# Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms

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## Summary

• Wood density and vessel characteristics are functionally interrelated, yet they may have distinct ecological associations.

• In a comparative study of 51 angiosperm species ranging from chaparral shrubs to riparian trees, we examined relationships among wood density and vessel traits and their ecological correlates.

• Mean vessel lumen area and vessel density (number $mm^{-2}$) varied widely (7- to 10-fold). In multivariate analyses, both vessel traits were negatively correlated with wood density, which varied more narrowly (< 2-fold). Vessel density and lumen area were inversely related across species, allowing a broad range of vessel traits within a narrow range of wood density. Phylogenetic independent contrasts indicated correlated inverse evolutionary change in vessel traits.

• Each trait had a distinct pattern of ecological correlation – wood density was most strongly associated with soil water, and vessel traits showed contrasting relationships with plant height. Within a narrow range of wood density, there was significant variation in vessel traits. Given their particular ecological associations, the results suggest that wood density and vessel traits describe two distinct ecological axes.

**Key words:** height, phylogenetic independent contrasts, phylogenetic signal, soil moisture, trait correlations, water potential, wood density, vessels.

## Introduction

Wood density is centrally important to the ecology of woody plants as it reflects carbon allocation to structural support, which in turn is the foundation for variation in several life history traits. Across a range of species, wood density is negatively associated with growth rate (Enquist *et al.*, 1999; Muller-Landau, 2004; Wikberg & Ögren, 2004; King *et al.*, 2005), and accordingly, species with denser wood tend to occur later in succession (ter Steege & Hammond, 2001; Falster & Westoby, 2005) and lower in the canopy (Worbes *et al.*, 2003; Falster & Westoby, 2005). Wood density also affects survivorship when it increases resistance to pathogens (Augspurger & Kelly, 1984) or to drought-induced xylem cavitation (Hacke *et al.*, 2001; Jacobsen *et al.*, 2005).

In vessel-bearing angiosperms, wood density is a complex trait, encompassing properties of the vessels and the matrix of fibers and other cell types surrounding them. The influence of vessels on density can be decomposed into two components – vessel area (the transverse lumen area of individual vessels) and vessel density (number of vessels per transverse area) – each with its own set of functional consequences and ecological correlates. Vessel lumen area strongly affects sapwood-specific conductivity, the capacity of wood to conduct water (Zimmermann, 1983). Wider vessels are also generally more vulnerable to cavitation as stems freeze and thaw, particularly when xylem water is under tension (Davis *et al.*, 1999). By contrast, the number of vessels in a given transverse area should have a relatively small effect on sapwood conductance. The significance of vessel density may instead lie in its

relationship to the interconnectedness of the vascular system within a stem (A. Zanne, unpublished data; Macquarie University, North Ryde, NSW, Australia). Specifically, closely spaced vessels may enhance conductivity when water is available but increase the spread of embolism when cavitation occurs (Carlquist & Hoekman, 1985; Hacke & Sperry, 2001). Moreover, vessel density directly influences bulk xylem composition, which affects both its strength and its resistance to vessel implosion under negative pressure (Jacobsen *et al.*, 2005).

These component traits, vessel area and vessel density, contribute to wood density in parallel by affecting the amount of lumen space in the wood. We might therefore expect both traits to vary inversely with wood density. However, on biophysical and functional grounds, these two variables should also be negatively associated with each other. Wood composed of closely spaced large vessels will have low density with high hydraulic conductivity (Fig. 1, upper right). In the extreme, such wood will likely be too weak to support most plants (Niklas, 1994; Jacobsen *et al.*, 2005). In contrast, wood that is composed of small vessels spaced widely within a fiber matrix will be very dense with low hydraulic conductivity (Fig. 1, lower left). At this extreme, an unsustainably large allocation of carbon to sapwood would be required to meet the hydraulic demands of the shoot (Taneda & Tateno, 2004). The alternative combinations – small, densely packed vessels and large, widely spaced vessels – do not appear so constrained.

Between extremes lies a band of operational wood density, where the same value of density can result from various combinations of vessel lumen area and vessel density (Fig. 1).
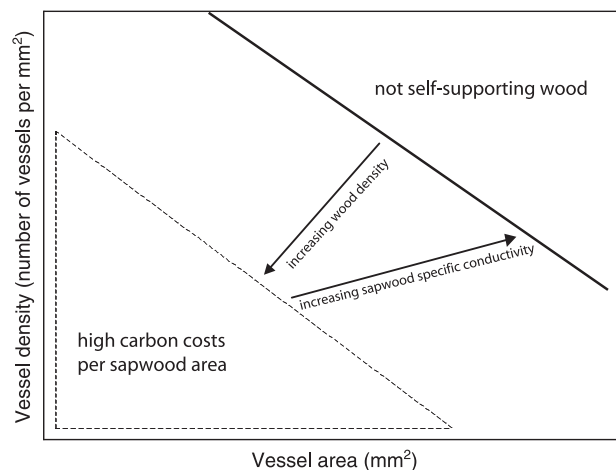


**Fig. 1** Predicted relationships among vessel traits and wood density. Wood density is a function of both vessel lumen area and the number of vessels for a given transverse area. Wood density should be low when both vessel area and density are high, whereas wood density should be high when both vessel lumen area and density are low. In theory, functional considerations should preclude very low wood density, whereas carbon costs should limit investment in high-density wood. Because sapwood conductivity increases exponentially with vessel area, the vector of increasing conductivity is not parallel to the wood density vector.

The interplay of vessel traits in determining wood density introduces a degree of independence between any pair of these traits as long as the third trait is allowed to vary. The ecology of a species will therefore reflect the influence of wood density itself and also the distinct consequences of its component vessel traits. In this light, it is especially instructive to decompose variation in wood density into its component parts and examine their ecological correlates.

