Vessel diameter is related to amount and spatial arrangement of axial parenchyma in woody angiosperms

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Abstract
Parenchyma represents a critically important living tissue in the sapwood of the secondary xylem of woody angiosperms. Considering various interactions between parenchyma and water transporting vessels, we hypothesize a structure–function relationship between both cell types. Through a generalized additive mixed model approach based on 2,332 woody angiosperm species derived from the literature, we explored the relationship between the proportion and spatial distribution of ray and axial parenchyma and vessel size, while controlling for maximum plant height and a range of climatic factors. When factoring in maximum plant height, we found that with increasing mean annual temperatures, mean vessel diameter showed a positive correlation with axial parenchyma proportion and arrangement, but not for ray parenchyma. Species with a high axial parenchyma tissue fraction tend to have wide vessels, with most of the parenchyma packed around vessels, whereas species with small diameter vessels show a reduced amount of axial parenchyma that is not directly connected to vessels. This finding provides evidence for independent functions of axial parenchyma and ray parenchyma in large vessels and further supports a strong role for axial parenchyma in long-distance xylem water transport.

KEYWORDS
angiosperms, climate, maximum plant height, parenchyma, precipitation, temperature, vessel diameter, water transport, wood anatomy, xylem
1 | INTRODUCTION

Water is critical for the growth of woody plants, but the transportation of this water to the sites of photosynthesis must overcome the challenges of long path lengths and negative pressures. In angiosperms, the transport of water is largely conducted through vessels, which trade off against other tissues (e.g., fibre and parenchyma) for a given amount of xylem cross section (Baas, Ewers, Davis, & Wheeler, 2004; Bittencourt, Pereira, & Oliveira, 2016; Gleason et al., 2016; Morris, Plavcová, et al., 2016; Ziemnińska, Butler, Gleason, Wright, & Westoby, 2013; Ziemnińska, Wright, & Westoby, 2015). Whereas vessels are dead at maturity, parenchyma is living and includes ray parenchyma and axial parenchyma. The parenchyma network is interwoven, sometimes together with living fibres, around the dead conduits (vessel elements and tracheids) to form a highly interconnected three-dimensional lattice in radial and axial orientations (Spicer, 2014). Importantly, axial parenchyma is highly variable in its abundance and spatial distribution patterns across angiosperms. Additionally, in angiosperms, the ray and axial parenchyma that are in contact with vessels are known as vessel-associated cells, which have direct functional connectivity to the water transport system (Czaninski, 1972, 1977).

Axial parenchyma differ greatly in the fraction of parenchyma, vessel cells, and fibres observed in cross sections of secondary xylem, and in the spatial organization of those cells. Axial parenchyma fraction is highly variable, ranging from ≤1% to ≥30% across angiosperm species, whereas ray parenchyma fraction is less variable, with mean values of 15% and 20% for temperate (including boreal) and tropical angiosperms (Morris, Plavcová, et al., 2016; Spicer, 2014). Vessel fraction is on average 15%, ranging from <5% to >20% across species, and vessel diameter ranges between 10 and 435 μm (Fichter & Wrobles, 2012; Morris, Plavcová, et al., 2016; Zanne et al., 2010a). Moreover, vessels may show some variation in their amount of interconnectivity, from mainly isolated (but connected to tracheoids) to highly interconnected with neighbouring vessels in radial multiples, clusters, and diagonal or tangential aggregations. Similarly, parenchyma can be arranged radially as in ray parenchyma or, in the case of axial parenchyma, always oriented axially. Axial parenchyma consists of two major types of arrangement, namely, apotracheal parenchyma, which has little or no contact with vessels (when viewed under light microscopy), and paratracheal parenchyma, which is associated with vessels (Carlquist, 2001, 2012; Metcalfe & Chalk, 1950; Morris & Jansen, 2016; Panshin & de Zeeuw, 1980). Both kinds of axial parenchyma, most notably paratracheal, have different distribution patterns (Figure 1, Table S1), which have been used frequently for their taxonomic and identification value, but have rarely been linked directly to function (Braun, 1984; Braun & Wolkinger, 1970; Carlquist, 2001; Kríbs, 1937).

Understanding the breadth of variation in the spatial arrangement of cells in the secondary xylem is essential to map out both the span of ecological plasticity as well as identify the limits imposed by selection on any given direction within this three-dimensional xylem network. The trade-off in amount of space occupied between the three principal cell types in angiosperm wood, that is, fibres, parenchyma, and vessels, is a topic of great current interest (Morris, Plavcová, et al., 2016; Pratt & Jacobsen, 2016; Zheng & Martinez-Cabrera, 2013; Ziemnińska et al., 2013, 2015). However, the functional significance of parenchyma in relation to vessels remains poorly understood.

