

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

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51 **Summary**

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

69

70 **Key words:** embolism, xylem, cavitation, hydraulic conductivity, pre-dawn water potential,
71 plant height, mean annual precipitation, mean annual temperature

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73

74 **Introduction**

75

76 Plants require water to maintain stomatal conductance and CO₂ uptake during photosynthesis.
77 Although the biological requirements for water are well-understood, the risks and tradeoffs
78 associated with water transport are less clear. Ever since the cohesion-tension theory was
79 proposed (Dixon, 1914), the risks of transporting water in a metastable state (under large
80 tension) have been appreciated. The most serious danger involves the expansion of small gas
81 bubbles (embolism) within the transpiration stream and the subsequent spread of this gas
82 across inter-conduit pits (hereafter abbreviated “pit”) (Tyree *et al.*, 1994). If most of the

83 conduits within the xylem become filled with gas, transport of water becomes limited until
84 new conduits are produced or conduits are refilled (Hacke & Sperry, 2001), although the
85 frequency and conditions of refilling remain unresolved (Cochard & Delzon, 2013; Rockwell
86 *et al.*, 2014; Trifilo *et al.*, 2014). Since plants benefit from a water transport system that is
87 both efficient and also safe from embolism, variation in both efficiency and safety are
88 expected to reflect ecological and evolutionary differences among species (Sperry, 2003;
89 Baas *et al.*, 2004).

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

100

101 **What are discernible benefits of efficiency and safety?**

102 At a given pressure gradient, higher efficiency either can deliver higher potential
103 transpiration and potential photosynthesis per unit xylem cross-section area, or else can
104 deliver the same water supply while requiring less xylem cross-section area. Supporting the
105 first possibility, efficiency has been reported as correlated with higher leaf-level
106 photosynthesis in angiosperms (Brodribb & Feild, 2000; Santiago *et al.*, 2004; Nardini &
107 Salleo, 2005; Choat *et al.*, 2011), gymnosperms (Brodribb & Feild, 2000; Hubbard *et al.*,
108 2001), and across pteridophytes, gymnosperms and angiosperms (Brodribb *et al.*, 2005).
109 Efficiency has also been found correlated with faster growth and greater leaf-area to xylem-
110 area ratio, i.e., leafier stems across angiosperm species (Tyree *et al.*, 1998; Sack *et al.*, 2003;
111 Poorter *et al.*, 2010; Gleason *et al.*, 2012). Alternatively, higher efficiency could also permit
112 lower xylem construction and maintenance costs per unit transpiration. For example,
113 efficient xylem may require less xylem tissue for a given amount of leaf area (thinner stems).
114 It is possible that differences among habitats, life histories, and plant life forms might be
115 associated with different safety-efficiency optimization strategies (Hacke *et al.*, 2010; Pratt *et*
116 *al.*, 2010; Markesteijn *et al.*, 2011; Plavcová *et al.*, 2011; Plavcová & Hacke, 2012; Pratt *et*

117 *al.*, 2012); however, even within these habitats and life forms, higher efficiency should allow
118 for less xylem cross-section area or a lower fraction of sapwood in stems.

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

125 Greater safety allows plants to operate at higher xylem tension (more negative water
126 potential) and with fewer gas obstructions within xylem conduits at a given tension. Benefits
127 of greater safety might allow plants to reduce root mass (shallower root penetration), operate
128 in soils with lower matric potential, or transpire through longer periods of the day or the year.
129 Species that must tolerate low xylem water potentials often exhibit markedly negative P_{50}
130 values (Brodribb & Hill, 1999; Choat, 2013; Urli *et al.*, 2013), although some arid-land plants
131 appear to tolerate significant losses of conductivity routinely (Jacobsen *et al.*, 2008; Hacke *et*
132 *al.*, 2009; Miranda *et al.*, 2010). These safety levels have evolved many times independently
133 in angiosperms (Maherali *et al.*, 2004; Sperry *et al.*, 2007; Hacke *et al.*, 2009), and there is
134 evidence for convergent evolution of safety in gymnosperms as well (Pittermann *et al.*,
135 2012).

136

137 **Should natural selection optimize efficiency and safety?**

138 Advantages of possessing efficient as well as safe xylem are self-evident, but the reasons why
139 these traits should trade off against one another are less clear. The tradeoff proposes that
140 xylem efficiency and safety are both direct outcomes of the characteristics of the pit
141 membranes and the nature of the connections within the xylem conduit network. For pits and
142 pit membranes, the thickness, the size of pit membrane-pores (Lens *et al.*, 2011; Lens *et al.*,
143 2013), and perhaps also the quantity of inter-conduit pits per vessel (Hargrave *et al.*, 1994),
144 are likely determinants of both safety and efficiency. A dominant hypothesis linking
145 efficiency and safety in angiosperms suggests that wider conduits (and therefore more
146 efficient conduits) tend to have more inter-conduit pits, more pit membranes, and a greater
147 chance of possessing a large membrane-pore through which air-seeding may proceed
148 (Hargrave *et al.*, 1994; Wheeler *et al.*, 2005). Xylem network traits such as lumen conduit
149 dimensions (length and diameter), the number of unique vessel connections among conduits
150 (conduit connectivity) (Carlquist, 1984; Loepfe *et al.*, 2007; Martínez-Vilalta *et al.*, 2012),

151 and the degree of conduit grouping (and therefore the number of interconduit connections)
152 (Carlquist, 1984; Lens *et al.*, 2011) are all important components of efficiency in
153 angiosperms, and could also possibly lead to decreased safety. Similarly across
154 gymnosperms, the size of the pit aperture as well as the relative sizes of the aperture and torus
155 (i.e., torus overlap) correlate with safety (Domec *et al.*, 2006; Domec *et al.*, 2008; Delzon *et*
156 *al.*, 2010; Pittermann *et al.*, 2010; Bouche *et al.*, 2014) although the relationship between
157 these traits and efficiency is less clear.