Consistent with functional predictions, several ecological patterns have been observed. High wood density is characteristic of slowly growing species, such as those found in the understory (Falster & Westoby, 2005), in dry soils (Hacke & Sperry, 2001; Ackerly, 2004a), or in nutrient-poor soils (Muller-Landau, 2004) and those with more shrub-like growth forms (Ackerly, 2004a). Theory predicts that wood density increases with water temperature in gymnosperms (Roderick & Berry, 2001). Smaller vessel lumen area has also been associated with dry soils (Carlquist & Hoekman, 1985; Pockman & Sperry, 2000), and with the risk of freezing (Carlquist & Hoekman, 1985). In the southern California flora, trees have larger, less dense vessels than shrubs, and the same trend is seen for water availability (Carlquist & Hoekman, 1985). Insofar as the same wood density can be achieved with different combinations of vessel traits, however, such patterns still do not address the possibility that different combinations of wood and vessel traits play particular ecological roles.

Compared with ecological trends, much less is known about evolutionary trends in wood density and vessel traits; however, it is plausible that density and its component vessel traits will show distinct patterns of evolutionary change or stasis. Recently developed metrics indicate that both vessel area and wood density show strong phylogenetic conservatism among 17 *Quercus* (Oak) species in Florida (Cavender-Bares *et al.*, 2004). Based on proportional differences in mean vessel traits between habitats, Carlquist & Hoekman (1985) have argued that vessel density 'changes more rapidly', or is more evolutionarily labile, than vessel area. In addition to estimating the degree of change, it is also possible to compare patterns of change among traits. We can ask, for example, how the evolution of wood density is related to changes in its constituent vessels, and whether evolutionary changes in vessel traits appear co-ordinated or relatively independent of each other.

Here we consider variation in wood density and vessel traits, together with their ecological correlates and phylogenetic distributions, among 51 woody angiosperm species occurring across a range of habitats within a biological preserve in California, USA. Our study had three primary goals. The first was to decompose variation in wood density into variation in its component vessel traits – average lumen area and vessel density. Patterns of covariation among these traits were of particular interest because, paradoxically, negative relationships were predicted among all three variables. Secondly, we sought to test existing hypotheses about the ecological correlates of wood density, vessel area, and vessel density, examining each

trait individually. We considered factors related to site (e.g. soil water and insolation) as well as growth habit and morphology (e.g. maximum height and canopy position) and site combined with morphology and physiology (e.g. minimum leaf water potential). Thirdly, we examined the evolutionary history of these functionally interdependent characters by quantifying the degree of morphological similarity among close relatives (phylogenetic signal) and correlated evolution among wood and vessel traits.

## Materials and Methods

### Field site and sampling

The field sampling for this project was carried out at Jasper Ridge Biological Preserve (JRBP). The 481-ha preserve, located in the eastern foothills of the Santa Cruz Coast range in California, contains a diverse array of woody vegetation types including riparian forest, evergreen broadleaf forest, oak woodland, open scrubland, and chaparral. The climate is Mediterranean-type, with mean annual rainfall of 605 mm, approx. 80% of which falls between November and March. On the basis of data from a previous vegetation survey (Cornwell *et al.*, 2006), we sampled the 51 most common native woody angiosperms at JRBP (Table A1), excluding one species, *Toxicodendron diversilobum*, which has been shown to be highly variable in wood anatomy (Gartner, 1991). Gymnosperms (*Sequoia sempervirens* and *Pseudotsuga menziesii*) were excluded from the study because their wood lacks the fiber matrix that decouples total lumen area from wood density (Roderick & Berry, 2001). Taxonomy follows Hickman (1993). Sampling protocols varied among traits as described in the next section.

### Trait measurement

In this study, we obtained new data on vessel area and density and the ratio of leaf area to sapwood area. These data were combined with available data including wood density, soil water, and species distributions (Cornwell *et al.*, 2006) and a more limited set of minimum seasonal leaf water potentials in evergreen chaparral shrubs (Ackerly, 2004a).

### Wood density

Wood density was measured on five individuals for each of the 51 species. The samples were taken from the same sites but not necessarily from the same individuals used for other traits. To obtain sufficient sample mass, wood density was measured on 3-year-old stem segments, as determined by examining annual growth rings. The pith and bark were removed, and fresh volume was measured by water displacement, accounting for the relationship between temperature and the density of water. Sample mass was determined after drying for at least 2 d at 70 C. Reported values are oven dry mass per fresh volume (g cm$^{-3}$).

### Vessel traits

Five individuals from each species were sampled for vessel traits. From each individual, we collected one distal segment of an undamaged representative shoot, including the complete leafy portion of the current year's growth. Shoots were bagged and kept cool for no more than 24 h until they were processed. Stem segments were then cut from the internode below the most basal leaf of the sampled shoot and stored cold in 70% EtOH. Mean vessel lumen area, vessel density, and total transverse sapwood area were determined from transverse stem sections of these segments. Images were captured from a microscope (Olympus CH-2) fitted with a digital camera (QColor 3; Qimaging, Burnaby, BC, Canada). Most sections were viewed at ×50 magnification, although some species with very small vessels were measured at ×125. Images at each magnification were calibrated with a slide-mounted micrometer.

Images were analyzed using the IMAGEJ program (http://rsb.info.nih.gov/ij/). For each stem, we measured the transverse

**Table 1** Results of the regression analyses of species means and phylogenetic independent contrasts (PICs)

| | Across species | | | PICs | | |
|---|---|---|---|---|---|---|
| | d.f. | $r^2$ | $P$ | d.f. | $r^2$ | $P$ |
| Simple regression | | | | | | |
| 1. Mean vessel area | 50 | 0.132 | 0.0081 | 43 | 0.026 | 0.3008 |
| 2. Vessel density | 50 | 0.026 | 0.2620 | 43 | 0.090 | 0.0479 |
| 3. The product, area × density | 50 | 0.312 | < 0.0001 | 43 | 0.271 | 0.0004 |
| Multiple regression | | | | | | |
| 4. Model | 49 | 0.320 | < 0.0001 | 42 | 0.266 | 0.0018 |
| Mean vessel area | | | < 0.0001 | | | 0.0032 |
| Vessel density | | | 0.0007 | | | 0.0007 |

Three models were tested using simple reduced major axis regression: 1, average vessel area alone; 2, vessel density alone; 3, the product of area and density, each as predictors of wood density. A fourth model included vessel area and density as independent variables in a multiple regression.

lumen area of each vessel within a chosen sector bounded by rays, adding sectors until at least 30 vessels had been measured (average 58 vessels per section). Vessel lumen areas were averaged to generate individual means; species means were calculated from individual means. For vessel density, a larger number of vessels were counted per stem (average 140, median 120 vessels per section) and divided by the total area of the vessels and surrounding matrix, excluding rays. Total sapwood area was determined either by tracing the outline of complete sections or by estimating the area based on average stem diameter when stem sections were very large or incomplete. In both cases, pith was excluded.