It is important to consider that vessels and parenchyma do not operate in isolation from one another but are anatomically and functionally integrated. The strength of this coupling between parenchyma and vessel functioning varies greatly across species and likely influences the rate and timing of long-distance water transport, as modified by climate and the conflicting requirements for carbohydrate storage, defence against pathogens, and mechanical stability. Many studies have linked parenchyma, and in particular vessel-associated cells, with long-distance water movement (Braun, 1984; Braun & Wolkinger, 1970; Canny, 1997, 1998; Clearwater & Goldstein, 2005; Johnson, McCulloh, Woodruff, & Meinzer, 2012; Schenk et al., 2017; Secchi, Pagliarani, & Zwieniecki, 2016; Trifilo, Barbera, Raimondo, Nardini, & Lo Gullo, 2014; Ursprung, 1935), suggesting that water transport cannot be considered to be a passive and purely a physical process only. However, it has been shown that for some species, vessel-associated parenchyma cells remained alive long after the adjacent vessels ceased to function, showing that these living cells must take on other functions post water transport cessation (Spicer & Holbrook, 2007).

Although advances have been made in understanding the links between vessel structure and functioning, the community has yet to integrate the multiple functions of parenchyma into this picture (Bittencourt et al., 2016; Gleason et al., 2016). Despite our poor understanding of how parenchyma might facilitate long-distance water transport, numerous studies have demonstrated a functional relationship between parenchyma and vessels, including two-way exchanges of solutes (van Bel, 1990), defence against pathogens (Cooper & Williams, 2004; Hilaire et al., 2001; Morris, Brodersen, Schwarze, & Jansen, 2016; Pouzolet, Pivovaroff, Santiago, & Rolshausen, 2014; Rioux, Nicole, Simard, & Ouellette, 1998), and the transition from sapwood to heartwood (Bamber & Fukazawa, 1985; Chattaway, 1949, 1952; Hillis, 1987). More controversial and poorly understood is the role of parenchyma in avoiding and/or refilling embolized conduits (Brodersen & McElrone, 2013; Brodersen, McElrone, Chaot, Matthews, & Shackel, 2010; Holbrook & Zwieniecki, 1999; Nardini, Salleo, & Jansen, 2011; Salleo, Trifilo, Espósito, Nardini, & Lo Gullo, 2009; Tyree, Salleo, Nardini, Lo Gullo, & Mosca, 1999), of which xylem hydraulic capacitance is also related (Goldstein et al., 1998; Meinzer, Johnson, Lachenbruch, McCulloh, & Woodruff, 2009). Vessel-associated cells are morphologically distinct from vessel-distant parenchyma in having smaller vacuoles and increased mitochondrial activity (Alves et al., 2001; Czaninski, 1972, 1977; Fromard et al., 1995; Sauter, 1988; Secchi et al., 2016), and in addition having an amorphous layer between the plasma membrane and parenchyma–vessel pit membrane, and a black cap on the exterior of the pit membrane (Schenk et al., 2017; Wisniewski & Davis, 1995).

Regarding the conductive efficiency of xylem (hereafter referred to as “specific hydraulic conductivity”), vessel diameter is traditionally assumed to represent the most important variable, with vessel length positively and vessel frequency negatively correlated to vessel diameter (Savage et al., 2010; Sperry, Hacke, & Pittermann, 2006; Zanne et al., 2010a; Zimmermann & Jeje, 1981). According to the Hagen–Poiseuille law, even a small increase in vessel diameter (μm) results in a large increase in conductivity, because conductance scales to the
fourth power of vessel diameter (Ewers, 1985; Kotowska, Hertel, Rajab, Barus, & Schuldt, 2015; Tyree & Ewers, 1991). High hydraulic efficiency has its advantages in terms of photosynthesis but is traditionally assumed to come at the price of increased vulnerability to embolism (Gleason et al., 2015). Freeze-induced embolism is likely linked to conduit size, where emboli form upon the thawing of frozen sap. Wider conduits facilitate the formation of larger emboli, which may expand more easily under increasing negative pressure than smaller emboli (Hacke, Spicer, Schreiber, & Plavcová, 2017). This dynamic sets an approximate critical threshold of 30 μm on conduit diameter in freezing habitats (Davis, Sperry, & Hacke, 1999), with a similar threshold of 40 μm in water-stressed habitats in walnut saplings.
Knipfer, Brodersen, Zedan, Kluepfel, & McElrone. 2015). For drought-induced embolism, there is also greater risk of embolism formation with increasing vessel diameter, an impairment of the hydraulic system that can lead to serious disruption or even death of the entire plant (Brodribb, Bienaimé, & Marmottant, 2016; Ewers, 1985; Scoffoni et al., 2017; Zimmermann & Brown, 1971). The resistance of angiosperm species to drought-induced embolism is complicated and likely to include conduit diameter, pit membrane properties, and the connectivity of the conduit network itself (Hargrave, Kolb, Ewers, & Davis, 1994; Lens et al., 2013; Li et al., 2016; Loepe, Martínez-Vilalta, Piñol, & Mencuccini, 2007; Martínez-Vilalta et al., 2012). It has been speculated that sheaths of axial parenchyma around vessels can counter negative pressure in vessels by reducing the likelihood of air entry via intervessel pits, although there is no experimental evidence for this idea (Braun, 1984; Braun & Walkinger, 1970; Mauseth, 1988). Positive hydrostatic pressure thought to be generated from root and/or stem xylem parenchyma is also known to occur in a range of temperate and tropical woody plants (Braun, 1984; Tibbetts & Ewers, 2000; Wegner, 2014). Parenchyma is also key to potential refilling of embolized vessels (Canny, 1997; Clearwater & Goldstein, 2005). Theoretical models show that the volumetric ratio of vessel-associated cells to vessels should be about 2:1 to enable successful refilling (Vesala, Hölttä, Perämäki, & Nikinmaa, 2003).