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

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

183

184 **Does the current literature support a safety-efficiency tradeoff?**

185 The largest test of this hypothesis to date reported insignificant correlation across extant
186 woody angiosperms ($r^2 = 0.03$; $P > 0.05$) and gymnosperms ($r^2 = 0.00$; $P > 0.05$) but weak
187 significant correlation when pooling both groups ($r^2 = 0.10$; $P < 0.05$) (Maherali *et al.*, 2004).
188 Interestingly in this analysis, and in other studies (Tyree *et al.*, 1994; Maherali *et al.*, 2004;
189 Westoby & Wright, 2006), many species representing a wide range in habitat and physiology
190 exhibited both low efficiency *and* low safety. The low efficiency and low safety species in
191 these studies appeared to contradict the proposition of a tradeoff between these two xylem
192 traits. Studies examining fewer species are divided, with ca 25% of studies providing support
193 for the safety-efficiency hypothesis and ca 75% not providing support, measured by linear
194 correlation between reported values of safety and efficiency. We note that the author's
195 interpretations of their own data may differ from ours, mainly due to differences in
196 correlation coefficients between data subsets (e.g., differences in site and phylogeny). For
197 this reason, we do not attempt here to categorize these individual reports as supporting or
198 refuting the tradeoff. However, it is likely that reporting a tradeoff has been encouraged by
199 the idea that a tradeoff between safety and efficiency should exist, at least at the level of the
200 inter-conduit pit membrane-pore (Sperry *et al.*, 2003). It is interesting therefore that over half
201 the studies quantifying this tradeoff in xylem have not found it. Thus, examining whether
202 efficiency and safety co-vary across a large subset of the world's plant species would provide
203 a more complete analysis of this tradeoff than is feasible within any single study.

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

217

218

219 Materials and Methods

220

221 **The dataset**

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

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

249 Climate data were taken from the original reports, where available, and otherwise
250 extracted from the Worldclim (elevation, temperature, precipitation) and the Climatic
251 Research Unit (number freezing days) databases (New *et al.*, 1999; Hijmans *et al.*, 2005).

252 When elevation data from the Worldclim database did not match elevations from published
253 reports, temperature was scaled to match published elevations using a lapse rate of $6.0\text{ }^{\circ}\text{C km}^{-1}$
254 increase in elevation.

255

256 **Analyses**

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

272 It is not well understood how P_X relates to irreversible damage and mortality across
273 species. As such, “safety” is a rather subjective concept. Although P_{50} relates to the steepest
274 part of the vulnerability curve, different points on the curve may reflect different aspects of
275 the dehydration process. The initial decline in maximal conductivity (P_{12}) relates to the air-
276 entry tension and is likely coordinated with decreasing stomatal conductance and increasing
277 hydraulic capacitance, i.e., accessible water stored in tissue outside the conduits (Kavanagh *et al.*,
278 1999; Domec & Gartner, 2001). At the other end of the range, P_{88} occurs at tensions well
279 beyond stomatal closure and likely relates to irreversible damage to the stem or root xylem
280 (Blackman *et al.*, 2009; Brodribb *et al.*, 2010; Urli *et al.*, 2013). Because the different
281 physiological processes conferring growth and fitness (such as stomatal conductance,
282 capacitance, embolism refilling) operate across different water potential ranges, it is
283 important to consider other definitions of hydraulic safety. With this in mind, we assessed
284 the K_S - P_X relationship at three points across each species’ vulnerability curve – at P_{12} , P_{50} ,
285 and P_{88} (Supporting Information Tables S1, S2, S3, S4, Figs S2, S3, S4, S5).

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

294 In addition to investigating whether third variables modified the safety-efficiency
295 relationship, we also wished to know whether or not these variables were more significantly
296 aligned with either the safety or efficiency axis. To do this, we fit an ordinary least squares
297 model, with the third variable set as the dependent variable and safety and efficiency as
298 predictor variables. To determine r^2 estimates for this analysis, we decomposed the r^2 value
299 into proportions of variation explained by efficiency or safety using the method proposed by
300 Lindberg, Merenda and Gold (1980), as implemented in the “relaimpo” package (“lmg”
301 function) for R (Grömping, 2006). This method uses an averaging technique to calculate
302 relative importance components for predictor variables that are insensitive to their ordering in
303 the model and uses a boot-strapping routine to generate confidence intervals.

304

305 **Comparing methods**

306 Hydraulic safety data were included in the analyses regardless of the methods employed to
307 build vulnerability curves. We note that some work has questioned the validity of
308 angiosperm safety data obtained by centrifuge-spinning short xylem segments for species
309 with relatively long vessels (Cochard *et al.*, 2013; Martin-StPaul *et al.*, 2014). Data obtained
310 via air-injection have also been disputed (Torres-Ruiz *et al.*, 2014). It is suggested that the
311 centrifuge technique may incur an “open vessel” artefact, resulting in an exponential “r-
312 shaped” curve. However, others have found no evidence for a long vessel artefact and have
313 found that r-shaped curves are valid when the standard centrifuge technique has been used
314 (Jacobsen & Pratt, 2012; Sperry *et al.*, 2012; Tobin *et al.*, 2013; Hacke *et al.*, 2015). Since
315 this appears to be a potentially important, but unresolved issue, all angiosperm analyses were
316 run a second time excluding all r-shaped vulnerability curves regardless of the technique
317 used. We have included the statistical results for all $K_S \sim P_{50}$ analyses using the reduced
318 dataset (Supporting Information Tables S5 & S6), but note that results from both analyses are
319 similar.

