranes and a greater chance of possessing a large membrane-pore through which air-seeding may proceed (Hargrave *et al.*, 1994; Wheeler *et al.*, 2005). Xylem network traits such as lumen conduit dimensions (length and diameter), the number of unique vessel connections among conduits (conduit connectivity) (Carlquist, 1984; Loepfe *et al.*, 2007; Martínez-Vilalta *et al.*, 2012) and the degree of conduit grouping (and therefore the number of interconduit connections) (Carlquist, 1984; Lens *et al.*, 2011) are all important components of efficiency in angiosperms, and could also possibly lead to decreased safety. Similarly across gymnosperms, the size of the pit aperture as well as the relative sizes of the aperture and torus (i.e. torus overlap) correlate with safety

(Domec *et al.*, 2006, 2008; Delzon *et al.*, 2010; Pittermann *et al.*, 2010; Bouche *et al.*, 2014), although the relationship between these traits and efficiency is not clear.

Many traits could contribute to the safety–efficiency tradeoff, and therefore there is opportunity for these traits to interact, and importantly, this may occur at multiple scales. It is apparent that if the pit membrane-pores through which sap must pass become smaller than the meniscus of an embolized conduit will be trapped at higher tension and prevent its spread into adjacent sap-filled conduits (Dixon & Joly, 1895). It is also apparent that this reduction in membrane-pore size would result in reduced efficiency. Moving up to the scale of a conduit, reduced efficiency at the level of the pit membrane-pore could be compensated for via changes in conduit features (e.g. more interconduit pits per conduit, greater conduit length, greater conduit diameter) or at the level of xylem cross-section (e.g. more conduits), and certainly at the level of the whole plant (Meinzer *et al.*, 2010). Thus, the hypothesized negative correlation between safety and efficiency may be unavoidable at the level of individual membrane-pores, but this correlation could weaken as the level of analysis broadens to include whole membranes, whole conduits and whole xylem tissue.

Within the constraints arising from the structure of xylem, we might expect natural selection to maximize efficiency at a given level of safety. Different levels of safety are expected in different habitats because xylem operates at widely different water potentials (Pockman & Sperry, 2000; Choat *et al.*, 2012). At a given level of safety, it should nearly always benefit a species to maximize xylem efficiency because this would result in either greater rates of photosynthesis or reduced xylem costs (as discussed earlier). It is possible that other xylem-specific tradeoffs could confound this relationship (Wagner *et al.*, 1998; Speck & Bergert, 2011; Lachenbruch & McCulloh, 2014). For example, if there were a tradeoff between efficiency and mechanical stability, and some habitats favoured higher mechanical stability than others, then we might expect species from different habitats or possessing different morphologies (e.g. wood density, Huber values) to occur in different zones of the safety–efficiency tradeoff space.

Does the current literature support a safety–efficiency tradeoff?

The largest test of this hypothesis to date reported insignificant correlation across extant woody angiosperms ($r^2 = 0.03$; $P > 0.05$) and gymnosperms ($r^2 = 0.00$; $P > 0.05$) but weak significant correlation when pooling both groups ($r^2 = 0.10$; $P < 0.05$) (Maherali *et al.*, 2004). Interestingly in this analysis, and in other studies (Tyree *et al.*, 1994; Maherali *et al.*, 2004; Westoby & Wright, 2006), many species representing a wide range in habitat and physiology exhibited both low efficiency and low safety. The low efficiency and low safety species in these studies appeared to contradict the proposition of a tradeoff between these two xylem traits. Studies examining fewer species are divided, with *c.* 25% of studies providing support for the safety–efficiency hypothesis and *c.* 75% not providing support, measured by linear correlation between reported values of safety and efficiency. We note that the

authors' interpretations of their own data may differ from ours, mainly due to differences in correlation coefficients between data subsets (e.g. differences in site and phylogeny). For this reason, we do not attempt here to categorize these individual reports as supporting or refuting the tradeoff. However, it is likely that reporting a tradeoff has been encouraged by the idea that a tradeoff between safety and efficiency should exist, at least at the level of the interconduit pit membrane-pore (Sperry *et al.*, 2003). It is interesting therefore that over half the studies quantifying this tradeoff in xylem have not found it. Thus, examining whether efficiency and safety covary across a large subset of the world's plant species would provide a more complete analysis of this tradeoff than is feasible within any single study.

We compiled branch xylem data across 335 angiosperms and 89 gymnosperm species, making this study five times larger than any previous work. We asked first whether there was evidence for a broad tradeoff between stem hydraulic efficiency (K_S) and safety (P_X) across angiosperm or gymnosperm species. Plotting efficiency against safety could result in several possible patterns (Fig. 1). If natural selection maximizes both traits within the limits of a tradeoff between them, we might expect a negative monotonic relationship (Fig. 1, Feature 3), and also unoccupied niche space outside this optimum zone (Fig. 1, Features 1 and 2). Second, we investigated why so many species appeared to lie outside of the optimum zone, having both low efficiency and low safety, as reported in previous analyses (Maherali *et al.*, 2004; Westoby & Wright, 2006) and as found again here. We asked whether plant structure, phenology, water availability, phylogeny or climate might be correlated with the distance that species were found away from the optimum zone. If the strength of other