Previous studies have weighted average vessel lumen area to account for size-dependent differences in conductivity, generating a hydraulic mean. Note that, in our study, we use the unweighted average vessel lumen area, as we are concerned with wood density and not whole-stem conductivity.

### Ratio of leaf area to sapwood area ($L_a$:$S_a$)

Whole-plant water use is strongly influenced by the ratio of total shoot leaf area to the transverse area of the sapwood that supports it, and this ratio has been shown to covary with other hydraulic traits (e.g. Vander Willigen *et al.*, 2000; Cavender-Bares & Holbrook, 2001; Preston & Ackerly, 2003). Between five and 20 individuals per species were used to estimate the ratio of leaf area to sapwood area on first-year shoots. We used the same shoots that had been collected for vessel traits but sampled up to 20 individuals of 29 species as part of another study. Total leaf area on a shoot was determined using a leaf area meter (LI-3100; Li-Cor, Lincoln, NE, USA).

### Maximum potential height

Forty-four randomly located $20 \times 20$ m plots were sampled across the woody plant communities at Jasper Ridge for species occurrence and abundance. In each plot, the tallest individual was measured, using a clinometer when necessary. Here we use the maximum observed height as a measure of the stature a species can attain given the environmental conditions at this location.

### Species distributions at Jasper Ridge

As part of a larger survey (Cornwell *et al.*, 2006), the distribution of each species was characterized with respect to abiotic gradients at Jasper Ridge. Briefly, to separate plots on an axis from xeric to mesic, gravimetric soil water content was measured from soil cores of 0–10 cm in depth at each plot in May of 2004. A Geographic Information System (GIS) layer of insolation (see Ackerly *et al.*, 2002) was used to characterize the solar radiation each plot receives over the course of a year. For each species, the mean value among plots of each variable across the species distribution was calculated, weighted

by the species abundance (per cent cover) in each plot. This resulted in a value that characterizes the average position on the environmental gradient for each species. For example, species that are found exclusively on mesic soils will have a high value for soil water, species on xeric soils will have a low value, and widespread species will have an intermediate value.

Canopy position has been shown to be a significant correlate of wood traits (Worbes *et al.*, 2003; Falster & Westoby, 2005). The proportion of a species' total cover that occurred in the understory was characterized as part of the survey described above (Cornwall *et al.*, 2006). Essentially, this value estimates the probability that a randomly encountered individual of a given species will be located in the understory.

### Minimum seasonal water potential

Previous work at Jasper Ridge (Davis & Mooney, 1985) has highlighted the importance of rooting depth in decoupling surface soil water content and the water potentials experienced by different species at the same site. Moreover, the ability to tolerate highly negative water potentials has emerged as an important and variable trait in the chaparral (Ackerly, 2004a). Here, we compared species mean values for wood-related traits to the seasonal minimum water potential experienced during the summer of 2001 at the same site, using data from Ackerly (2004a). Data were available for 11 of the evergreen chaparral species in our sample.

### Statistical analysis

**Correlations among traits and ecological variables** Correlations were calculated for all pairwise combinations of wood traits – vessel area, vessel density, leaf area-to-sapwood area ratio, and bulk wood density – and between wood traits and ecological measures of species distributions – soil water, insolation, per cent of cover in the understory, maximum height, and minimum seasonal water potential. Species mean values of vessel area, vessel density, $L_a$:$S_a$, and soil water were log-transformed before analysis. Reduced major axis (RMA) regression was used to calculate scaling relationships among wood traits.

Theory suggests that bulk wood density should be related to the amount of space in the wood dedicated to water transport:

$$d_w = d_m(1 - \bar{a}_v n_v) \qquad \text{Eqn 1}$$

[$d_w$, the density of wood; $\bar{a}_v$, the average vessel lumen area; $n_v$, the number of vessels per unit area (vessel density); $d_m$, the density of the matrix of fibers, cell walls, parenchyma and other cells.]

The matrix density is also influenced by the amount of water bound to cell walls, which generally increases with increasing wood density (Berry & Roderick, 2005). Eqn 1 suggests that

wood density should vary more closely with the product of vessel area and vessel density than with either variable alone. The product of vessel area and density is the lumen fraction of the stem.

We therefore tested four models relating wood density to its component vessel traits: (1) a model with average vessel lumen area, $\bar{a}_v$, as the only predictor variable; (2) a model with vessel density, $n_v$, as the only predictor variable; (3) a model with the product of $\bar{a}_v$ and $n_v$, the lumen fraction, as a single independent variable; and (4) a multiple regression model with both vessel area and vessel density as predictors. With respect to the multiple regression model, we tested for colinearity using the COLLIN and VIF options in SAS version 9.1 (SAS Institute, Inc., Cary, NC, USA). As measured in this study, $\bar{a}_v$ and $n_v$ showed a moderate amount of colinearity [variance inflation factor (VIF) = 1.45]. In some cases, this can cause instability in partitioning variance between predictor variables (Graham, 2003), and the multiple regression results should be interpreted in that light.

Principal components analysis (PCA) was used to describe patterns of covariation among wood traits (wood density, vessel area, vessel density and lumen fraction), leaf area to sapwood area ratio, maximum plant height, and soil water.