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

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

337

338

339 Results

340

341 **Is there evidence for a safety-efficiency tradeoff?**

342 Regardless of what definition of safety was used (P_{12} , P_{50} , P_{88}) several common results
343 emerged from the data. Most safety-efficiency plots exhibited an empty quadrant in the
344 upper right-hand corner (Figs 2, 3, 4, S2, S3, S4, and S5), confirming that species have not
345 been able to achieve both high efficiency and high safety (feature 1 in Fig. 1). On the other
346 hand, many species were found in the lower left quadrant of the safety-efficiency plots
347 (feature 2 in Fig. 1). The strength of the safety-efficiency tradeoff on log-transformed data
348 was generally significant but weak (without meaningful predictive power) and differed
349 slightly among the three definitions of safety. Angiosperm r^2 values ranged from 0.053 (P_{50})
350 to 0.075 (P_{12}) and gymnosperm r^2 values ranged from 0.004 (P_{88}) to 0.086 (P_{50}) (Tables 1,
351 S1, S3). Tradeoffs (P_{50}) were also similarly weak among evergreen ($r^2 = 0.023$; $P = 0.035$),
352 winter deciduous ($r^2 = 0.031$; $P = 0.086$), and drought deciduous ($r^2 = 0.014$; $P = 0.428$)
353 angiosperms (Table 1).

354

355 **Is there evidence for clade-specific safety-efficiency tradeoffs?**

356 Within particular clades (Fig. 3b, c for angiosperms, Fig. 4a-c for gymnosperms) there
357 appeared in some instances to be a clear safety-efficiency tradeoff. Considering all
358 definitions of safety, within the families Anacardiaceae, Asteraceae, Cupressaceae,
359 Euphorbiaceae, and Sapindaceae negative correlation accounted for 38-46% of variation
360 (Table 1), although the strength of within-family relationships did vary among definitions of
361 safety (Tables 1, S1, S3). In other clades there was weak or no correlation, and among
362 *Ericaceae* there was a clear *positive* relationship between safety (P_{50} & P_{88}) and efficiency
363 (Tables 1, S1).

364

365 **Is the safety-efficiency tradeoff altered by other plant or climate variables?**

366 Considering safety defined as P_{50} , wood density explained a small but significant amount of
367 residual variation in the safety-efficiency relationship across angiosperm species ($r^2 = 0.02$; P
368 $= 0.049$) (Table 2, Fig. 3d). Angiosperms with high density xylem tended weakly to be
369 positioned away from the tradeoff diagonal and towards the origin (intersection of the x and y
370 axes). Leaf-area to sapwood-area ratio explained a significant amount of residual variation
371 across gymnosperm species ($r^2 = 0.21$; $P = 0.021$) (Table 2, Fig. 4d), although with only 24
372 species in this analysis, this result should not be over-interpreted.

373 Results differed depending on the definition of safety considered. For angiosperms,
374 safety-efficiency relationships using P_{50} and P_{88} were similar, with most third variables
375 explaining only markedly small amounts of residual variation (0 – 4%), suggesting that the
376 relationship between safety and efficiency was not modified meaningfully by precipitation
377 nor by differences in plant structure (Tables 2 & S2, Figs 3 & S2). However, when safety
378 was defined as P_{12} , these results changed somewhat. In particular, wood density explained
379 12% of the residual variation across angiosperms, and leaf-area to sapwood-area, maximum
380 height, and mean annual precipitation also explained small (< 7%) but significant percentages
381 of residual variation (Supporting Information Table S4, Fig. S4). As such, short stature
382 species with high wood density, low leaf-area to sapwood-area ratios, and in drier locations
383 tended to be located slightly away from the diagonal, towards the origin.

384 Mean annual temperature and number of freezing days explained no residual variation
385 for angiosperms or gymnosperms when safety was defined as P_{50} (Table 2). However, when
386 considering safety as P_{88} , mean annual temperature and number of freezing days explained
387 3.4% and 7.7% of the residual variation in the efficiency~safety relationship (Supporting

388 Information Table S2). Species living in colder climates tended to be located away from the
389 efficiency~safety trendline, slightly towards the low efficiency and low safety quadrant. This
390 result was similar even after removing drought and winter deciduous species, which avoid
391 functioning during unfavourable seasons. Interestingly, number of freezing days was weakly
392 correlated with efficiency across all angiosperms ($r^2 = 0.056$; $P < 0.001$), but this correlation
393 strengthened markedly after removing deciduous species from the analysis ($r^2 = 0.199$; $P <$
394 0.001). In contrast, neither mean annual temperature nor number of freezing days were
395 correlated with efficiency across gymnosperm species.

396

397 **Is a safety-efficiency tradeoff confounded by experimental methods?**

398 Comparison of methods did not reveal any differences that were likely to have modified the
399 relationship between safety and efficiency (Supporting Information Figs S6 & S7). Neither
400 the Cavitron method (Cochard, 2002) nor the effect of not ‘flushing’ xylem prior to
401 measuring maximal conductivity could be evaluated because hydraulically weighted
402 diameters were generally not reported in these publications. However, conductivity loss
403 curves that exhibited an exponential shape, as well as data obtained using air injection
404 methods, had *lower* efficiency values at a given hydraulically weighted vessel diameter than
405 curves of different shape or data obtained via other methods (Supporting Information Figs S6
406 & S7). Nevertheless, these differences in efficiency were small relative to the shift away
407 from the expected tradeoff space observed in the safety-efficiency plot (feature 3 in Fig. 1).
408 They are not likely to have been responsible for the large number of species with low
409 efficiency and low safety in the lower left-hand corner of Fig. 2.

410

411

412 Discussion

413

414 **Is there a safety-efficiency tradeoff across woody species?**

415 It seems clear that high safety together with high efficiency has not evolved in stem xylem
416 (feature 1 in Fig. 1). This strongly suggests that the combination may not be achievable, and
417 to that extent a tradeoff may exist. On the other hand, many species seem to have low
418 efficiency together with low safety, which cannot be understood by reference to a tradeoff.
419 Furthermore, the distance species lie away from the hypothesized “tradeoff zone” was not
420 strongly correlated with any of the other traits or climate variables examined in this study,

421 suggesting that these variables cannot explain why so many species have xylem with low
422 efficiency and low safety (feature 2 in Fig. 1).