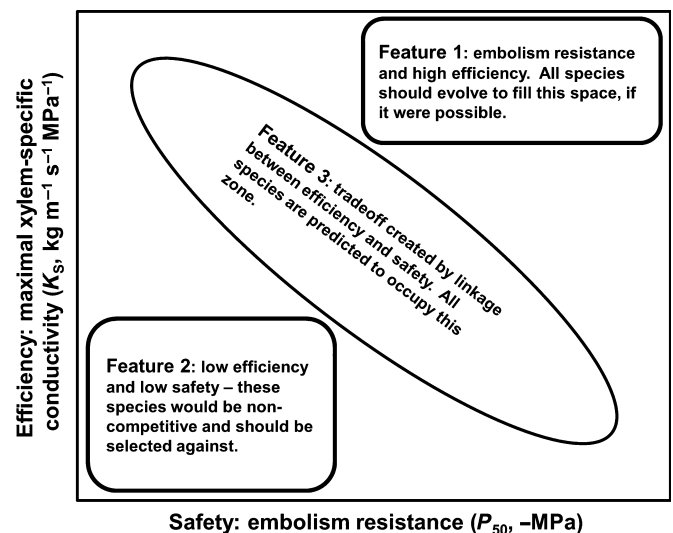


Fig. 1 Schematic diagram explaining three hypothetical features that might be expected in a tradeoff between hydraulic safety and hydraulic efficiency in xylem. Feature 1, upper right quadrant not occupied because both high safety and high efficiency cannot be achieved in the same species. Feature 2, Natural selection is expected to drive species upwards and rightwards because efficiency and safety are advantageous (taken in isolation). This should result in negative cross-species correlation between safety and efficiency (Feature 3).

tradeoffs differed across habitats or plant structural types, then we might expect this to be the case.

Materials and Methods

The dataset

The dataset used in this study (Xylem Functional Traits Database; XFT) can be accessed from the TRY Plant Traits Database (<https://www.try-db.org/TryWeb/Home.php>) and was an outcome from a working group assembled through the Australia–New Zealand Research Network for Vegetation Function, Macquarie University, Australia. Most data came from previously published reports (Choat *et al.*, 2012), but the dataset also included 31 unpublished safety–efficiency observations (Supporting Information Notes S1). We included species in these analyses only when safety and efficiency were measured on small branch samples (*c.* 0.4–1.0 cm diameter) because these were the sizes most commonly measured in the literature and because stem diameter is known to correlate with conduit structure (Jacobsen *et al.*, 2012). When multiple measures of efficiency or safety were available from the literature, mean values (across studies) were used in all cases. Water potentials measured at predawn (Ψ_{PD}), wood density, and leaf- to sapwood-area traits in most cases were provided in the same published reports as hydraulic safety; when absent, these data were extracted from the literature. We interpreted leaf or xylem water potential measured at predawn (Ψ_{PD}) as the soil water potential experienced by an individual plant at that time. Ψ_{PD} should be interpreted with some caution because it not only varies with species and site, but also reflects vagaries in precipitation throughout the year, as well as differences in night transpiration (Bucci *et al.*, 2004) and soil–xylem osmotic potential (Donovan *et al.*, 2003). In addition, we combined leaf and stem xylem Ψ data, as these were statistically indistinguishable from one another in this dataset (Choat *et al.*, 2012). Although leaf Ψ must be lower than xylem Ψ for water transport to take place, variation in Ψ among species and habitats is likely to be much greater than the error associated with this simplification.

Data were mainly taken from naturally occurring plant populations, but glasshouse and common garden experiments were included, providing that safety and efficiency values were both measured in these studies. For climate comparisons, only naturally occurring plant locations were included in the analyses.

Climate data were taken from the original reports, where available, and otherwise extracted from the Worldclim (elevation, temperature, precipitation) and the Climatic Research Unit (number freezing days) databases (New *et al.*, 1999; Hijmans *et al.*, 2005). When elevation data from the Worldclim database did not match elevations from published reports, temperature was scaled to match published elevations using a lapse rate of $6.0^{\circ}\text{C km}^{-1}$ increase in elevation.

Analyses

All analyses were performed across species using log-transformed mean values for each species. Safety and efficiency data were log-transformed because the raw means were markedly right-skewed (Fig. 2). We fitted standard major axis (SMA) linear functions through log-transformed data (Fig. S1). This corresponds to assuming that the association between efficiency and safety is approximated by a power function, with the slope of the log-log transformed model equal to the scaling exponent. We used this transformation because it had the effect of producing an approximately linear (though loose) association between efficiency and safety (Fig. 2). Although this is consistent with previously published findings (Martínez-Vilalta *et al.*, 2002), we accept that other models may also be appropriate. Safety–efficiency data were analysed using the ‘smatr’ package (Warton *et al.*, 2006) for R 3.1.0 (R Core Team, 2014), which gave estimates of the SMA slope and also the per cent covariation between these traits (r^2). To evaluate if the correlation between safety and efficiency differed among plant clades, SMA models were fit to species belonging to individual clades (e.g. family), provided at least eight species were present per clade.

It is not well understood how P_X relates to irreversible damage and mortality across species. As such, ‘safety’ is a rather subjective concept. Although P_{50} relates to the steepest part of the

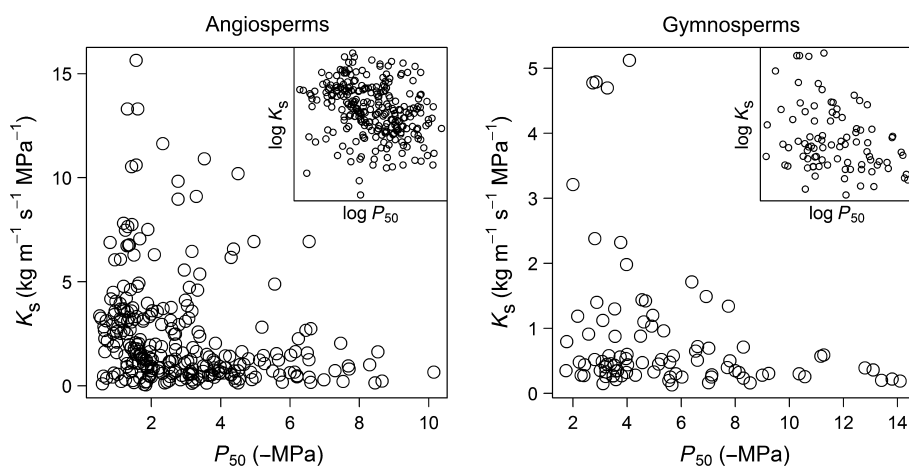


Fig. 2 Hydraulic safety (P_{50}) – efficiency plots for all angiosperm and gymnosperm species. Inset plots have been drawn to show log-transformed relationships. K_s , hydraulic conductivity.