**Phylogenetic signal and correlated evolution** Patterns of trait variation among species sometimes reflect phylogenetic relationships such that more closely related taxa share similar trait values. Traits with this pattern are said to show phylogenetic signal (*sensu* Blomberg *et al.*, 2003). We tested for phylogenetic signal in wood density and vessel traits using Analysis of Traits (AOT), version 3.0 (D. Ackerly), a module of PHYLOCOM version 3.21 (C. Webb, S. Kempel & D. Ackerly; http://www.phylodiversity.net/phylocom). This algorithm reconstructs contrasts in trait values between sister taxa and calculates the mean of all contrasts over a phylogeny. For significance testing, the observed mean value for a trait was compared to the distribution of mean contrasts derived from repeated randomization (*n* = 999) of trait values across the tips of the phylogeny. We generated a phylogenetic tree for the analysis using PHYLOMATIC (Webb & Donoghue, 2004) and were able to resolve two of the remaining polytomies using published phylogenetic hypotheses (Rosaceae: Evans *et al.*, 2000; Ackerly, 2004b; *Quercus*: Nixon, 2002). We assumed equal branch lengths for all analyses.

When phylogenetic signal is significant, trait correlations may reflect a shared evolutionary history in addition to any functional association. To account for the phylogenetic signal, contrast values may be used to infer patterns of evolutionary change in single traits. These phylogenetic independent contrasts (PICs) may then be used to test for correlated evolutionary change among traits (Felsenstein, 1985; Garland *et al.*, 1992). We tested for correlated evolution among morphological traits using PICs calculated in AOT. The final tree with 51 species provided 44 evolutionary contrasts as a result of a few

unresolved polytomies. We also analyzed vessel trait contrasts as predictors of wood density contrasts in a multiple regression. As with the analysis of species means, there was moderate colinearity between vessel trait contrasts (VIF = 1.54).

## Results

### Correlations among wood density, vessel traits, and $L_a:S_a$

The observed relationships among vessel traits and wood density were in accord with the expectations presented in Fig. 1. There was a strong negative relationship between average vessel size, measured as lumen area, and vessel density, measured as the number of vessels per unit area ($r = -0.557$, $P < 0.0001$; Fig. 2a). Vessel size and density showed near-perfect negative isometry, as the reduced major axis slope of their relationship was $-1.05$ [95% confidence interval (CI) = 0.25].

Both vessel traits also varied inversely with wood density; however, vessel area showed the stronger relationship in the univariate models (Table 1). Average vessel lumen area alone explained a significant amount of the observed variation in wood density, whereas vessel density did not. Nevertheless, vessel density did influence wood density. The product of vessel area and vessel density, which is essentially the fraction of the stem occupied by vessel lumen, was highly significantly related to wood density, explaining more of the variation than either variable alone. An alternative analysis including both vessel area and vessel density in the same model using multiple regression led to a very similar result (Table 1).

Wood and vessel traits were also related to the relative amount of leaf area supported by a given area of sapwood, $L_a:S_a$ (Table 2). There was a strong positive relationship between vessel lumen area and $L_a:S_a$. In other words, stems supporting a relatively high leaf area tended to have larger vessels. $L_a:S_a$ was negatively related to wood density and was largely independent of vessel density. Overall, the correlations among shoot-level characters were strongest between vessel area and both wood density and $L_a:S_a$, whereas vessel density was associated primarily with vessel area.

### Ecological correlates of wood density and vessel traits

Wood density, vessel lumen area, and vessel density showed distinct patterns of ecological correlation (Table 2, Fig. 3). Wood density was most closely associated with soil water content; denser wood was found in drier soils (Fig. 3d) and was associated with more negative minimum seasonal leaf water potentials ($\Psi_{min}$) among evergreen chaparral species (Ackerly, 2004a). A weaker relationship was found between wood density and maximum plant height (Fig. 3a).

Vessel area was also correlated with soil water and plant height, although the relative importance of these variables was reversed (Table 2; Fig. 3b,e vs Fig. 3a,d). Larger vessels were
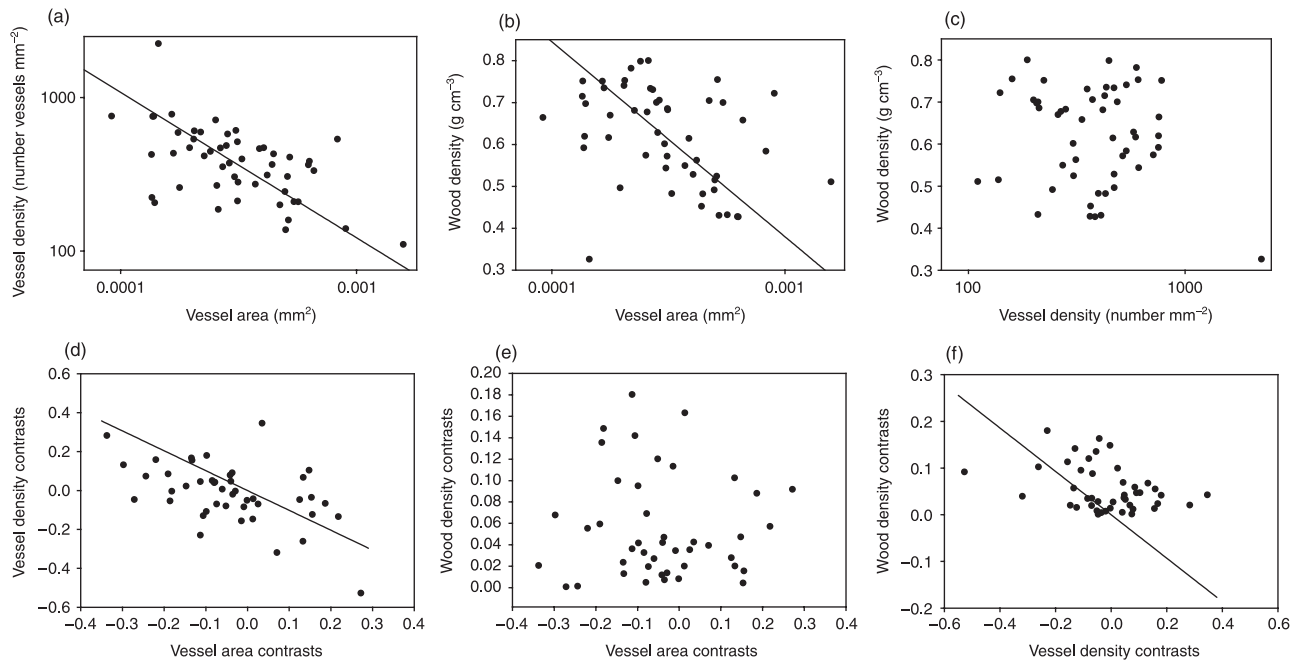
**Fig. 2** Correlations among wood density and vessel traits. (a–c) Correlations among species means; (d–f) correlations among phylogenetic independent contrasts (PICs). Reduced major axis (model II) regression lines are shown for significant pairwise relationships.