423 Two main questions arise from these results. Firstly, what are the wood anatomical
424 features that permit safety to vary so widely at a given level of efficiency (as in Fig. 2), and
425 vice versa, efficiency to vary widely at a given level of safety? Total xylem efficiency may
426 result from different anatomical features in different species (e.g. inter-conduit pit membrane-
427 pore size, inter-conduit pit membrane area per conduit, conduit diameter/length, conduit
428 connectivity, sapwood area) and each of these features may have separate and different
429 effects on safety as has been suggested for *Sequoia sempervirens* (Burgess *et al.*, 2006) and
430 across *Acer* species (Lens *et al.*, 2011). Similarly, different anatomical features could confer
431 different levels of safety, although these mechanisms remain largely unstudied except for air-
432 seeding through pores in pit membranes (Cochard, 2006; Jansen *et al.*, 2009; Lens *et al.*,
433 2011; Brodersen *et al.*, 2015). The second question that arises from these results is, why
434 should any particular anatomical arrangement of the xylem result in both low efficiency and
435 low safety? Given that efficiency should nearly always enhance fitness (result in higher rates
436 of gas exchange or lower xylem construction and maintenance costs), the presence of so
437 many species that have both low efficiency and low safety suggests that the anatomical basis
438 for high efficiency may be trading off with important traits other than safety. We note that
439 this observation holds whether we consider all species in the dataset or omit those exhibiting
440 r-shaped vulnerability curves. Considering that such a large portion of the world's woody
441 species are achieving neither high efficiency nor high safety, these unidentified traits have
442 likely confounded our understanding of plant strategies, and as such, represent a very
443 significant research question.

444

445 **Why might we not expect a safety-efficiency tradeoff?**

446 *Different sources of xylem efficiency*

447 Differences in xylem efficiency may arise through many mechanisms: 1) conduit dimensions
448 (Hacke *et al.*, 2006; Sperry *et al.*, 2006), 2) conduit lumen fraction or the fraction of cross-
449 section area that is composed of conduit lumens, independent of vessel width (McCulloh *et*
450 *al.*, 2010; Zanne *et al.*, 2010), 3) changes in inter-conduit pit and pit membrane ultrastructure
451 (Choat *et al.*, 2008; Lens *et al.*, 2011; Brodersen *et al.*, 2015), 4) differences in perforations
452 between angiosperm vessel elements (Sperry *et al.*, 2005; Christman & Sperry, 2010), 5)
453 non-conductive vs conductive ground-tissue, i.e., hydraulically functional tracheids or
454 vasicentric tracheids (Sano *et al.*, 2011), 6) conduit connectivity and “network” efficiency

455 (Loepfe *et al.*, 2007; Martínez-Vilalta *et al.*, 2012), and 7) ion-mediated changes in the pit
456 membrane ultrastructure that modify efficiency (Zwieniecki *et al.*, 2001; Nardini *et al.*,
457 2011).

458 Importantly, we should not expect that efficiency improvements via each of these
459 components to result in reduced safety. For example, the direct effects of increasing
460 efficiency via conduit dimensions (Tyree *et al.*, 1994), conductive ground-tissue (Sano *et al.*,
461 2011), or ion-mediated physiology (Tyree *et al.*, 1994; Sperry *et al.*, 2006; Cochard *et al.*,
462 2010) appear to have near-negligible effects on xylem safety (at least in the case of drought),
463 whereas changes in efficiency associated with pit and membrane ultrastructure are likely to
464 have a strong influence on xylem safety (Pickard, 1981; Zimmermann, 1983; Wheeler *et al.*,
465 2005; Jansen *et al.*, 2009; Lens *et al.*, 2011; Brodersen *et al.*, 2015). Thus, unless natural
466 selection acts on only one source of efficiency (e.g., pit membrane-pore size), or acts on all
467 sources similarly in all cases, we might not expect a strong safety-efficiency tradeoff across
468 species. Assuming closely related species have more similar xylem anatomy than distantly
469 related species, we might expect stronger negative correlation between safety and efficiency
470 within families, especially those spanning a large range in habitat aridity. This was partially
471 supported by the analyses, with Asteraceae, Euphorbiaceae, Sapindaceae, and Cupressaceae
472 all showing significant negative correlation, and all spanning a large range in mean annual
473 precipitation.

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

484

485 *Climate and ecophysiology*

486 Plant structure and climate appeared to have a moderate influence on the hypothesised safety-
487 efficiency tradeoff. Considering each separately, wood density, leaf-area to sapwood-area,
488 plant height, mean annual precipitation, mean annual temperature, and number of freezing

489 days explain at most 12% of the residual variation in the efficiency~safety relationship.
490 Species from cold climates did have reduced efficiency at a given level of safety, but only
491 among angiosperms and when defining safety as P_{88} or P_{12} . The analyses also show that the
492 shift in cold-habitat species occurred more strongly on the efficiency axis than the safety axis,
493 with clear correlations between number of freezing days and efficiency (wider conduits) in
494 most cases (Table 2, S2, S4). This is in line with our present understanding of freeze-thaw
495 embolism. According to the “thaw expansion hypothesis” (e.g., Ewers, 1985; Hacke &
496 Sperry, 2001; Pittermann & Sperry, 2003; Mayr & Sperry, 2010), gas bubbles formed in
497 conduits on freezing expand on thawing when xylem tension is high. Small conduits contain
498 less air and therefore result in smaller bubbles, which increases safety (Pittermann & Sperry,
499 2006). Similarly, air-seeding processes, similar to drought-induced cavitation, likely occur
500 during freezing and may be exacerbated by lower temperature (Charrier *et al.*, 2014) as well
501 as more frequent frost cycles (Mayr *et al.*, 2007). Our data are in rough agreement with this
502 theory and further suggests that high efficiency via larger conduits may not be possible for
503 many species in cold habitats.