vulnerability curve, different points on the curve may reflect different aspects of the dehydration process. The initial decline in maximal conductivity (P_{12}) relates to the air-entry tension and is likely coordinated with decreasing stomatal conductance and increasing hydraulic capacitance, that is, water released from embolizing conduits as well as water stored in tissue outside the conduits (Tyree & Yang, 1990; Kavanagh *et al.*, 1999; Domec & Gartner, 2001; Hölttä *et al.*, 2009). At the other end of the range, P_{88} occurs at tensions well beyond stomatal closure and likely relates to irreversible damage to the stem or root xylem (Blackman *et al.*, 2009; Brodribb *et al.*, 2010; Urli *et al.*, 2013). Because the different physiological processes conferring growth and fitness (such as stomatal conductance, capacitance, embolism refilling) operate across different water potential ranges, it is important to consider other definitions of hydraulic safety. With this in mind, we assessed the K_S – P_X relationship at three points across each species' vulnerability curve – at P_{12} , P_{50} and P_{88} (Tables S1–S4; Figs S2–S5).

The majority of species in our dataset did not sit close to the standard major axis trend-line (e.g. Fig. 1, Feature 3), suggesting that safety or efficiency were trading off against other, as yet unknown, variables. To test this hypothesis, we assessed whether variation in other plant traits (e.g. wood density) or climate variables (e.g. temperature, precipitation) were correlated with variation orthogonal to the fitted safety–efficiency trend-line. To do this, the residuals from the safety–efficiency SMA fit were saved and regressed against our 'third' variables (plant traits, climate). Third variables were transformed as necessary to meet the assumptions of the analyses.

In addition to investigating whether third variables modified the safety–efficiency relationship, we also wished to know whether or not these variables were more significantly aligned with either the safety or efficiency axis. To do this, we fitted an ordinary least-squares model, with the third variable set as the dependent variable and safety and efficiency as predictor variables. To determine r^2 estimates for this analysis, we decomposed the r^2 value into proportions of variation explained by efficiency or safety using the method proposed by Lindeman *et al.* (1980), as implemented in the 'relaimpo' package ('lmg' function) for R 3.1.0 (Grömping, 2006). This method uses an averaging technique to calculate relative importance components for predictor variables that are insensitive to their ordering in the model and uses a boot-strapping routine to generate confidence intervals.

Comparing methods

Hydraulic safety data were included in the analyses regardless of the methods employed to build vulnerability curves. We note that some work has questioned the validity of angiosperm safety data obtained by centrifuge-spinning short xylem segments for species with relatively long vessels (Cochard *et al.*, 2013; Martin-StPaul *et al.*, 2014). Data obtained via air-injection have also been disputed (Torres-Ruiz *et al.*, 2014). It is suggested that the centrifuge technique may incur an 'open vessel' artefact, resulting in an exponential 'r-shaped' curve. However, others have found

no evidence for a long vessel artefact and have found that r-shaped curves are valid when the standard centrifuge technique has been used (Jacobsen & Pratt, 2012; Sperry *et al.*, 2012; Tobin *et al.*, 2013; Hacke *et al.*, 2015). Because this appears to be a potentially important, but unresolved issue, all angiosperm analyses were run a second time excluding all r-shaped vulnerability curves regardless of the technique used. We have included the statistical results for all K_S – P_{50} analyses using the reduced dataset (Tables S5, S6), but note that results from both analyses are similar.

Recent work suggests that native emboli (emboli present upon collecting the sample) must first be flushed to obtain representative vulnerability curves, and thus, accurate efficiency and safety data (Hacke *et al.*, 2015). We had hoped to evaluate this potential artefact by plotting $\log K_S$ as a linear function of the hydraulically weighted diameter ($\log D_H$) and then comparing slopes and intercepts from flushed versus nonflushed xylem. Unfortunately, those publications that did clearly describe their flushing procedure did not usually report D_H .

Also of concern were effects that different methods may have had on the measurement accuracy of hydraulic efficiency. Particularly, we were interested if centrifuged samples had higher efficiency at a given hydraulically weighted diameter ($\log D_H$), as might be the case if an open-vessel artefact was significant (Cochard *et al.*, 2013), that is, fewer interconduit pits, and thus, less interconduit resistance. In addition to centrifuged samples, we also evaluated the air injection and 'bench-top' methods by comparing the SMA slopes and intercepts extracted from K_S – D_H plots. Similarly, we constructed K_S – D_H plots to compare conductivity loss curves exhibiting exponential, sigmoidal, or 'other' shapes. Thus, any method that had used branch segments too short, relative to vessel length, would yield an erroneously high maximal K_S value, that is, a high SMA y -intercept coefficient.

Results

Is there evidence for a safety–efficiency tradeoff?

Regardless of what definition of safety was used (P_{12} , P_{50} , P_{88}) several common results emerged from the data. On the one hand, most safety–efficiency plots exhibited an empty quadrant in the upper right-hand corner (Figs 2–4, S2–S5), confirming that species have not been able to achieve both high efficiency and high safety (Fig. 1, Feature 1). On the other hand, many species were found in the lower left quadrant of the safety–efficiency plots (Fig. 1, Feature 2). The strength of the safety–efficiency tradeoff on log-transformed data was generally significant but weak (without meaningful predictive power) and differed slightly among the three definitions of safety. Angiosperm r^2 values ranged from 0.053 (P_{50}) to 0.075 (P_{12}) and gymnosperm r^2 values ranged from 0.004 (P_{88}) to 0.086 (P_{50}) (Tables 1, S1, S3). Tradeoffs (P_{50}) were also weak or absent among evergreen ($r^2 = 0.023$; $P = 0.035$), winter deciduous ($r^2 = 0.031$; $P = 0.086$) and drought deciduous ($r^2 = 0.014$; $P = 0.428$) angiosperms (Table 1).