Tropical tree species generally have greater conduit diameters than do temperate diffuse-porous woody plants, with the exception of ring-porous temperate species (McCulloh et al., 2010; Wheeler, Baas, & Rodgers, 2007). Wet and warm climatic conditions are traditionally regarded as favoring species with wider conduits, whereas cold or dry environments support smaller conduits (Baas, 1973; Carlquist, 2001; Tyree & Zimmermann 2002; Zanne et al., 2014). However, vessel diameter is suggested to be related primarily to plant stature (conductive path length) and not climate, with vessels widening with increasing distance from the stem tip (Olson et al., 2014; Rosell, Olson, & Anfodillo, 2017). Although researchers are currently divided over the height versus climate debate in explaining variation in mean vessel diameter between individuals (e.g., Olson et al., 2014; Pfautsch et al., 2016), axial parenchyma fractions were found to be determined by climate, in particular temperature (Morris, Plavcová, et al., 2016). This represents a complex interaction spanning a range of xylem attributes, including plant size, vessel diameter, ray and axial parenchyma fractions, axial parenchyma spatial arrangements, and climate. Apart from speculation that a correlation exists between axial parenchyma arrangements and vessels (Braun, 1984; Kribs, 1937), there is no quantitative study that has investigated a statistical link between them.

The primary goal of this study was to quantitatively explore the relationship between the amount of axial parenchyma and vessel diameter, testing the hypothesis that the former increases with the latter. In addition, we tested the relationship between axial parenchyma arrangements and mean vessel diameter by means of a large-scale qualitative approach, demonstrating that as vessel diameter increases, the axial parenchyma arrangement becomes increasingly more paratracheal (a more grouped living cell arrangement surrounding a vessel or vessel group). This hypothesis would be in agreement with previous structure–function findings of a relationship between paratracheal axial parenchyma and water transport (Borchert, 1994; Borchert & Pockman, 2005; Goldstein et al., 1998; Tyree et al., 1999; Zheng & Martínez-Cabrera, 2013). In addition, we conducted a global-scale analysis between maximum plant height (height_{max}, m), mean vessel diameter, and a range of climate parameters to elucidate the degree to which both stem length and climate predict vessel diameter by measuring their effect sizes through a generalized additive mixed model (GAMM) approach. We also postulate that vessel diameter scales with both plant size and climate, but that climate has a significant predictive capacity on vessel diameter after partialling out the influence of plant size. Overall, the questions we address here improve our understanding of the structure–function relationships of xylem, and especially how the large spatial variation in axial parenchyma may contribute to plant hydraulic strategies.

2 | MATERIALS AND METHODS

2.1 | Compilation of the datasets

To test the hypothesis that axial parenchyma fraction scales with mean vessel diameter, it was important to include data from as wide a spectrum of climates as possible across a large phylogenetic span. Two separate and independent datasets were compiled. The first dataset was composed of 3,259 specimens (2,332 individual species) to investigate the relationships between height_{max}, climate, and vessel diameter. We included woody plants with a range of heights (the maximum height known for the species) between 0.5 and 114 m. The second dataset of 1,008 specimens (832 individual species) focussed on the relationship between vessel diameter, axial and ray parenchyma fractions, axial parenchyma arrangement, and climate. All anatomical records included in this analysis reported values for trunk wood only and not branch wood.

The vessel diameter data were based on the “Global Vessel Anatomy Database,” including 3,005 species (Zanne et al., 2010a, 2010b; available from the Dryad Digital Repository; http://dx.doi.org/10.5061/dryad.d1138), and various additional datasets (Ruelle, Clair, Beauchêne, Prévost, & Fournier, 2006; Wagenführ, 2007; Martínez-Cabrera, Jones, Espino, & Schenk, 2009; Poorter et al., 2010; Fichtler & Worbes, 2012; Olson & Rosell, 2013; Zheng & Martínez-Cabrera, 2013; Table 1). The measuring method for vessel diameter differed between authors. The majority of references, which were post-1989, used the IAWA Committee (1989) as a guideline for the measurement of vessel diameter, where the tangential diameter of at least 25 vessels was randomly measured at the widest point of the lumen (excluding cell walls). Pre-1989 publications often included the cell wall, such as in Baas, Werker, and Fahn (1983), which may overestimate the vessel diameter by up to 10 μm assuming a vessel wall is up to 5 μm. A more recent approach includes the equivalent circle diameter, which is the diameter of the circle having the same vessel cross-sectional area as the vessel measured (Scholz, Klepsch, Karimi, & Jansen, 2013).

Axial parenchyma, ray parenchyma, and ray and axial parenchyma (combined) tissue fractions were from Morris, Plavcová, et al. (2016) and Table S1 and are accessible via the TRY Plant Trait Database (https://www.try-db.org/tryweb/home.php; Kattge et al., 2011). Different methods to quantify parenchyma were used by various authors.
The methodology of all authors was checked for differences in approaches to measuring tissue fractions. Validation of the parenchyma fraction measurements was provided by Morris, Plavcová, et al. (2016), who found no significant difference between parenchyma fractions from literature and own measurements using a standard method. Axial and ray parenchyma were based on thin transverse wood sections using light microscopy (e.g., Martínez-Cabrera et al., 2009; Ruelle et al., 2012) or on polished wood surfaces using stereomicroscopy (Fichtler & Worbes, 2012; Poorter et al., 2010). The relative fraction of parenchyma tissue can be analysed by measuring the entire area covered by the tissue or by estimating this area using stereomicroscopy (Fichtler & Worbes, 2012; Poorter et al., 2010). The methodology of all authors was checked for differences in their interpretation.