504 Similarly, species may not require high safety. It has been suggested that effective
505 regulation at the stomata may reduce the need for high safety even in dry habitats, i.e., if
506 plants avoid damaging tensions (Skelton *et al.*, 2015). We suggest that even plants in arid
507 habitats experience water loss after stomatal closure (Borchert & Pockman, 2005; Brodribb *et al.*
508 *et al.*, 2014; Gleason *et al.*, 2014) and xylem tension will eventually increase to critical levels
509 during prolonged periods of water stress. Also, if safety is indeed not required, then natural
510 selection should then favour higher efficiency to save xylem construction and maintenance
511 costs. Similar arguments can be made for plant strategies that avoid embolism (e.g.,
512 capacitance), strategies that repair embolized conduits or produce new conduits quickly, e.g.,
513 post-disturbance resprouters or recovery via secondary growth (Brodribb *et al.*, 2010; Pratt *et al.*
514 *et al.*, 2010; Pratt *et al.*, 2012), as well as strategies that allow for surplus or redundant
515 efficiency (Ewers *et al.*, 2007), as has been proposed for leaves (Wagner, 1979; Sack *et al.*,
516 2008) and other biological networks (Tononi *et al.*, 1999). Clearly, all these differences in
517 habitat, physiology, and life history are good reasons why plants may not *need* high
518 efficiency or high safety. However, this does diminish one of the important benefits of
519 efficiency – efficient xylem can transport the same volume of water as inefficient xylem, but
520 do so with a smaller cross-section of living wood. As such, these reasons do not address why
521 natural selection does not increase efficiency to the extent possible in all cases, unless high
522 efficiency comes with costs or risks that are not yet understood.

523

524 *The need for mechanical safety*

525 It has been suggested that hydraulic efficiency may trade off against mechanical safety (Long
526 *et al.*, 1981; Wagner *et al.*, 1998; Niklas & Spatz, 2004; Pratt *et al.*, 2007), particularly in
527 gymnosperm xylem, where the tracheids perform both mechanical support and sap transport
528 functions, and up to 90% of the cross-sectional area may consist of conduit lumens (Domec
529 & Gartner, 2002; Pittermann *et al.*, 2006). In contrast, conduit lumens comprise only ca 14%
530 of xylem cross-section in self-supporting angiosperm stems, though the fraction may be
531 larger in roots (Pratt *et al.*, 2007). Vessel lumen fraction varies nearly orthogonally to stem
532 wood density in angiosperms (Zanne *et al.*, 2010; Gleason *et al.*, 2012; Ziemińska *et al.*,
533 2013). Furthermore, mechanical safety manifests at the level of whole-plants and involves
534 many traits beyond the xylem and in many cases neither mechanical safety nor damage by
535 wind correlate with wood density (Gleason *et al.*, 2008; Butler *et al.*, 2011). Thus, species
536 with low density xylem are *not* inherently less mechanically stable than species with high
537 wood density. Considering that the mechanical stability of *angiosperms* is largely decoupled
538 from wood density, vessel lumen fraction, and therefore hydraulic efficiency, we should not
539 expect a strong tradeoff between hydraulic efficiency and mechanical safety across
540 angiosperm species.

541

542 **Conclusion**

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

555 Clearly, the fitness of individual species reflects whole-plant hydraulic function, not
556 only xylem function. The effects of climate and habitat on the whole-plant may alter the

557 relative favourability of either increased efficiency or safety along the trade-off, but they
558 would not necessarily obviate a trade-off that arose from the design properties of the xylem
559 tissue itself. Assuming that there is no arrangement of xylem anatomy that would allow for
560 orthogonal variation in safety and efficiency, we might expect the tradeoff between efficiency
561 and safety to be ineluctable, regardless of the plant or habitat conditions existing beyond the
562 xylem. However, the existing data clearly do not support this idea. The considerable number
563 of species with both low efficiency and low safety, and their broad distribution across
564 habitats, poses a substantial research question. We suggest that efforts to address this
565 question will require a stronger understanding of xylem efficiency – its costs, risks, and
566 relationships with other aspects of xylem functioning, e.g., hydraulic safety, storage,
567 biomechanics. We should seek to identify specific tradeoffs arising from the structure of pits
568 (membrane thickness, size, quantity), conduit lumens (size, diameter), as well interconduit
569 connectivity and grouping. Computer models, biological systems (e.g., hybrids, mutant lines,
570 knockouts), comparative physiology, and advanced imaging methods (e.g., high-resolution
571 computed tomography, magnetic resonance imaging) could all be used effectively towards
572 this goal.

573

574

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576

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581

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875 **Supporting Information**

876

877 Data References. Published references from which data were extracted for analyses.

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

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

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

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

884 Table S5 Standard major axis (SMA) comparisons after omitting “r-shaped” vulnerability
885 curves.

886 Table S6 Fit statistics for linear multiple regression models after omitting “r-shaped”
887 vulnerability curves.

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

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

- 890 Fig. S3 Hydraulic efficiency-safety (P_{88}) plots for gymnosperm species.
891 Fig. S4 Hydraulic efficiency-safety (P_{12}) plots for angiosperm species.
892 Fig. S5 Hydraulic efficiency-safety (P_{12}) plots for gymnosperm species.
893 Fig. S6 Comparison of ‘curve shapes’ exhibited by fitted bivariate models (i.e., P_{50} curve).
894 Fig. S7 Comparison of methods used for generating P_{50} data.
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896 **Table 1.** Standard major axis (SMA) efficiency~safety models fit to individual angiosperm
 897 and gymnosperm groups.