**Table 2** Pearson's coefficients of correlation between pairs of traits

|  | Wood density | Vessel density | Mean vessel area | Lumen fraction | $L_a$:$S_a$ | Soil water[1] | Maximum height | $\Psi_{min}$[2] |
|---|---|---|---|---|---|---|---|---|
| Wood density |  | −0.159 | **−0.363** | **−0.560** | **−0.438** | **−0.375** | **−0.279** | **−0.655** |
| Vessel density | **−0.303** |  | **−0.557** | **0.426** | −0.107 | −0.069 | **−0.441** | **0.629** |
| Mean vessel area | −0.235 | **−0.485** |  | **0.514** | **0.652** | **0.298** | **0.597** | **0.750** |
| Lumen fraction (area × density) | **−0.521** | **0.537** | **0.473** |  | **0.600** | 0.246 | 0.194 | **0.847** |
| $L_a$:$S_a$ | −0.234 | −0.014 | **0.689** | **0.634** |  | **0.432** | 0.172 | **0.862** |
| Soil water | −0.166 | −0.082 | 0.238 | 0.100 | **0.343** |  | 0.057 | 0.412 |
| Maximum height | −0.196 | −0.255 | **0.474** | 0.196 | 0.047 | 0.005 |  | 0.147 |

Significant correlations are shown in bold ($P < 0.05$). Correlations among species means are given above the diagonal, and correlations among phylogenetic independent contrasts (PICs) are given below it.
[1]For soil water, $n = 48$ (40 contrasts); otherwise $n = 51$ (44 contrasts).
[2]Note that for $\Psi_{min}$, $n = 11$ and data are from evergreen chaparral shrubs only. Contrasts were not calculated for $\Psi_{min}$ because of low sample size.

typical of taller trees and, to a lesser degree, of moister soils. In addition, vessel area was strongly related to $\Psi_{min}$ among the subset of evergreen chaparral species for which we had data.

Across all 51 species, vessel density was strongly associated with only one ecological variable, maximum plant height (Fig. 3c). The relationship between vessel density and height was negative, the inverse of the relationship between height and both vessel area and wood density. Consequently, taller species tended to have lighter wood despite their lower density of vessels, perhaps in part because vessels were larger. Among evergreen chaparral species, vessel density was greatest among species with the least negative seasonal $\Psi_{min}$.

The ratio of leaf area to sapwood area was positively related to water availability, measured either as soil water content or as $\Psi_{min}$ (Table 2). There was also a weak trend for understory species to have a higher $L_a$:$S_a$ ($r = 0.274$, $P < 0.07$; data not shown). None of the wood traits or $L_a$:$S_a$ was significantly related to insolation ($| r | < 0.15$ in all cases; data not shown).

It is significant that soil water and maximum plant height varied independently in our data, suggesting that the two most important ecological variables emerging in this study represent orthogonal axes of variation (Table 2). It is also important to note that soil water content and minimum seasonal water potentials were only weakly correlated. Minimum
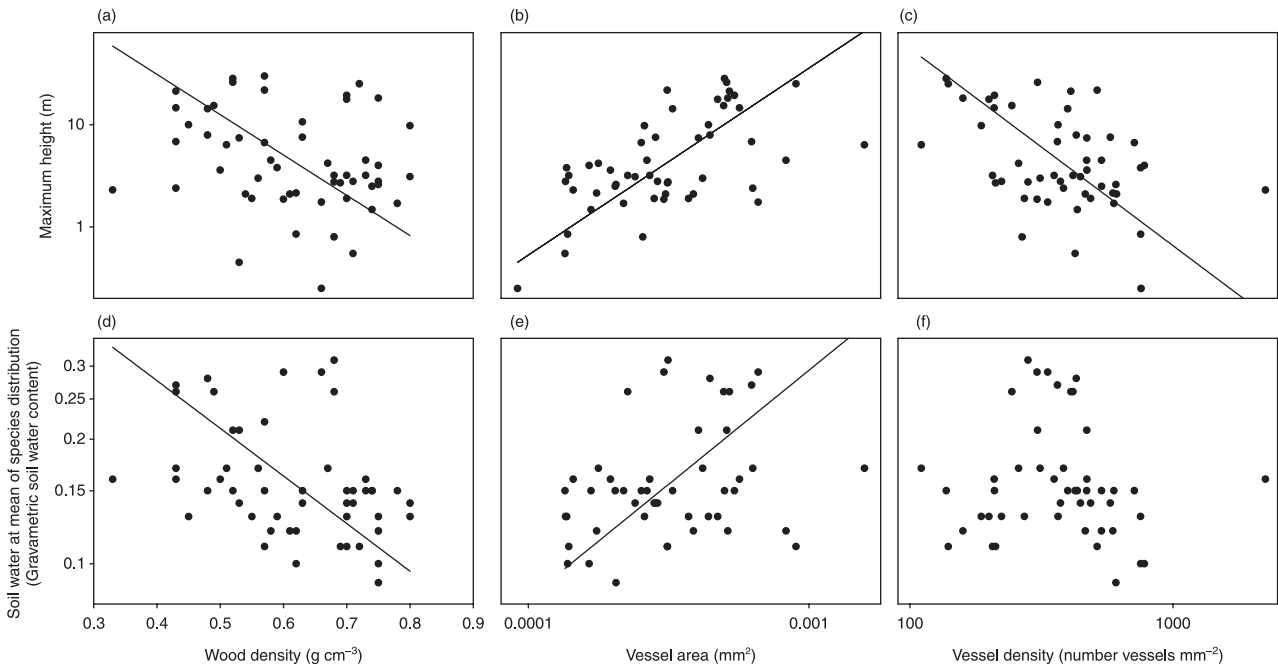
**Fig. 3** Correlations between species means of wood and vessel traits and two aspects of life history, maximum height for these species at Jasper Ridge Biological Preserve (JRBP) and the centroid of the species distributions with respect to a gradient in gravimetric soil water content. Reduced major axis (RMA) regression lines are shown for significant pairwise relationships.

seasonal water potential depends on various characteristics of a species, such as rooting depth and stomatal sensitivity, which allows some decoupling of leaf water potential and water content of the upper 10 cm of soil. Moreover, water potential data were collected only for co-occurring chaparral species, which would tend to share soil water data measurements.

## Principal components analysis

The first two axes of the PCA explained 42 and 26% of the variation in the seven included traits, respectively (Fig. 4). Wood density loaded strongly on the first axis, along with negative loadings of per cent lumen (the product of vessel area and density), $L_a$:$S_a$, and soil water. Vessel area and vessel density loaded strongly on the second axis, along with maximum plant height. The vectors for vessel area and vessel density were nearly orthogonal to the wood density vector.

## Phylogenetic signal and correlated evolution

All three wood-related characters showed strong phylogenetic signal across the 51 angiosperm taxa in our study. In each case, the mean contrast values were significantly less than the null expectation in one-tailed tests (wood density, $P < 0.0004$; vessel density, $P < 0.0024$; vessel area, $P < 0.0104$). By contrast, the phylogenetic signal was much weaker for the leaf area to sapwood area ratio and was only marginally significant (one-tailed, $P = 0.0477$). Although phylogenetic signal was evident
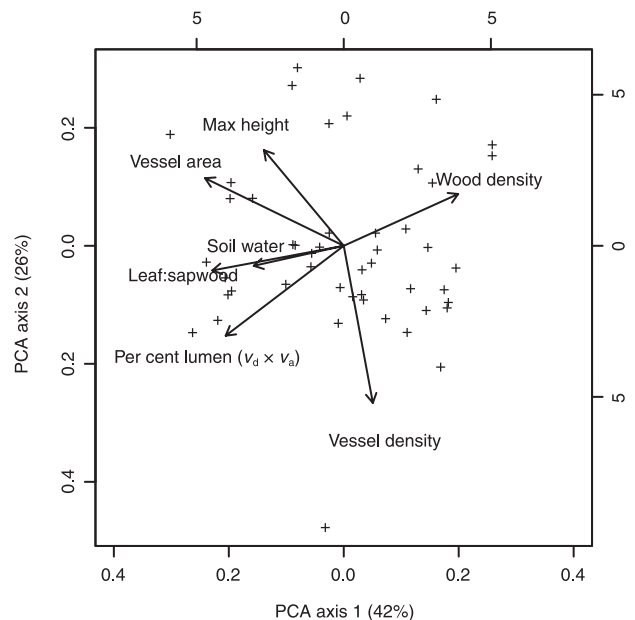


**Fig. 4** Position of traits on the first and second axes of a principal components analysis (PCA). Crosses indicate the loadings of individual species on these axes.

for all the xylem traits, they differed in their degree of variation among species: wood density varied less than 3-fold among species, and less than 2-fold without the outlier *Dirca occidentalis*, whereas vessel density varied 7-fold and vessel area varied nearly

10-fold (excluding the extreme outliers *D. occidentalis* from vessel density and *Juglans californica* from the vessel area data).

Analysis of PICs suggested that evolutionary changes in wood-related characters have been co-ordinated; however, the evolutionary correlations did not always mirror the cross-species trait correlations (Table 2, Fig. 2). For example, wood density and vessel density were not related across species, but they showed a moderate degree of correlated evolutionary change (Fig. 2c,f). The relationship between vessel area and $L_a:S_a$ PICs was stronger than the cross-species correlation, whereas the relationship between wood density and $L_a:S_a$ PICs was considerably weaker. Strong cross-species and contrast relationships were found between vessel area and vessel density (negative; Fig. 2a,d) and between wood density and lumen fraction (positive).

We also found evidence for correlated evolution between stem characteristics and ecological variables (Table 2). Significant contrast correlations included vessel area and maximum plant height, and $L_a:S_a$ and soil water content. Overall, correlations among PICs represented a subset of the ecological correlations seen across species, and, notably, vessel density contrasts were not significantly related to contrasts in any ecological variables.

## Discussion

The goals of this study were to decompose wood density into two of its component vessel traits and examine their contributions to variation in wood density with respect to both ecology and phylogeny. Globally, wood density ranges from approximately 0.2 to 1.3 g cm$^{-3}$ (Borchert, 1994; Detienne & Chanson, 1996; ter Steege & Hammond, 2001; Kohyama *et al.*, 2003); however, extremely light or dense wood is rare in most ecosystems (Detienne & Chanson, 1996). In this study, wood density ranged more narrowly – from 0.33 to 0.8 g cm$^{-3}$ – with 75% of the species falling between 0.48 and 0.75 g cm$^{-3}$ (mean 0.619 g cm$^{-3}$). This relatively small range in wood density nevertheless accommodated a much greater range of vessel traits and, potentially, a range of functional strategies (Fig. 4).

### Correlations among wood density and vessel traits

In this data set, a significant proportion of the variation in wood density was attributable to variation in vessel traits, primarily vessel size. The effect of these particular vessel traits on wood density follows directly from their structure because the fraction of wood volume occupied by lumen area is the product of vessel size and density (Eqn 1). Indeed, variation in lumen fraction accounted for much, but not all, of the variation in bulk wood density. The remaining tissue – the vessel walls and the matrix surrounding them – must then explain much of the remaining variation in bulk wood density. This component of wood density is also very important, as

the structure of the fibers in the matrix appears to contribute directly to biomechanical strength and cavitation resistance (Berry & Roderick, 2005; Jacobsen *et al.*, 2005).

As predicted, vessel lumen area and vessel density both varied inversely with wood density, yet they were also strongly negatively related to each other. It is unlikely that this correlation arose from a simple geometrical trade-off between size and number, as vessels are usually not tightly packed within stems (Carlquist & Hoekman, 1985). Rather, the observed pattern apparently represents the set of vessel trait combinations that maintain wood density within functional limits (Fig. 1). It is worth noting that if $d_w$ and $d_m$ (or their ratio) are held constant in Eqn 1, $v_a$ and $v_d$ necessarily have a scaling relationship of −1. Although wood density was not constant among the species we measured, the scaling relationship between vessel traits nevertheless fell very close to −1 (RMA slope = −1.05; 95% CI = 0.25). This result is consistent with our observation that a limited range of $d_w$ values can be obtained across a wide range of either vessel area or vessel density.

Functional constraints on wood density were apparent in our study. A recent model has shown that optimal carbon allocation would produce stems that maximized conductivity (via large vessels) and minimized wood density while just maintaining adequate support (Taneda & Tateno, 2004). In our study, those species that fell closest to this optimum – along the upper right margin of the vessel area–density relationship – were not strongly self-supporting. These included three vines (*Rubus ursinus*, *Clematis lasiantha*, and *Lonicera hispidula*) and *Dirca occidentalis*, which has unusually pliable stems. Along the other margin, species with small vessels at low density were represented by drought-tolerant evergreen chaparral shrubs (*Ceanothus cuneatus*, *C. oliganthus*, *Cercocarpus betuloides*, and *Rhamnus crocea*).

### Ecological correlates of wood density and vessel traits

In this study, wood density, vessel area, and vessel density each showed a distinct pattern of ecological association. Across all 51 species, the most important ecological factors to emerge were maximum plant height and soil water content. Among evergreen chaparral shrubs, minimum seasonal water potential was also highly predictive of wood characters.

**Maximum plant height** In our data set, plant height varied 100-fold, from 0.3 to 30 m. Taller species had larger vessels but also lower vessel density than shorter species. In combination, these opposing relationships tended to loosen the relationship between height and wood density, resulting in a weak negative correlation.

Our results are in line with those from another comparative study of 207 woody species in California, in which trees were found to have larger vessels and lower vessel density than shrubs (Carlquist & Hoekman, 1985). Results from many other investigations of height and vessel characteristics are

not directly comparable to ours because they were based on intraspecific ontogenetic comparisons of vessel size and focused on hydraulic limits on plant height (see Discussion in Mencuccini, 2003; Phillips *et al.*, 2003; Koch *et al.*, 2004). Nevertheless, those studies generally found that vessel lumen area increased as individuals grew taller, thereby counteracting some of the increased hydraulic resistance associated with height (e.g. Mencuccini & Magnani, 2000). The positive correlation between vessel area and height that we observed among species thus appears to be functionally appropriate given fundamental biophysical constraints on water transport to canopies (Niklas & Spatz, 2004). A functional hydraulic interpretation was also supported by independent contrasts which suggest that plant height and vessel area have undergone co-ordinated evolutionary change, such that hydraulic adjustment seems to have accompanied changes in stature.

We found that wood density in our species was weakly negatively correlated with maximum plant height. Both negative and positive interspecific relationships between wood density and stature have been reported, and in each case the relationship is mediated by a trade-off between wood density and growth rate. Negative correlations typically arise across light gradients within tropical forests (Thomas, 1996; Worbes *et al.*, 2003; see also Falster & Westoby, 2005), whereas positive correlations are associated with successional gradients (ter Steege & Hammond, 2001; Worbes *et al.*, 2003; Falster & Westoby, 2005). Variation in density with height across a light gradient would not explain our results, because wood density was not related to the proportion of individuals in a species found in the understory. Our study was also unlikely to detect a successional trend as our species were drawn from a range of communities, including chaparral, oak woodland, and riparian habitats.

Instead, the weak negative relationship between wood density and height most likely reflected the opposing influence of the two vessel traits. Increasing vessel area with height would tend to decrease wood density with height, but this relationship was counterbalanced somewhat by a reduction in vessel density with height (Fig. 3a–c). Variation in vessel density may thus allow species to maintain sufficient wood density even while increasing lumen area.

It is also notable that the phylogenetic contrast correlations between vessel lumen area and height were significantly positive, but vessel density and wood density PICs were not independently related to height (Table 2). Instead, evolutionary changes in wood density appeared to be at least partially decoupled from height evolution because correlated changes in vessel density tended to counterbalance changes in vessel area.

**Soil water content and $\Psi_{min}$** In this study, species growing in wetter soils generally had less dense wood with larger vessels and a higher ratio of leaf area to sapwood area on a shoot. Of the wood-related traits, wood density was most strongly correlated with soil water content. A similar pattern has been reported among oak species in Florida (Cavender-Bares *et al.*, 2004). Vessel size and the ratio of leaf to sapwood area on a shoot are part of a suite of traits influencing leaf hydraulic supply (Whitehead *et al.*, 1984; Margolis *et al.*, 1995; Maherali *et al.*, 1997; Villar-Salvador *et al.*, 1997; Tausend *et al.*, 2000; Vander Willigen *et al.*, 2000; Cavender-Bares & Holbrook, 2001; Preston & Ackerly, 2003), and thus it is not surprising that they were also related to soil water content.

Wood density in angiosperms is tied to the tolerance of the species of low xylem water potentials (Hacke *et al.*, 2001; Ackerly, 2004a; Jacobsen *et al.*, 2005) and mean diurnal variation in leaf water potential (Meinzer, 2003). Results from our study were consistent with these trends; wood density was correlated with the minimum seasonal water potentials of 11 evergreen chaparral shrubs. Very small vessels together with low vessel density appeared to be associated with resistance to xylem cavitation under tension, as the species with this combination of vessel traits had the most negative values of $\Psi_{min}$. By contrast, larger denser vessels were generally found among the drought-deciduous species.

## Phylogenetic signal and correlated evolution

Few studies have addressed the evolutionary lability of wood traits, although Carlquist & Hoekman (1985) have argued that vessel density shows more rapid evolutionary change than does vessel area, and Cavender-Bares *et al.* (2004) found a high degree of phylogenetic signal in both wood density and vessel area in oaks. Among the 51 angiosperm species in our study, wood density and vessel traits showed similar signals. If there had been large differences among traits in phylogenetic signal, this might have suggested that certain evolutionary trajectories would be more likely than others; for example, low signal (higher lability) in vessel density could indicate that changes in wood density would be driven by that vessel trait. Our data, however, offered no evidence for such a bias in xylem evolution.

It is worth noting here that a high degree of phylogenetic signal does not necessarily indicate homogeneity in wood traits within clades, only that on balance close relatives are more similar to each other than to distantly related species. For example, both the lowest and highest density wood were found in a large and ecologically diverse clade comprised of members of the Rosaceae: *Rubus ursinus* had the lowest wood density (after the outlier *D. occidentalis*), and *Cercocarpus betuloides* and *Amelanchier utahensis* had the two highest wood densities. Among the 11 species we sampled from that family, the range in vessel area was 70% of the full range and the range in vessel density was 89% (excluding *D. occidentalis*).

We also found evidence for correlated evolutionary changes in wood traits. Most strikingly, vessel lumen area and vessel density showed a strong negative contrast correlation, indicating that evolutionary increases in one trait have generally been accompanied by decreases in the other. However, evolutionary changes in wood density were significantly related to vessel

changes only when both vessel traits were considered together in a multivariate analysis (Table 1). One possible explanation for this pattern could be a relatively common evolutionary trajectory that holds wood density constant while vessel area and vessel density change in opposite directions. Such evolutionary decoupling may allow vessel traits to respond to ecological pressures independently of wood density.

## Conclusions

This study demonstrates the benefits of considering vessel traits that contribute to wood density along with wood density itself. Wood density has been shown to be a reliable predictor of some fundamental plant characteristics, including growth rate and resistance to xylem failure. Nevertheless, it is worth noting that, even within a narrow range of wood densities, there is room for significant variation in vessel traits, and that this variation has its own ecological consequences. There are additional vessel traits not included in our study – for example, length, pore size and frequency, and sculpturing – which must also vary at a given wood density and which bear crucially on stem function (e.g. Wheeler *et al.*, 2005). Our data also provide evidence for correlated evolutionary change in vessel traits, which suggests that there may be a range of ecologically significant vessel strategies available to species, independent of wood density *per se*.

## Acknowledgements

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## Supplementary Material

The following supplementary material is available for this article online:

**Fig. S1** Pairwise relationships among eight plant traits and environmental variables. Scatter plots above the diagonal correspond to Pearson correlation coefficients given below the diagonal. For soil water n = 48; for minimum seasonal water potential n = 11; otherwise n = 51.

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## Appendix A

**Table A1** Species sampled in this study

| Family | Species |
| --- | --- |
| Asteraceae | *Artemisia californica*<br>*Baccharis pilularis*<br>*Eriophyllum confertiflorum* |
| Betulaceae | *Alnus rhombifolia*<br>*Corylus cornuta* |
| Boraginaceae | *Eriodictyon californicum* |
| Caprifoliaceae | *Lonicera hispidula*<br>*Sambucus mexicana*<br>*Symphoricarpos albus*<br>*Symphoricarpos mollis* |
| Cornaceae | *Cornus glabrata*<br>*Cornus sericea* |
| Ericaceae | *Arbutus menziesii* |
| Fabaceae | *Lotus scoparius* |
| Fagaceae | *Quercus agrifolia*<br>*Quercus douglasii*<br>*Quercus durata*<br>*Quercus kelloggii*<br>*Quercus lobata* |
| Grossulariaceae | *Ribes californicum*<br>*Ribes divaricatum*<br>*Ribes malvaceum*<br>*Ribes sanguineum* |
| Juglandaceae | *Juglans californica* |
| Lamiaceae | *Lepechinia calycina* |
| Lauraceae | *Umbellularia californica* |
| Ranunculaceae | *Clematis lasiantha* |
| Rhamnaceae | *Ceanothus cuneatus*<br>*Ceanothus oliganthus*<br>*Rhamnus californica*<br>*Rhamnus crocea* |
| Rosaceae | *Adenostoma fasciculatum*<br>*Amelanchier utahensis*<br>*Cercocarpus betuloides*<br>*Heteromeles arbutifolia*<br>*Holodiscus discolor*<br>*Oemleria cerasiformis*<br>*Prunus ilicifolia*<br>*Rosa californica*<br>*Rosa spithamea*<br>*Rubus parviflorus*<br>*Rubus ursinus* |
| Salicaceae | *Populus balsamifera*<br>*Salix lasiolepis*<br>*Salix lucida* |
| Sapindaceae | *Acer macrophyllum*<br>*Acer negundo*<br>*Aesculus californica* |
| Scrophulariaceae | *Mimulus aurantiacus* |
| Solanaceae | *Solanum umbelliferum* |
| Thymelaeaceae | *Dirca occidentalis* |