### Data summary of tissue fractions for ray and axial parenchyma

<table>
<thead>
<tr>
<th></th>
<th>Total parenchyma (%)</th>
<th>Axial parenchyma (%)</th>
<th>Ray parenchyma (%)</th>
<th>Vessel diameter (μm)</th>
<th>Height(_{\text{max}}) (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(n) entries</td>
<td>1,259</td>
<td>1,008</td>
<td>1,008</td>
<td>3,259</td>
<td>3,259</td>
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<tr>
<td>(n) sources</td>
<td>39</td>
<td>39</td>
<td>39</td>
<td>8</td>
<td>&gt;200</td>
</tr>
<tr>
<td>(n) species/genera/families</td>
<td>832/400/104</td>
<td>832/400/104</td>
<td>832/400/104</td>
<td>2,332/890/184</td>
<td>2,332/890/184</td>
</tr>
<tr>
<td>Mean</td>
<td>26.27</td>
<td>4.60</td>
<td>17.45</td>
<td>94.43</td>
<td>17.25</td>
</tr>
<tr>
<td>Median</td>
<td>22.32</td>
<td>2.23</td>
<td>16.97</td>
<td>80</td>
<td>15</td>
</tr>
<tr>
<td>Min</td>
<td>6.88</td>
<td>0</td>
<td>5.23</td>
<td>10</td>
<td>0.2</td>
</tr>
<tr>
<td>Max</td>
<td>64.2</td>
<td>44.10</td>
<td>42.47</td>
<td>435.12</td>
<td>114</td>
</tr>
<tr>
<td>CV</td>
<td>22.32</td>
<td>134.25</td>
<td>30.26</td>
<td>62.88</td>
<td>76.26</td>
</tr>
</tbody>
</table>

Note. Total parenchyma, ray parenchyma, and axial parenchyma fractions and their literature sources were derived from Morris, Pavclova, et al. (2016).

### 2.2 Climate data

Locations for all 2,783 species were obtained from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/), which were matched to the corresponding location. Climate data for the locations were obtained from Bioclim layers based on the WorldClim Global Climate Database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) for the years 1950–2000. The following criteria were used for GBIF locations: (a) the record was not a duplicate according to the spatial coordinates of the sample, (b) a cut-off of a minimum of 10 records was imposed for calculating the median location and corresponding climatic computations, and (c) the record was not located within 0.01 decimal degrees of the GBIF headquarters in Copenhagen (55.68°N, 12.59°E) to reduce the chance that a record might be given a coordinate that matched to where the data were housed instead of where the plant was actually collected. In addition, we excluded nonnumeric coordinates, coordinates without a reasonable range, coordinates equal to exactly 0, records with similar latitude and longitude values, records with coordinates less than two decimal places of precision, and records located within 0.01 decimal degrees of a country’s centroid.

To investigate the relationships between climate and axial parenchyma amount, we assigned the species into three broad climatic zones: temperate, subtropical, and tropical. We used the climatic classification system created by Köppen (1936), as opposed to the later Köppen-Geiger version (Geiger, 1961), where broader classifications have been used rather than subdivided as in the latter climate system. In the Köppen (1936) classification, temperate includes boreal, maritime, and continental types, with subtropical ranging from permanent wet to summer dry and winter dry, and tropical including permanent wet, summer dry, winter dry, and monsoonal.

### 2.3 Statistical analyses

For all analyses in this study, model selection was carried out using the Akaike information criterion (AIC; Burnham & Anderson, 2002). The weight of support of each candidate model is assessed using the AIC weight (\(\omega\); Burnham & Anderson, 2002). We also measured the goodness of fit of models using the Nagelkerke pseudo-\(R^2\) (Nagelkerke, 1991). Partial correlation coefficient \(r\) (Nakagawa & Cuthill, 2007) and Cohen’s \(D\) (Cohen, 1988) were calculated for, respectively.
continuous and categorical variables of interest using the top-ranked candidate model. All analyses were carried out in R (R Core Team, 2015), and model selection was carried out using the package MuMln (Bartoń, 2016). When fitting models with non-linear continuous explanatory variables, all models were GAMMs using a Gaussian distribution with a maximum likelihood estimation method and were fitted using the mgcv package (Wood, 2006). For smoother terms, the maximum estimated degrees of freedom were limited to 5, and if the estimated degrees of freedom were close to 1, then we replaced the smoother term with a linear term. If the full model of the candidate set of models contained no smoother term, we fitted generalized linear mixed models using a Gaussian distribution with maximum likelihood estimation with the lme4 package instead of fitting GAMMs (Bates, Maechler, Bolker, & Walker, 2015). The random factor in all models was species nested within family. In all analyses, vessel diameter and height_{max} were log10 transformed to meet conditions of normality, and also because it is known that correlation between these variables can be approximated with a power function (Olson et al., 2014; Rosell & Olson, 2014).