899	Angiosperms	r^2	slope	intercept	P	df
901	All angiosperm species	0.053	-1.65	0.65	<0.001	333
903	Phenology					
904	evergreen	0.023	-1.92	0.81	0.035	189
905	winter deciduous	0.031	-1.35	0.56	0.086	94
906	drought deciduous	0.014	-1.89	0.58	0.428	46
908	Families					
909	Anacardiaceae	0.375	-2.69	1.03	0.034	10
910	Asteraceae	0.463	-0.90	0.18	0.011	11
911	Boraginaceae	0.056	-2.79	1.44	0.539	7
912	Ericaceae	0.463	2.12	-1.39	0.015	10
913	Euphorbiaceae	0.377	-1.92	0.62	0.004	18
914	Fabaceae	0.028	-1.21	0.54	0.420	23
915	Fagaceae	0.092	-1.00	0.47	0.170	20
916	Proteaceae	0.132	-1.38	0.52	0.271	9
917	Rhamnaceae	0.028	-1.23	1.02	0.622	9
918	Rosaceae	0.066	-2.26	1.73	0.262	19
919	Sapindaceae	0.375	-3.04	1.38	0.045	9
921	Genera					
922	<i>Acer</i>	0.429	-3.36	1.58	0.040	8
923	<i>Ceanothus</i>	0.024	-1.19	1.00	0.740	5
924	<i>Cordia</i>	0.010	2.46	-0.23	0.812	6
925	<i>Quercus</i>	0.145	-0.88	0.37	0.119	16

	r^2	slope	intercept	P	df
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 with bold text.

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

962		r^2_{P50}	r^2_{Ks}	r^2_{resid}	df
964	<hr/>				
965	Angiosperms				
966					
967	Wood density	0.060**	0.189***	0.020*	194
968	Leaf-area to sapwood-area	0.056**	0.188***	0.020	160
969	Maximum height	0.049*	0.165***	0.019	128
970	Pre-dawn water potential	0.236***	0.184***	0.002	118
971	Mean annual precipitation	0.029*	0.106***	0.003	307
972	Mean annual temperature	0.063***	0.020	0.006	307
973	Number of freezing days	0.003	0.032**	0.002	227
974					
975	Gymnosperms				
976					
977	Wood density	0.133**	0.196***	0.004	67
978	Leaf-area to sapwood-area	0.008	0.485***	0.209*	22
979	Maximum height	0.042	0.147**	0.017	62
980	Pre-dawn water potential	0.249	0.629**	0.065	7
981	Mean annual precipitation	0.044	0.078	0.009	51
982	Mean annual temperature	0.016	0.002	0.013	51
983	Number of freezing days	0.001	0.013	0.000	51
984	<hr/>				

985
 986 Safety is defined as the xylem water potential at which maximal conductivity declines by
 987 50%. Coefficient of determination values represent the proportion of total variation in the
 988 third variable explained by hydraulic safety (r^2_{P50}) and hydraulic efficiency (r^2_{Ks}). The
 989 percent residual variation in the safety-efficiency fit (orthogonal variation, i.e., standard
 990 major axis residuals) that is explained by the third variable (r^2_{resid}) is also reported and
 991 indicates whether the third variable is a meaningful predictor of where species are located
 992 away from the safety-efficiency trend-line. Asterisks indicate levels of significance (* =
 993 0.05, ** = 0.01, *** = 0.001).

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 999

1000 Figure legends

1001

1002 **Fig. 1.** Schematic explaining three hypothetical features that might be expected in a tradeoff
1003 between hydraulic safety and hydraulic efficiency in xylem. (1) Upper right quadrant not
1004 occupied because both high safety and high efficiency cannot be achieved in the same
1005 species. (2) Natural selection is expected to drive species upwards and rightwards because
1006 efficiency and safety are advantageous (taken in isolation). This should result in negative
1007 cross-species correlation between safety and efficiency, and (3) an empty zone in the lower
1008 left quadrant.

1009

1010 **Fig. 2.** Hydraulic safety-efficiency (P_{50}) plots for all angiosperm and gymnosperm species.
1011 Inset plots have been drawn to show log-transformed relationships.

1012

1013 **Fig. 3.** Hydraulic safety-efficiency (P_{50}) plots for angiosperm species. Axes have been log10
1014 scaled. Different colours represent different leaf habits (panel a), taxonomic groups (panels
1015 b, c), plant structural traits (panels d, e, f), and site factors (g, h, i). Continuous variables
1016 were binned in roughly equal groups of four, with bin ranges denoted in the legends.

1017

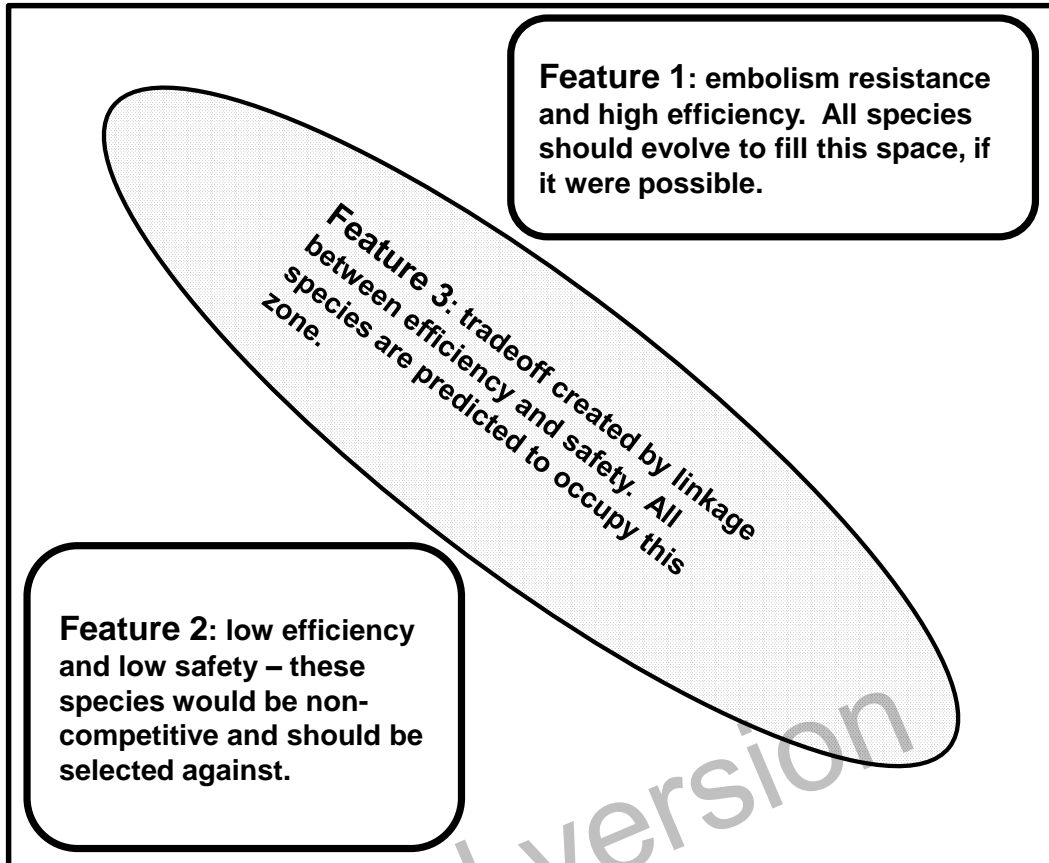
1018 **Fig. 4.** Hydraulic safety-efficiency (P_{50}) plots for gymnosperm species. Axes have been
1019 log10 scaled. Different colours represent different taxonomic groups (panels a, b, c), plant
1020 structural traits (panels d, e, f), and site factors (g, h, i). Continuous variables were binned in
1021 roughly equal groups of four, with bin ranges denoted in the legends.