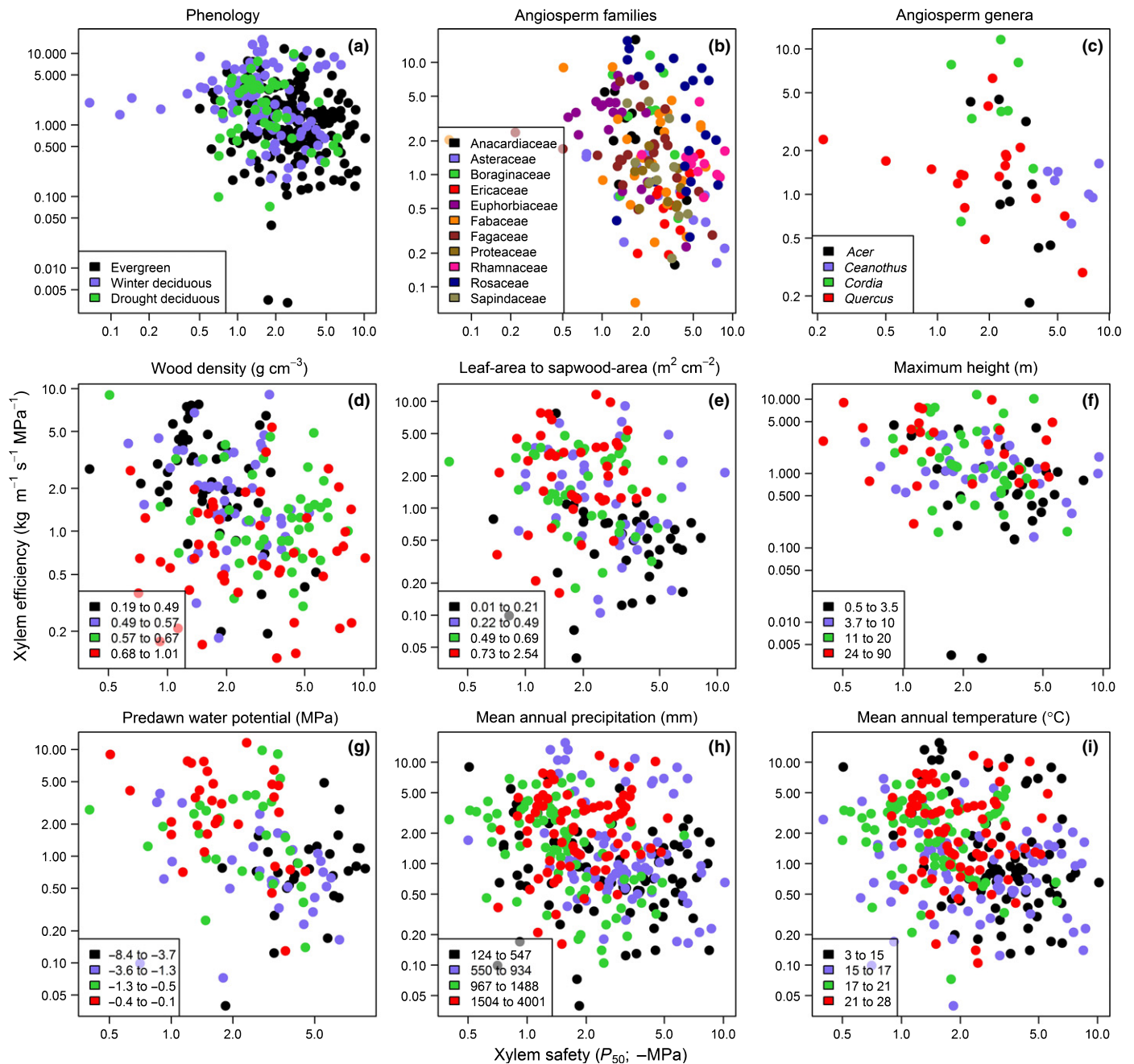


Fig. 3 Hydraulic safety (P_{50}) – efficiency plots for angiosperm species. Axes have been \log_{10} scaled. Different colours represent different (a) leaf habits, (b, c) taxonomic groups, (d–f) plant structural traits and (g–i) site factors. Continuous variables were binned in roughly equal groups of four, with bin ranges denoted in the legends.

Is there evidence for clade-specific safety–efficiency tradeoffs?

Within particular clades (Figs 3b,c for angiosperms, 4a–c for gymnosperms) there appeared in some instances to be a clear safety–efficiency tradeoff. Considering all definitions of safety, within the families Anacardiaceae, Asteraceae, Cupressaceae, Euphorbiaceae and Sapindaceae, negative correlation accounted for 38–46% of variation (Table 1), although the strength of within-family relationships did vary among definitions of safety

(Tables 1, S1, S3). In other clades there was weak or no correlation, and among *Ericaceae* there was a clear *positive* relationship between safety (P_{50} and P_{88}) and efficiency (Tables 1, S1).

Is the safety–efficiency tradeoff altered by other plant or climate variables?

Considering safety defined as P_{50} , wood density explained a small but significant amount of residual variation in the safety–efficiency relationship across angiosperm species ($r^2 = 0.02$;