To investigate the effect of climate on log-transformed vessel diameter, we fitted a model with the explanatory variables climate (temperate, subtropical, and tropical) and log-transformed maximum height. Due to collinearity, we did not enter ray and axial parenchyma combined fractions in the same models as axial parenchyma and ray parenchyma, with the latter being interpreted separately. We therefore applied model selection using two separate full models. To investigate the effect of axial parenchyma and ray parenchyma fractions, along with axial parenchyma arrangement on log-transformed vessel diameter, while controlling for climate, we fitted a full model prior to model selection with log-transformed height_{max}, elevation, mean annual precipitation, mean annual temperature, axial parenchyma arrangement, axial parenchyma, and ray parenchyma fractions. The maximum variance inflation was 1.92. A second full model prior to model selection had the explanatory variables log-transformed height_{max}, elevation, mean annual temperature, mean annual precipitation, axial parenchyma arrangement, axial parenchyma, and ray parenchyma fractions. The maximum variance inflation was 1.21.

As geographical location is likely to be highly collinear with meteorological environmental factors, latitude was not entered into the same models as mean annual temperature and mean annual precipitation, which were interpreted separately. We therefore applied model selection using two separate models. The first had the explanatory variables height_{max}, elevation, mean annual temperature, and mean annual precipitation. The maximum variance inflation factor (O’Brien, 2007) was 1.55. The second had the explanatory variables log-transformed for height_{max}, elevation, and latitude. The maximum variance inflation factor was 1.06.

3 | RESULTS

3.1 | Relationships between vessel diameter, axial parenchyma arrangements, and climate

Model selection strongly supports that log-transformed vessel diameter is related to log-transformed height_{max}, axial parenchyma category, axial parenchyma fraction, and mean annual temperature (Model 9, Table 2b, ΔAIC = 36.85, cumulative ω = 1). However, there was no support for an effect of ray parenchyma on vessel diameter (Models 1 and 3 of Table 2b). We used Model 3 in Table 2b to estimate effect size because it was the most parsimonious model (ΔAIC < 6).

Percentage axial parenchyma had a non-linear relationship with log-transformed vessel diameter, whereby there was a strong positive linear relationship until 10% axial parenchyma, after which the positive relationship weakened (Figure 2a). Model selection also supported a positive relationship between ray and axial parenchyma combined fraction and log-transformed vessel diameter (Table 2c; ΔAIC = 10.50, cumulative ω = .995; Figure 2b). However, the top-ranked model with the ray and axial parenchyma combined fraction (Model 1 in Table 2c) was less well supported than was the top-ranked model with axial parenchyma when separated from ray parenchyma (Model 3 in Table 2b and Model 1 in Table 2c; ΔAIC = 38.52), further suggesting that the effect is mainly driven by axial parenchyma and not ray parenchyma.

Parameter estimates revealed that the “absent/ extremely rare” (β = 1.453, 95% CI [1.379, 1.528]; Figure 2c) and “low apotracheal” 95% confidence intervals overlapped in their relation to vessel diameter (β = 1.461, 95% CI [1.413, 1.509]; Figure 2c). However, there was strong support that parenchyma categories “high apotracheal” (β = 1.664, 95% CI [1.591, 1.737]), “low paratracheal” (β = 1.578, 95% CI [1.531, 1.626]), “medium paratracheal” (β = 1.612, 95% CI [1.558, 1.666]), and “high paratracheal” (β = 1.598, 95% CI [1.530, 1.667]) were all significantly higher in relation to vessel diameter than were both the “absent/ extremely rare” and “low apotracheal” categories (Figure 2c).

3.2 | Effects of maximum plant height, elevation, and climate on vessel diameter

Model comparisons strongly supported a model that retained the effect of plant height_{max}, elevation, mean annual precipitation, and mean annual temperature (Model 1, Table 3a, ΔAIC = 14.55, ω = .999) on vessel diameter. Log-transformed vessel diameter was positively associated with mean annual temperature (Figure 3a), mean annual precipitation (Figure 3b), log-transformed plant height_{max} (Figure 4a), and elevation (Figure 4b). Considering the independent contributions from each of these predictor variables on vessel diameter, log-transformed plant height_{max} and mean annual temperature had medium to small effects (r = .360 and .241; β = 0.231, 95% CI [0.217, 0.249] and β = 0.027, 95% CI [0.023, 0.030]), whereas mean annual precipitation and elevation had negligible effects (r = .085 and .075; β = 0.00007, 95% CI [0.00004, 0.00009] and β = 0.00005, 95% CI [0.00003, 0.00007]). The effect of latitude on vessel diameter was also strongly supported by model selection (Table 3b, ΔAIC = 287.28). Latitude had a quadratic relationship with log-transformed vessel diameter, whereby log-transformed vessel diameter was at its largest near the equator (Figure 3d). Further confirming the effect of latitude, the effect of climate on log-transformed vessel diameter was strongly supported by model selection (Table 2a, ΔAIC = 15.97, ω = 1; temperate, β = 1.721, 95% CI [1.662, 1.781]; subtropical, β = 1.720, 95% CI [1.690, 1.750]; tropical, β = 1.774, 95% CI [1.747, 1.802]). Cohen’s D...
suggested a small but meaningful difference in log-transformed vessel diameter between the temperate and tropical climate (Cohen's $D = 0.314$; Figure 3c) as well as between the subtropical climate and tropical climate (Cohen's $D = 0.280$; Figure 3c). However, the difference in log-transformed vessel diameter between the temperate and subtropical climate was negligible (Cohen's $D = 0.038$; Figure 3c).

4 | DISCUSSION

4.1 | Relationships between vessel diameter, parenchyma fractions, and climate

The most important outcome of our GAMM approach is the positive relationship between mean vessel diameter and axial parenchyma (Figure 2a), and lack of relationship between mean vessel diameter and ray parenchyma fraction. The finding that temperature (Figure 3a), and not precipitation (Figure 3b), results in a mean vessel diameter increase (slope $= 0.027$ in Figure 3a) is in agreement with many wood ecological studies on latitudinal and altitudinal trends in vessel size (e.g., Baas, 1973; Carlquist, 2001; Fisher, Goldstein, Jones, & Cordell, 2007; Noshiro & Baas, 2000). Similar to vessel diameter, in a recent study, the ray and axial parenchyma combined fraction, and in particular axial parenchyma, were found to also increase with temperature (Figures 6, 55, and 56 in Morris, Plavcová, et al., 2016), with both mean vessel diameter (Figure 3d) and ray and axial parenchyma combined fractions increasing along a latitudinal gradient (Figure 7 in Morris, Plavcová, et al., 2016). These relations suggest a parallel trend between vessel diameter and parenchyma but may also indicate that the functions of ray parenchyma and axial parenchyma in relation to vessel diameter become increasingly more independent as temperature rises. However, the effect size of mean vessel diameter on axial parenchyma

### Table 2

A comparison of candidate models that relate log-transformed vessel diameter to (a) log-transformed plant height$_{max}$ and climate (including temperate, subtropical, and tropical) using generalized linear mixed models (GLMMs); (b) log-transformed plant height$_{max}$, axial parenchyma category, axial parenchyma (%), ray parenchyma (%), elevation, precipitation, and temperature using generalized additive mixed models; and (c) log-transformed plant height$_{max}$, axial parenchyma category, axial parenchyma, ray parenchyma, elevation, precipitation, and temperature using GLMMs.

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Model parameters</th>
<th>$k$</th>
<th>LL</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>$\omega$</th>
<th>Pseudo-$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Height$_{max}$ Climate</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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Note. The parameters included in the model are indicated by "+" and the number of parameters ($k$), log likelihood (LL), Akaike information criterion (AIC) of the models, change in AIC compared to the best ranked model ($\Delta$AIC), AIC model weights ($\omega$), and pseudo-$R^2$ are reported. The smoother was applied to axial parenchyma only because preliminary analyses revealed no non-linear relationships for ray parenchyma, parenchyma, elevation, mean annual precipitation, and mean annual temperature. The random factor in the GLMM was the species nested within the family. AP = axial parenchyma; RAP = ray and axial parenchyma; RP = ray parenchyma.
fraction weakened after axial parenchyma fractions reached approximately 10% (Figure 2a). A possible explanation for this weakened trend after approximately 10% may lie in the occupation of xylem space between axial parenchyma and vessels, where the size and frequency of the latter may pose an upper limit on the amount of axial parenchyma surrounding them. The addition of more axial parenchyma would trade off for space with the vessels and/or the mechanical tissues, which would be counterintuitive.

Furthermore, mean vessel diameter was related to the spatial distribution of axial parenchyma (Figure 2c). Therefore, when controlling for maximum height, paratracheal arrangements of axial parenchyma (Table S1) were more frequent in wide vessels (common in tropical species), whereas species with relatively narrow vessels typically show little apotracheal axial parenchyma (common in temperate regions). However, the arrangement “high apotracheal” was an anomaly (Table S1; Figure 2c), with high axial parenchyma amounts corresponding to large vessels, which was due to bias from ring-porous Quercus species with very large early-wood vessels. In Quercus, vessels are surrounded by vasicentric tracheids, with little or no contact from axial parenchyma. The frequency of paratracheal arrangements (Table S1) around wide vessels shows that selection appears to favour paratracheal axial parenchyma patterns in warmer climates, where
vessels are in general wider. Kribs (1937) suggested a correlation between vessel perforation type and axial parenchyma patterns, with the paratracheal arrangement thought to be the most derived form of association. Moreover, large vessel diameters in association with the paratracheal arrangement thought to be the most derived form between vessel perforation type and axial parenchyma patterns, with vessels are in general wider. Kribs (1937) suggested a correlation between vessel perforation type and axial parenchyma patterns, with the paratracheal arrangement thought to be the most derived form of association. Moreover, large vessel diameters in association with the paratracheal arrangement thought to be the most derived form between vessel perforation type and axial parenchyma patterns, with vessels are in general wider. Kribs (1937) suggested a correlation between vessel perforation type and axial parenchyma patterns, with the paratracheal arrangement thought to be the most derived form of association. Moreover, large vessel diameters in association with

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Note. The parameters included in the model are indicated by “+” and the number of parameters (k), log likelihood (LL), Akaike information criterion (AIC) of the models, change in AIC compared to the best ranked model (ΔAIC), AIC model weights (ω), and pseudo-R² are reported. The smoother was applied to elevation only because preliminary analyses revealed no non-linear relationships for elevation, precipitation, and temperature. The random factor in the GLMM was the species nested within the family.

On the basis of categorizing plants into broad climate types, our finding that mean vessel diameter is slightly higher in tropical than subtropical and temperate zones (3.1% higher on average; Figure 3c), when controlling for stem length, follows a similar trend for axial parenchyma (Figure 4 in Morris, Plavcová, et al., 2016). In a previous study, axial parenchyma tissue fractions were shown to increase abruptly above 14 °C (significantly higher in the tropics), with a negligibly different difference between temperate and subtropical zones (see Figures 6 and S5a in Morris, Plavcová, et al., 2016). Ray parenchyma tissue fractions, however, remained relatively unchanged across biomes (Figure 4 in Morris, Plavcová, et al., 2016). Due to categorization of vessel sizes and parenchyma into broad climate types being superficial in that many species span across ecoregions, the latitudinal trends are more informative (Figure 3d). The parallel trend between axial parenchyma fraction and mean vessel diameter supports a close relationship between them, where we speculate that temperature is strongly tuning vessel diameter to prevent thaw-induced embolism (Davis et al., 1999; Knipfer et al., 2015; Zanne et al., 2014); abundant axial parenchyma around narrow vessels would not be necessary to repair thaw-induced embolism. As there was no difference found between species of temperate and subtropical biomes (Figure 3c), where freezing temperatures are possible, only the tropical species are likely to have evolved in the complete absence of freezing temperatures and, therefore, have wider vessels and the support of more abundant high apotracheal and paratracheal axial parenchyma (Figure 2c).
4.2 Relationships between vessel diameter, maximum plant height, and climate

To understand the relationship between axial parenchyma and vessel diameter, factoring in height\(_{\text{max}}\) is crucial due to the influence of the latter on vessel diameter (Figure 4a). The global analysis of plant height\(_{\text{max}}\), climate, and mean vessel diameter shows that plant stature has the largest influence on vessel diameter due to the scaling effect (slope = 0.231; Figure 4a), where there is a gradual tapering of vessel diameter from the trunk to the leaves between species and within species, which occurs irrespectively of the environment the plant grows and is evident among all plant forms (i.e., shrubs, trees, succulents, and lianas; Coomes, Jenkin, & Cole, 2007; Martínez-Cabrera et al., 2009; Olson et al., 2014; Olson & Rosell, 2013; Rosell et al., 2017; Rosell & Olson, 2014). This vessel widening is a general phenomenon that has been recognized for many years (Grew, 1682; Sanio, 1872; De Bary, 1884). Without vessel widening, hydraulic conductivity per unit cross-sectional area of twig would decrease significantly with tree size, leading to reductions in productivity (Becker, Gribben, & Lim, 2000; Becker & Gribben, 2001; but see Savage et al., 2010). However, hydraulic conductivity of woody tissues varies little, if at all, with tree size as a result of vessel widening, which is found universally within vascular plants (Drake, Price, Poot, & Veneklaas, 2015; Petit & Anfodillo, 2009; Price, Enquist, & Savage, 2007; West, Brown, & Enquist, 1997, 1999).

**FIGURE 3** The effect of (a) mean annual temperature, (b) mean annual precipitation (MAP), (c) the biome type, and (d) latitude on log-transformed vessel diameter in angiosperm wood. (a, b) Based on the generalized linear mixed model (GLMM) 1 of Table 2a, which is based on 3,259 specimens out of 2,332 species. (c) Based on the GLMM 1 in Table 2a, which is based on 1,008 specimens out of 832 species. (d) Based on the GAMM 1 in Table 2b, including 3,259 specimens and 2,783 species. Data points represent partial residuals. The locations for all species were derived from the Global Biodiversity Information Facility, whereas the climate data corresponding to the locations were gathered from WorldClim. The solid line represents the fitted line (a and b), parameter estimates (c), or smoother (d), whereas the 95% confidence intervals are marked by the shaded zone. For the GAMMs, estimated degrees of freedom are limited to 5. Partial correlation coefficient \(r\) and the slope, with 95% confidence intervals, are shown in (a) and (b). For (c), the biggest vessel diameter sizes were found in tropical species, whereas differences between temperate and subtropical biomes were found to be negligible for mean vessel diameter.
When controlling for height_{max}, we found temperature to have a small but significant effect on vessel diameter (Figure 3a), whereas precipitation (Figure 3b) and elevation (Figure 4b) had an almost negligible effect. This demonstrates that climate has an influence on mean vessel diameter after controlling for height_{max}, a finding which supports studies reporting wider vessels in warmer climates (e.g., Pfautsch et al., 2016; Zanne et al., 2014). However, the latter study did not factor in plant height, which is accountable for most of the variation in vessel diameter (Figure 4a). This reveals that where most of the influence on vessel diameter is due to plant height, variation in vessel diameter between species is also attributable to climate (temperature specifically), as climate itself indirectly influences height. For example, trees are, on average, shorter in more northern and southern hemispheres than in midrange latitudes, with exceptions such as the woody angiosperms of tropical savanna and cool temperate regions of south east Australia (see latitudinal trends in Figure 3d). Whether plant height determines vessel diameter through water transport requirements, or vessel diameter determines transport capacity, and thus plant height being the less relevant, is not answered here and is perhaps unanswerable.

4.3 Functional significance of vessel–parenchyma–climate associations

Due to different plant strategies in temperate, subtropical, and tropical biomes along with wet versus arid habitats, there is likely to be a divergence in the functions related to axial parenchyma, with hydraulic maintenance being among numerous possibilities. Greater dependence on axial parenchyma for hydraulic maintenance likely occurs in the tropics, where many tropical families (e.g., Fabaceae, Bignoniaceae, Meliaceae, and Moraceae) have higher axial parenchyma fractions and paratracheal axial parenchyma arrangements (confluent, aliform, and vasicentric) around wide vessels (Figure 1c, e).

The amount and distribution of axial parenchyma were positively correlated with hydraulic capacitance in tropical evergreen species during dehydration (Borchert, 1994; Borchert & Pockman, 2005; Goldstein et al., 1998). With little or no direct, visual evidence of vessel refilling under negative pressure (Brodersen & McElrone, 2013; Charrier et al., 2016; Zwieniecki, Melcher, & Ahrens, 2013), the frequency of embolism formation is possibly related to a diurnal buffering effect via hydraulic capacitance, where controlled water release from vessel-associated cells (axial or ray parenchyma in contact with vessels) buffer extreme tensions in times of reduced water availability (Borchert, 1994; Holbrook, 1995; Meinzer et al., 2009; Sperry, Meinzer, & McCulloh, 2008; Vergeynst, Dierick, Bogaerts, Cnudde, & Steppe, 2015). Therefore, paratracheal axial parenchyma and vessel-associated cells may avert embolism in wide vessels, which might not have the capacity to reverse emboli due to shear volume limitations (Ewers, 1985), or axial parenchyma cells may not be plentiful enough or may not have sufficient connectivity to the vessel network to enable refilling. If a 2:1 ratio of ray and axial parenchyma combined fraction to vessel area is required for successful refilling to occur (Vesala et al., 2003), most angiosperm species would not fulfill this criterion because total ray and axial parenchyma tissue fractions are typically below 30%, especially in temperate trees (Morris, Plavcová, et al., 2016). However, the amount of parenchyma may not be the only important factor determining capacitance: The connectivity to the vessel network and to the living tissues in bark and pith may also be crucial (Morris et al., Submitted; Spicer, 2014).

Small vessels, but with greater vessel density (Aloni & Zimmermann, 1983), may not require extensive paratracheal axial parenchyma arrangements to avoid embolism formation because of an increased redundancy of the hydraulic system and small vessel volumes. Moreover, selection towards less axial parenchyma in temperate regions might be owing to energy demands to protect parenchyma against frost (Sperling, Earles, Secchi, Godfrey, & Zwieniecki, 2015; Wisniewski & Davis, 1995).

Nonstructural carbohydrates stored in the parenchyma were shown to have an important function in drought resistance through osmoregulation in tropical tree seedlings (O’Brien, Leuzinger, Philipson,
Parenchyma fractions in temperate tree species provide a useful proxy for nonstructural carbohydrate storage (Plavcová, Hoch, Morris, Ghiasi, & Jansen, 2016), with large paratracheal axial parenchyma fractions potentially keeping vessels hydrated during short drought periods. Large paratracheal axial parenchyma fractions, however, may reduce mechanical strength, possibly resulting in a trade-off between embolism risk and mechanical support (Zheng & Martínez-Cabrera, 2013). Finally, a recent hypothesis suggests that paratracheal axial parenchyma may produce surfactants (insoluble, amphiphilic lipids) in xylem sap, which has considerable consequences for water transport under negative pressure (Morris et al., in press; Jansen & Schenk, 2015; Schenk et al., 2017).

5 | CONCLUSION

This study is the first major global analysis of angiosperms to include parenchyma fractions and axial parenchyma spatial arrangement, vessel diameter, height_{max}, and climatic factors. We show that trees with wide vessels tend to have a high fraction of axial parenchyma, which is mainly packed around the vessels. However, the relationship between vessel diameter and axial parenchyma does not explain all the variation and tells us that other factors are at play in explaining xylem structure and trade-offs, where wide vessels for some taxa are decoupled from axial parenchyma, demonstrating an evolutionary independence (e.g., Allantoma decandra; Figure 1f). In summary, we have calculated the proportion of variation attributed independently to vessel diameter versus climate, and height_{max} versus climate. However, plant height, vessel diameter, and axial parenchyma likely exhibit correlation with climate via natural selection acting on these traits as a coordinated assemblage, which has not been directly tested here. This study provides evidence that water transport in plants is not only controlled by structural and physico-chemical attributes of dead conduits but is also likely to be affected by the living cells.

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STATEMENT OF AUTHORSHIP

HM conceived the study with SJ, LP, MAFG, SMG, EW, and MAE. MAFG and HM conducted the analyses. Data were contributed by LP, MEO, HM, DAC, EF, MMK, HIMC, DJMG, JAR, EAW, JZ, and KZ. HM and SJ wrote the manuscript in collaboration with MAFG, SMG, and MAE. All other authors contributed substantially to manuscript revisions.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found online in the supporting information tab for this article.

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