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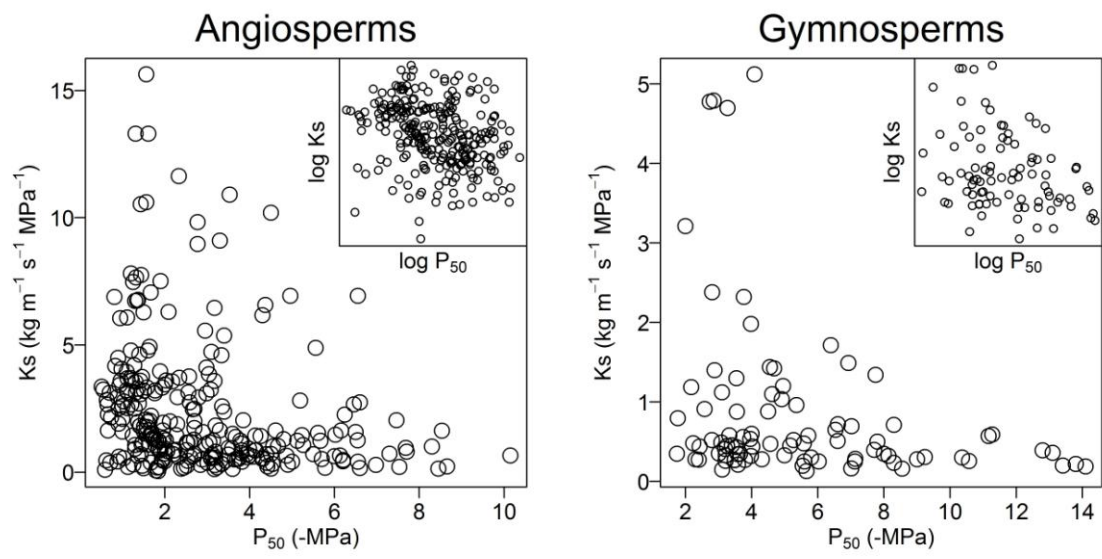
Fig. 1

Efficiency: maximal xylem-specific conductivity (K_s , $\text{kg m}^{-1} \text{sec}^{-1} \text{Mpa}^{-1}$)



Safety: embolism resistance (P_{50} , -MPa)