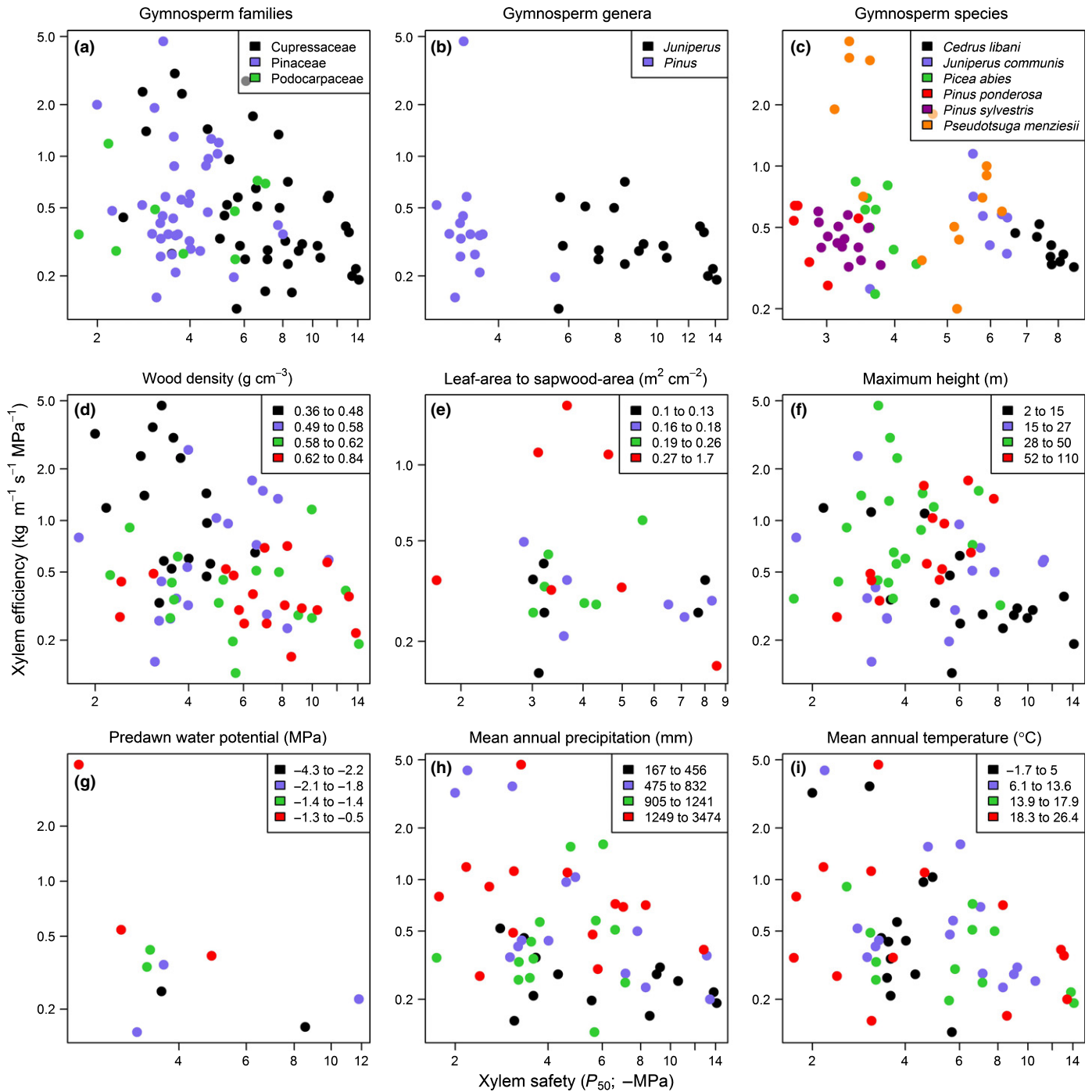


Fig. 4 Hydraulic safety (P_{50}) – efficiency plots for gymnosperm species. Axes have been \log_{10} scaled. Different colours represent different (a–c) taxonomic groups, (d–f) plant structural traits and (g–i) site factors. Continuous variables were binned in roughly equal groups of four, with bin ranges denoted in the legends.

$P=0.049$) (Table 2; Fig. 3d). Angiosperms with high-density xylem tended weakly to be positioned away from the tradeoff diagonal and towards the origin (intersection of the x - and y -axes). Leaf- to sapwood-area ratio explained a significant amount of residual variation across gymnosperm species ($r^2=0.21$; $P=0.021$) (Table 2; Fig. 4d), although with only 24 species in this analysis, this result should not be overinterpreted.

Results differed depending on the definition of safety considered. For angiosperms, safety–efficiency relationships using P_{50} and P_{88} were similar, with most third variables explaining only markedly small amounts of residual variation (0–4%), suggesting that the relationship between safety and efficiency was not modified meaningfully by precipitation nor by differences in plant structure (Tables 2, S2; Figs 3, S2). However, when safety was

Table 1 Standard major axis (SMA) efficiency–safety models fitted to individual angiosperm and gymnosperm groups

Angiosperms	r^2	Slope	Intercept	P	df
All angiosperm species	0.053	−1.65	0.65	< 0.001	333
Phenology					
Evergreen	0.023	−1.92	0.81	0.035	189
Winter deciduous	0.031	−1.35	0.56	0.086	94
Drought deciduous	0.014	−1.89	0.58	0.428	46
Families					
Anacardiaceae	0.375	−2.69	1.03	0.034	10
Asteraceae	0.463	−0.90	0.18	0.011	11
Boraginaceae	0.056	−2.79	1.44	0.539	7
Ericaceae	0.463	2.12	−1.39	0.015	10
Euphorbiaceae	0.377	−1.92	0.62	0.004	18
Fabaceae	0.028	−1.21	0.54	0.420	23
Fagaceae	0.092	−1.00	0.47	0.170	20
Proteaceae	0.132	−1.38	0.52	0.271	9
Rhamnaceae	0.028	−1.23	1.02	0.622	9
Rosaceae	0.066	−2.26	1.73	0.262	19
Sapindaceae	0.375	−3.04	1.38	0.045	9
Genera					
<i>Acer</i>	0.429	−3.36	1.58	0.040	8
<i>Ceanothus</i>	0.024	−1.19	1.00	0.740	5
<i>Cordia</i>	0.010	2.46	−0.23	0.812	6
<i>Quercus</i>	0.145	−0.88	0.37	0.119	16
Gymnosperms					
All gymnosperm species	0.086	−1.57	0.80	0.005	87
Families					
Cupressaceae	0.255	−1.86	1.23	0.001	37
Pinaceae	0.019	−2.66	1.26	0.433	33
Podocarpaceae	0.008	1.01	−0.92	0.820	7
Genera					
<i>Juniperus</i>	0.046	−1.35	0.77	0.391	16
<i>Pinus</i>	0.066	−5.13	2.31	0.354	14
Species					
<i>Cedrus libani</i>	0.615	−2.37	1.69	0.012	7
<i>Juniperus communis</i>	0.216	2.40	−2.08	0.246	7
<i>Picea abies</i>	0.250	−5.57	2.90	0.171	7
<i>Pinus ponderosa</i>	0.121	−3.43	1.22	0.399	6
<i>Pinus sylvestris</i>	0.172	−2.38	0.86	0.124	13
<i>Pseudotsuga menziesii</i>	0.413	−3.64	2.38	0.013	12

Safety is defined as the xylem water potential at which maximal conductivity declines by 50%. Statistically significant P -values ($\alpha = 0.05$) are denoted in bold.

defined as P_{12} , these results changed somewhat. In particular, wood density explained 12% of the residual variation across angiosperms, and leaf- to sapwood-area, maximum height and mean annual precipitation also explained small (< 7%) but significant percentages of residual variation (Table S4; Fig. S4). As such, short stature species with high wood density, low leaf- to sapwood-area ratios and in drier locations tended to be located slightly away from the diagonal, towards the origin.

Mean annual temperature and number of freezing days explained no residual variation for angiosperms or gymnosperms when safety was defined as P_{50} (Table 2). However, when considering safety as P_{88} , mean annual temperature and number of freezing days explained 3.4% and 7.7% of the residual variation

Table 2 Fit statistics for linear multiple regression models, with efficiency and safety as predictor variables and various structural and climatological traits as the dependent third variable

	r^2_{P50}	r^2_{Ks}	r^2_{resid}	df
Angiosperms				
Wood density	0.060**	0.189***	0.020*	194
Leaf-area to sapwood-area	0.056**	0.188***	0.020	160
Maximum height	0.049*	0.165***	0.019	128
Predawn water potential	0.236***	0.184***	0.002	118
Mean annual precipitation	0.029*	0.106***	0.003	307
Mean annual temperature	0.063***	0.020	0.006	307
Number of freezing days	0.003	0.032**	0.002	227
Gymnosperms				
Wood density	0.133**	0.196***	0.004	67
Leaf-area to sapwood-area	0.008	0.485***	0.209*	22
Maximum height	0.042	0.147**	0.017	62
Predawn water potential	0.249	0.629**	0.065	7
Mean annual precipitation	0.044	0.078	0.009	51
Mean annual temperature	0.016	0.002	0.013	51
Number of freezing days	0.001	0.013	0.000	51

Safety is defined as the xylem water potential at which maximal conductivity declines by 50%. Coefficient of determination values represent the proportion of total variation in the third variable explained by hydraulic safety (r^2_{P50}) and hydraulic efficiency (r^2_{Ks}). The percent residual variation in the safety–efficiency fit (orthogonal variation, i.e. standard major axis residuals) that is explained by the third variable (r^2_{resid}) is also reported and indicates whether the third variable is a meaningful predictor of where species are located away from the safety–efficiency trend-line. Asterisks indicate levels of significance (*, $P = 0.05$; **, $P = 0.01$; ***, $P = 0.001$).

in the efficiency–safety relationship (Table S2). Species living in colder climates tended to be located away from the efficiency–safety trendline, slightly towards the low efficiency and low safety quadrant. This result was similar even after removing drought and winter deciduous species, which avoid functioning during unfavourable seasons. Interestingly, number of freezing days was weakly correlated with efficiency across all angiosperms ($r^2 = 0.056$; $P < 0.001$), but this correlation strengthened markedly after removing deciduous species from the analysis ($r^2 = 0.199$; $P < 0.001$). By contrast, neither mean annual temperature nor number of freezing days were correlated with efficiency across gymnosperm species.

Is a safety–efficiency tradeoff confounded by experimental methods?

Comparison of methods did not reveal any differences that were likely to have modified the relationship between safety and efficiency (Figs S6, S7). Neither the Cavitron method (Cochard, 2002) nor the effect of not ‘flushing’ xylem before measuring maximal conductivity could be evaluated because hydraulically weighted diameters were generally not reported in these publications. However, conductivity loss curves that exhibited an exponential shape, as well as samples obtained using air injection methods, had *lower* efficiency values at a given hydraulically weighted vessel diameter than curves of different shape or data obtained via other methods (Figs S6, S7). Nevertheless, these

differences in efficiency were small relative to the shift away from the expected tradeoff space observed in the safety–efficiency plot (Fig. 1, Feature 3). They are not likely to have been responsible for the large number of species with low efficiency and low safety in the lower left-hand corner of Fig. 2.

Discussion

Is there a safety–efficiency tradeoff across woody species?

It seems clear that high safety together with high efficiency has not evolved in stem xylem (Fig. 1, Feature 1). This strongly suggests that the combination may not be achievable, and to that extent a tradeoff may exist. However, many species seem to have low efficiency together with low safety, which cannot be understood by reference to a tradeoff. Furthermore, the distance that species lie away from the hypothesized ‘tradeoff zone’ was not strongly correlated with any of the other traits or climate variables examined in this study, suggesting that these variables cannot explain why so many species have xylem with low efficiency and low safety (Fig. 1, Feature 2).

Two main questions arise from these results. First, what are the wood anatomical features that permit safety to vary so widely at a given level of efficiency (as in Fig. 2), and vice versa, efficiency to vary widely at a given level of safety? Total xylem efficiency may result from different anatomical features in different species (e.g. interconduit pit membrane-pore size, interconduit pit membrane area per conduit, conduit diameter/length, conduit connectivity, sapwood-area) and each of these features may have separate and different effects on safety, as has been suggested for *Sequoia sempervirens* (Burgess *et al.*, 2006) and across *Acer* species (Lens *et al.*, 2011). Similarly, different anatomical features could confer different levels of safety, although these mechanisms remain largely unstudied except for air-seeding through pores in pit membranes (Cochard, 2006; Jansen *et al.*, 2009; Lens *et al.*, 2011; Brodersen *et al.*, 2015). The second question that arises from these results is why should any particular anatomical arrangement of the xylem result in both low efficiency and low safety? Given that efficiency should nearly always enhance fitness (result in higher rates of gas exchange or lower xylem construction and maintenance costs), the presence of so many species that have both low efficiency and low safety suggests that the anatomical basis for high efficiency may be trading off with important traits other than safety. We note that this observation holds whether we consider all species in the dataset or omit those exhibiting r-shaped vulnerability curves. Considering that such a large portion of the world’s woody species are achieving neither high efficiency nor high safety, these unidentified traits have likely confounded our understanding of plant strategies, and as such, represent a very significant research question.

Why might we not expect a safety–efficiency tradeoff?

Different sources of xylem efficiency Differences in xylem efficiency may arise through many mechanisms: conduit dimensions (Hacke *et al.*, 2006; Sperry *et al.*, 2006); conduit lumen fraction

or the fraction of cross-section area that is composed of conduit lumens, independent of vessel width (McCulloh *et al.*, 2010; Zanne *et al.*, 2010); changes in interconduit pit and pit membrane ultrastructure (Choat *et al.*, 2008; Lens *et al.*, 2011; Brodersen *et al.*, 2015); differences in perforations between angiosperm vessel elements (Sperry *et al.*, 2005; Christman & Sperry, 2010); nonconductive vs conductive ground-tissue, that is, hydraulically functional tracheids or vasicentric tracheids (Sano *et al.*, 2011); conduit connectivity and ‘network’ efficiency (Loepfe *et al.*, 2007; Martínez-Vilalta *et al.*, 2012); and ion-mediated changes in the pit membrane ultrastructure that modify efficiency (Zwieniecki *et al.*, 2001; Nardini *et al.*, 2011).

Importantly, we should not expect that efficiency improvements via each of these components will result in reduced safety. For example, the direct effects of increasing efficiency via conduit dimensions (Tyree *et al.*, 1994), conductive ground-tissue (Sano *et al.*, 2011) or ion-mediated physiology (Tyree *et al.*, 1994; Sperry *et al.*, 2006; Cochard *et al.*, 2010) appear to have near-negligible effects on xylem safety (at least in the case of drought), whereas changes in efficiency associated with pit and membrane ultrastructure are likely to have a strong influence on xylem safety (Pickard, 1981; Zimmermann, 1983; Wheeler *et al.*, 2005; Jansen *et al.*, 2009; Lens *et al.*, 2011; Brodersen *et al.*, 2015). Thus, unless natural selection acts on only one source of efficiency (e.g. pit membrane-pore size), or acts on all sources similarly in all cases, we might not expect a strong safety–efficiency tradeoff across species. Assuming that closely related species have more similar xylem anatomy than distantly related species, we might expect stronger negative correlation between safety and efficiency within families, especially those spanning a large range in habitat aridity. This was partially supported by the analyses, with Asteraceae, Euphorbiaceae, Sapindaceae and Cupressaceae all showing significant negative correlation, and all spanning a large range in mean annual precipitation.

Possible relationships between xylem traits, safety and efficiency also strongly depend on how embolism events and air-seeding actually occur. It has recently been suggested that small gas ‘nanobubbles’ stabilized with surfactants may often be produced as gas passes through angiosperm pit membranes (Schenk *et al.*, 2015). This would allow pressure differentials to be increased without necessarily giving rise to embolism in a previously hydrated conduit. Furthermore, a safety–efficiency tradeoff may not be expected at all in gymnosperms, considering that safety appears to arise mainly from the amount of overlap between the sap-impermeable torus relative to the size of the pit aperture (Delzon *et al.*, 2010; Pittermann *et al.*, 2010; Bouche *et al.*, 2014), which may have minimal influence on efficiency (but see Domec *et al.*, 2008).

Climate and ecophysiology Plant structure and climate appeared to have a moderate influence on the hypothesized safety–efficiency tradeoff. Considering each separately, wood density, leaf- to sapwood-area, plant height, mean annual precipitation, mean annual temperature, and number of freezing days explain at most 12% of the residual variation in the efficiency–safety relationship. Species from cold climates did have reduced

efficiency at a given level of safety, but only among angiosperms and when defining safety as P_{88} or P_{12} . The analyses also showed that the shift in cold-habitat species occurred more strongly on the efficiency axis than the safety axis, with clear correlations between number of freezing days and efficiency (wider conduits) in most cases (Tables 2, S2, S4). This is in line with our present understanding of freeze–thaw embolism. According to the ‘thaw expansion hypothesis’ (e.g. Ewers, 1985; Hacke & Sperry, 2001; Pittermann & Sperry, 2003; Mayr & Sperry, 2010), gas bubbles formed in conduits on freezing expand on thawing when xylem tension is high. Small conduits contain less air and therefore result in smaller bubbles, which increases safety (Pittermann & Sperry, 2006). Similarly, air-seeding processes, similar to drought-induced cavitation, likely occur during freezing and may be exacerbated by lower temperature (Charrier *et al.*, 2014) as well as more frequent frost cycles (Mayr *et al.*, 2007). Our data are in rough agreement with this theory and further suggest that high efficiency via larger conduits may not be possible for many species in cold habitats.

Similarly, species may not require high safety. It has been suggested that effective regulation at the stomata may reduce the need for high safety even in dry habitats, that is, if plants avoid damaging tensions (Mencuccini *et al.*, 2015). We suggest that even plants in arid habitats experience water loss after stomatal closure (Borchert & Pockman, 2005; Brodribb *et al.*, 2014; Gleason *et al.*, 2014) and xylem tension will eventually increase to critical levels during prolonged periods of water stress. Also, if safety is indeed not required, natural selection should then favour higher efficiency to save xylem construction and maintenance costs. Similar arguments can be made for plant strategies that avoid embolism (e.g. capacitance), strategies that repair embolized conduits or produce new conduits quickly, for example, postdisturbance resprouters or recovery via secondary growth (Brodribb *et al.*, 2010; Pratt *et al.*, 2010, 2012), as well as strategies that allow for surplus or redundant efficiency (Ewers *et al.*, 2007), as has been proposed for leaves (Wagner, 1979; Sack *et al.*, 2008) and other biological networks (Tononi *et al.*, 1999). Clearly, all of these differences in habitat, physiology and life history are good reasons why plants may not *need* high efficiency or high safety. However, this does not diminish one of the important benefits of efficiency – efficient xylem can transport the same volume of water as inefficient xylem, but does so with a smaller cross-section of living wood. As such, these reasons do not address why natural selection does not increase efficiency to the maximum extent possible in all cases, unless high efficiency comes with costs or risks that are not yet understood.

The need for mechanical safety It has been suggested that hydraulic efficiency may trade off against mechanical safety (Long *et al.*, 1981; Wagner *et al.*, 1998; Niklas & Spatz, 2004; Pratt *et al.*, 2007), particularly in gymnosperm xylem, where the tracheids perform both mechanical support and sap transport functions, and up to 90% of the cross-sectional area may consist of conduit lumens (Domec & Gartner, 2002; Pittermann *et al.*, 2006). By contrast, conduit lumens comprise only *c.* 14% of xylem cross-section in self-supporting angiosperm stems,

although the fraction may be larger in roots (Pratt *et al.*, 2007). Vessel lumen fraction varies nearly orthogonally to stem wood density in angiosperms (Zanne *et al.*, 2010; Gleason *et al.*, 2012; Ziemińska *et al.*, 2013). Furthermore, mechanical safety manifests at the level of whole plants and involves many traits beyond the xylem and in many cases neither mechanical safety nor damage by wind correlate with wood density (Gleason *et al.*, 2008; Butler *et al.*, 2011). Thus, species with low-density xylem are *not* inherently less mechanically stable than species with high wood density. Considering that the mechanical stability of *angiosperms* is largely decoupled from wood density, vessel lumen fraction, and therefore hydraulic efficiency, we should not expect a strong tradeoff between hydraulic efficiency and mechanical safety across angiosperm species.

Conclusion

Species have not achieved high values of both efficiency and safety in stem xylem, as indicated by the vacant area at upper right in the safety–efficiency trait space (Fig. 2). However, when neither of these traits is near their maximum value, it appears that they vary widely and near-independently of one another. This suggests that the xylem safety–efficiency tradeoff, although holding great appeal, may not have contributed to the divergence of species to the extent previously thought. This is not to say that safety–efficiency tradeoffs do not exist within the xylem. For example, increasing the efficiency through individual interconduit pit membrane-pores will likely reduce safety against air-seeding at the level of the pit membrane (Sperry *et al.*, 2003; Choat *et al.*, 2008), but see Schenk *et al.* (2015). However, this tradeoff with safety may be avoided if other sources of efficiency are under selection. We suggest that understanding these sources of efficiency and their specific tradeoffs with safety, as well as other functional traits, is necessary to understand hydraulic strategies.

Clearly, the fitness of individual species reflects whole-plant hydraulic function, not only xylem function. The effects of climate and habitat on the whole plant may alter the relative favourability of either increased efficiency or safety along the tradeoff, but they would not necessarily obviate a tradeoff that arose from the design properties of the xylem tissue itself. Assuming that there is no arrangement of xylem anatomy that would allow for orthogonal variation in safety and efficiency, we might expect the tradeoff between efficiency and safety to be ineluctable, regardless of the plant or habitat conditions existing beyond the xylem. However, the existing data clearly do not support this idea. The considerable number of species with both low efficiency and low safety, and their broad distribution across habitats, poses a substantial research question. We suggest that efforts to address this question will require a stronger understanding of xylem efficiency – its costs, risks and relationships with other aspects of xylem functioning, for example, hydraulic safety, storage or biomechanics. We should seek to identify specific tradeoffs arising from the structure of pits (membrane thickness, size, quantity), conduit lumens (size, diameter), as well interconduit connectivity and grouping. Computer models, biological systems (e.g. hybrids, mutant lines, knockouts), comparative

physiology and advanced imaging methods (e.g. high-resolution computed tomography, magnetic resonance imaging) could all be used effectively towards this goal.

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Author contributions

S.M.G., M.W., S.J., B.C., U.G.H., R.B.P., R.B., T.J.B., S.J.B., K-F.C., H.C., S.D., J-C.D., Z-X.F., T.S.F., A.L.J., D.M.J., F.L., H.M., J.M-V., S.M., K.A.M., M.M., P.J.M., H.M., A.N., J.P., L.P., S.G.S., J.S.S., I.J.W. and A.E.Z. contributed data, ideas and assisted with writing the final manuscript. S.M.G. and M.W. analysed the data and wrote the first manuscript draft. S.J. and B.C. led the initial data compilation and assisted substantially with manuscript development.

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Supporting Information

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

Fig. S1 Schematic describing the calculation of standard major axis residuals (SMA).

Fig. S2 Hydraulic efficiency–safety (P_{88}) plots for angiosperm species.

Fig. S3 Hydraulic efficiency–safety (P_{88}) plots for gymnosperm species.

Fig. S4 Hydraulic efficiency–safety (P_{12}) plots for angiosperm species.

Fig. S5 Hydraulic efficiency–safety (P_{12}) plots for gymnosperm species.

Fig. S6 Comparison of ‘curve shapes’ exhibited by fitted bivariate models (i.e. P_{50} curve).

Fig. S7 Comparison of methods used for generating P_{50} data.

Table S1 Standard major axis (SMA) comparisons in the safety–efficiency relationship when safety is considered as P_{88}

Table S2 Fit statistics for linear multiple regression models when safety is considered as P_{88}

Table S3 Standard major axis (SMA) comparisons in the safety–efficiency relationship when safety is considered as P_{12}

Table S4 Fit statistics for linear multiple regression models when safety is considered as P_{12}

Table S5 Standard major axis (SMA) comparisons after omitting ‘r-shaped’ vulnerability curves

Table S6 Fit statistics for linear multiple regression models after omitting ‘r-shaped’ vulnerability curves

Notes S1 Published references from which data were extracted for analyses.

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