Fig. 2



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Fig. 3

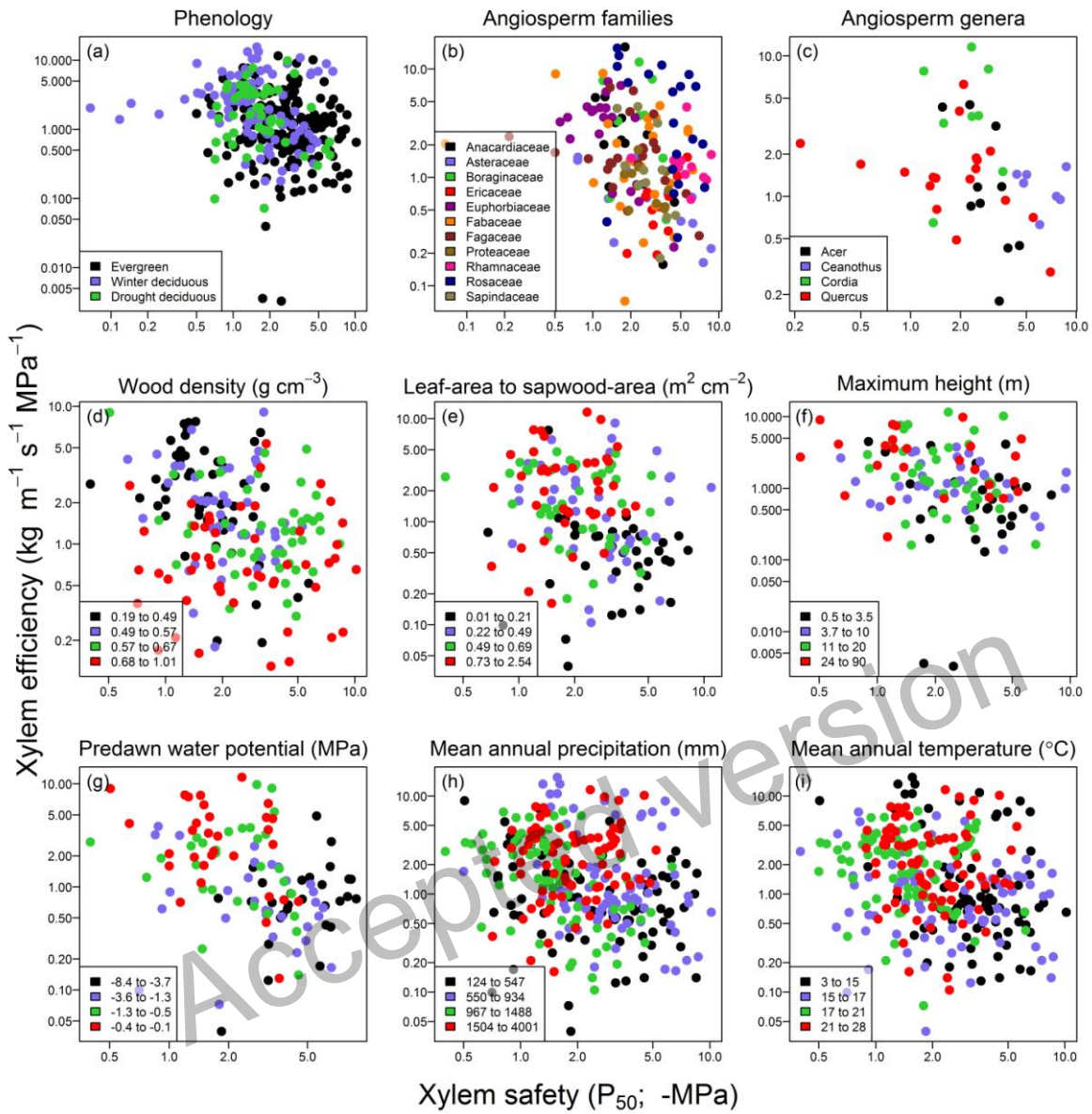
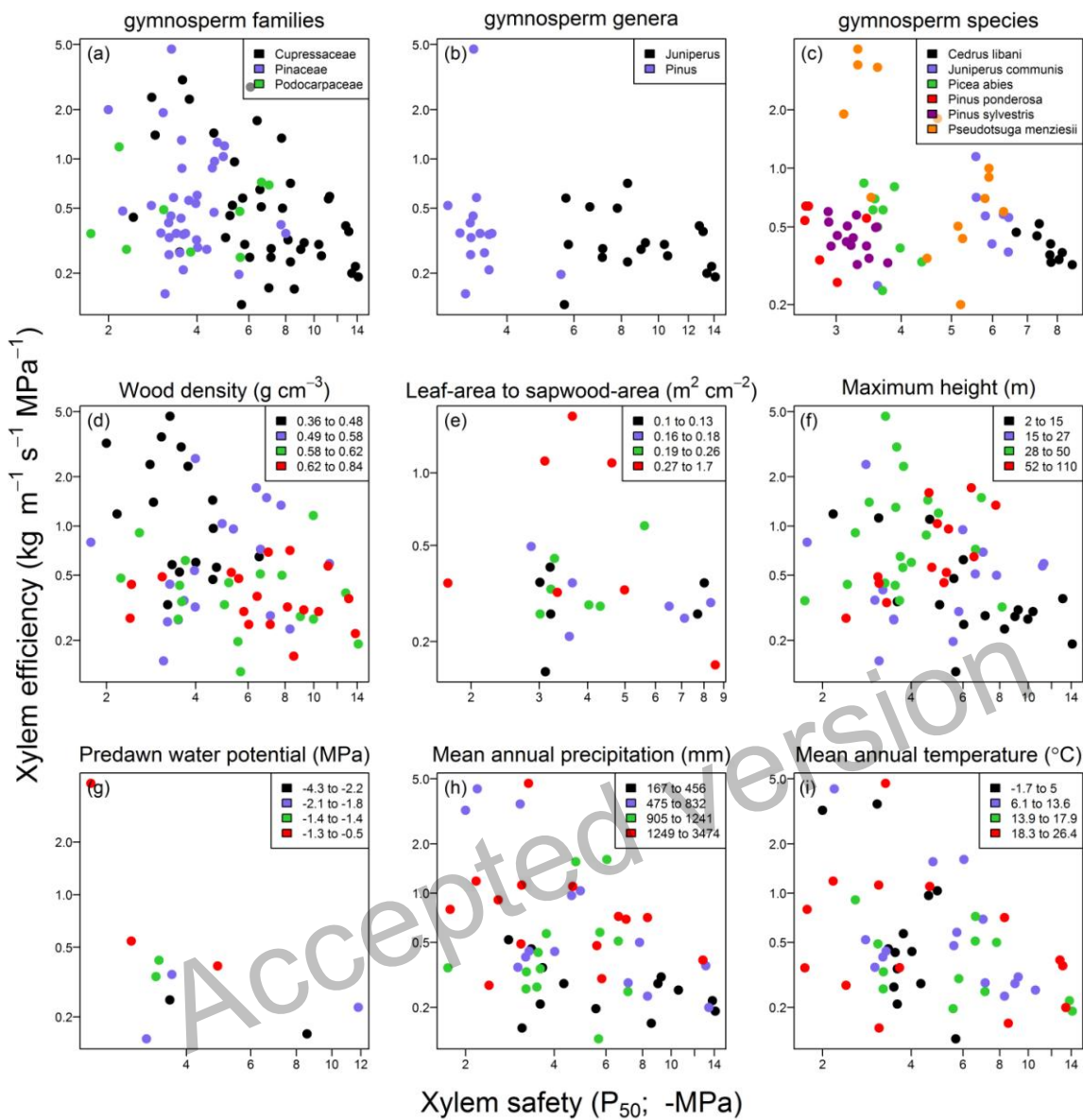


Fig. 4



This is the accepted version of the following article: Gleason, Sean M. et al. "Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species" in New phytologist (Ed. Wiley), vol. 209, issue 1 (Jan. 2016), p. 123-136, which has been published in final form at DOI 10.1111/nph.13646. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving