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Tree height predicts the shape of radial sap flow profiles of Costa-Rican tropical dry forest tree species

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1. Introduction

Accurate estimates of stand-level transpiration are indispensable for an improved understanding of water fluxes in terrestrial ecosystems, which in turn is required to predict the response of forests to changing precipitation regimes (Schlesinger and Jasechko, 2014). A common way of estimating stand-level transpiration is by scaling up predictions of whole-tree water-use of individual trees that are based on measurement with thermal sap flux probes placed into the conductive part of the sapwood (Oishi et al., 2008; Wang and Dickinson, 2012). While transpiration estimates based on water-use estimates of individual trees have the advantage of preserving information on functional links between plants and their environment (Meinzer et al., 2001; Wilson et al., 2001; Caylor and Dragoni, 2009), uncertainties regarding the spatial distribution of sap flux in the stem can result in large inaccuracies when scaling up to tree- and stand-level (Hatton et al., 1995; Ford et al., 2004b; Oishi et al., 2008; Reyes-Acosta and Lubczynski, 2013).

It has long been known that sap flux is highly variable across the sapwood area, both in radial (Edwards and Booker, 1984; Čermák et al., 1992) and azimuthal direction (Miller et al., 1980). In recent years, radial gradients in sap flux density (in the following, radial profiles) have received special attention, as many commonly used sap flux probes only measure the sap flux density in the outermost few
centimeters of the sapwood, which potentially leads to large errors in whole-tree water-use estimates when assuming uniform flux across the sapwood in the presence of pronounced radial changes (Caylor and Dragoni, 2009; Reyes-Acosta and Lubczynski, 2014; Zhang et al., 2015).

As sap flux density tends to decline with increasing distance from the cambium (Delzon et al., 2004), ignoring radial variation when scaling up to whole-tree water-use has been found to lead to an over-estimation of tree water-use by up to 154% (Čermák and Nadezhdina, 1998; Ford et al., 2004b).

Notwithstanding the obvious importance of accounting for radial gradients when scaling up sap flux density measurements to estimates of tree water-use, a literature survey by Berdanier et al. (2016) found that a majority of 58% of a sample of 122 papers published between 2013 and 2015 assumed constant sap flux density throughout the sapwood, while 27% of the papers used a simple correction based on weighted means in different annuli and only 15% used continuous radial profile models. We concur with the notion of these authors that there is a need for transferrable models that enable to account for radial profiles in the absence of species- or site-specific radial sap flux measurements. This is especially true when studying tree water-use in tropical forests, where the determination of species-specific radial profiles may often not be feasible due to the high species diversity.

The shape of radial gradients in sap flux density has been linked to a multitude of explanations, such as ontogenetic changes in wood anatomy related to sapwood maturation and aging (Spicer and Gartner, 2001), anatomical differences between conifers, ring-porous and diffuse-porous trees (Berdanier et al., 2016), connection with roots situated in different soil layers (Nadezhdina et al., 2007) and even small-scale differences between early- and latewood tracheids in conifers (Fan et al., 2018). As a consequence, radial profiles may differ considerably between species even in the same habitat (Gebauer et al., 2008). It has further been shown in some instances that the shape of radial profiles can be linked to other tree traits, e.g. tree size (Delzon et al., 2004; Zhang et al., 2018) and wood anatomical traits (Guyot et al., 2015; Zhao et al., 2018). This indicates that when measuring radial profiles for all present species is not feasible, a promising way to reduce the uncertainty in upscaled estimates of tree water-use is to identify surrogate traits that predict their shape.

In this study, we use a dataset of daily averages of sap flux measurements performed with the heat field deformation method (Nadezhdina et al., 1998, 2012, 2018) to model the radial sap flux profiles of 38 trees belonging to eight Costa Rican tropical dry forest species using a Bayesian hierarchical modeling framework. We hereby follow the approach of Caylor and Dragoni (2009), who proposed to separate sap flux measurements into a time-dependent component describing the response of stem conductance to environmental conditions and a time-invariant component describing the relative spatial distribution of sap flux density along the tree radius. In this work, we focus on the time-invariant component of sap flux, extending upon the hierarchical modeling approach of Berdanier et al. (2016) by expressing the parameters determining the shape of the radial sap flux profiles as functions of a set of structural and functional traits.

We hypothesize that (i) the parameters governing the shape of the radial profiles can be predicted by wood density, tree height and radial growth rate, and (ii) there are credible differences in the relative shape of radial profiles between trees of the same species. We further use the predicted radial profiles to obtain estimates of whole-tree water-use for each tree with the propagated uncertainty from our model, and investigate their relationship with a set of predictor variables. We then compare these estimates of whole-tree water-use against simple water-use estimates based on the average sap flux density in the outermost 2 cm of sapwood to test the hypothesis that (iii) single-sensor methods that assume constant sap flux density across the sapwood depth consistently overestimate tree water-use compared to methods based on radial profiles.

2. Analytical framework

When upscaling from sap flux density measurements to whole-tree water-use, the instantaneous whole-tree sap flow \( F_i(t) \) at a time \( t \) can be described as the product of the average sap flux density \( \tau_i(t) \) at that time and the sapwood area \( A_i \):

\[
F_i(t) = \tau_i(t)A_i \tag{1}
\]

Under the simplifying assumption of a homogeneous radial sap flux profile (i.e., no azimuthal variation in sap flux density) and expressing the sap flux profile with regard to a relative radial coordinate \( r \) describing the distance from the cambium relative to the radius \( R \) of the tree, it is possible to compute the average sap flux density by integrating over the radial profile, yielding the following expression for \( F_i(t) \) (Caylor and Dragoni, 2009; Berdanier et al., 2016):

\[
F_i(t) = 2\pi R^2 \int_0^1 (1 - r) \psi_i(r, t) \, dr \tag{2}
\]

In this study, we follow the framework of Caylor and Dragoni (2009), who proposed to decompose the instantaneous sap flux density \( \psi_i(r, t) \) at any point \( r \) in the radial profile into a product of a time-invariant component \( \rho_i(r) \) describing the radial sap flux profile and a time-dependent component \( c_i(t) \) describing stem conductance:

\[
\psi_i(r, t) = \rho_i(r)c_i(t) \tag{3}
\]

Like Caylor and Dragoni (2009), we describe the radial component based on the probability density function of a beta distribution, but express it based on the (biologically more interpretable) relative distance \( r \) from the cambium instead of a relative distance from the tree center. In addition, we reparameterize it with its expected value \( \mu = \alpha/(\alpha + \beta) \) and a concentration parameter \( K = \alpha + \beta \) instead of the commonly used shape parameters \( \alpha \) and \( \beta \) (cf. Ferrari and Cribari-Neto, 2004):

\[
\rho_i(r|\mu, K) = \frac{\mu^{K-1}(1 - r)^{1 - \mu K - 1}}{B(\mu K, (1 - \mu) K)}, \tag{4}
\]

where \( B(a, b) \) is the beta function. This reparameterization has the advantage that it results in biologically directly interpretable parameters describing the ‘average profile depth’ \( \mu \) (weighted average of relative distance of the cambium weighted by the sap flux density at that position) and the concentration \( K \) showing how narrowly the profile is centered around \( \mu \). The possible radial profile shapes that can be described by Eq. (4) are illustrated in Fig. 1; it can be seen that larger values of \( \mu \) move the bulk of sap flow away from the cambium, while larger values of \( K \) center the profile more strongly around \( \mu \).

Inserting Eq. (3) into Eq. (2) yields

\[
F_i(t) = 2\pi R^2 c_i(t) \int_0^1 (1 - r) \rho_i(r) \, dr, \tag{5}
\]

which has a simple closed form solution for the beta distribution, as the integral in Eq. (5) is equal to \( 1 - \mu \), yielding the following expression for the whole-tree sap flow \( F_i(t) \) (cf. Caylor and Dragoni, 2009):

\[
F_i(t) = \rho_i c_i(t) A_i = 2\pi R^2 (1 - \mu) c_i(t) \tag{6}
\]

Accordingly, under the given assumptions, the entire influence of the shape of the radial profile on the whole-tree water use can be expressed based on the average profile depth \( \mu \), which can be directly estimated from the data when expressing the radial profile according to Eq. (4).

3. Material and methods

3.1. Study site

The sap flow measurements were performed on eight tropical dry
forest tree species at the Estación Experimental Forestal Horizontes (EEFH) in the Guanacaste area in northwestern Costa Rica (10.718° N, 85.594° W) during the rainy season of 2015. The climate in the region is characterized by a pronounced annual pattern in precipitation with an almost rain-free dry season that lasts from December until May. The mean annual temperature is 25 °C, and annual precipitation at the nearby Santa Rosa climate station ranges from 880 to 3030 mm with a 30-year average of 1765 mm (Instituto Meteorológico de Costa Rica, 2015; Werden et al., 2018). The measured trees are situated in permanent sample plots managed by the School of Forestry Engineering of the Instituto Tecnológico de Costa Rica that were established in 2012. The vegetation in the sample plots consists of secondary forests on former pastures that were abandoned between 21 and 40 years before the measurement campaign in 2015 (Reyes Cordero, 2012). The trees in the sample plots belong to mostly deciduous tropical dry forest species and constitute a mosaic of relatively young secondary forest trees interspersed by large emergent trees that were left uncut by farmers as shading trees for livestock (mostly *Hymenaea courbaril*). The soils of the plots are Inceptisols and Vertisols (Alfaro et al., 2001; Reyes Cordero, 2012).

### 3.2. Selection of experimental trees

Out of the species present in the permanent sample plots, eight species were selected to represent a gradient in wood density (WD) and tree height at maturity (H). To achieve this, the 30 most common species were stratified by average wood density and diameter at breast height (DBH) as a proxy for tree H, and eight species representing gradients in both variables were selected taking into account species-specific information such as the presence of abundant latex or resins that interfere with hydraulic measurements. Of each of these species, five individuals were sampled from the 50th to 100th percentile of the diameter distribution to ensure selecting mature individuals.

All experimental trees were equipped with dendrometer bands (UMS GmbH, München, Germany) in August 2015 to measure DBH and radial growth rates. Annual stem increment (ASI) was determined as the slope of the regression line of DBH against time using a dataset of bimonthly growth measurements from August 2015 until October 2017. The height of the experimental trees was determined in November 2015 using a Vertex IV Hypsometer with Transponder T3 (Haglöf, Längsele, Sweden). WD of the sapwood was measured from 5 to 7 cm long samples taken with a 5.15 mm increment corer (Haglöf, Långsele, Sweden) as the oven-dry weight (dried at 105 °C) divided by the wet volume. The volume was estimated from length and four diameter measurements with a caliper (two at each end along a coordinate plane). A list of the sampled species with the averages of H, DBH and WD is provided in Table 1.

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>WD (g cm⁻³)</th>
<th>Height (m)</th>
<th>DBH (cm)</th>
<th>ASI (mm yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bursera simaruba</em> (L.) Sarg.</td>
<td>Burseraceae</td>
<td>0.39 (0.37 - 0.45)</td>
<td>16.5 (15.1 - 19.0)</td>
<td>50.8 (33.2 - 73.6)</td>
<td>6.7 (3.0 - 13.6)</td>
</tr>
<tr>
<td><em>Cordia panamensis</em> L. Riley</td>
<td>Cordiaceae</td>
<td>0.40 (0.37 - 0.43)</td>
<td>11.0 (9.6 - 14.6)</td>
<td>18.3 (17.8 - 33.8)</td>
<td>3.5 (0.9 - 5.4)</td>
</tr>
<tr>
<td><em>Machaerium biovulatum</em> Micheli</td>
<td>Fabaceae</td>
<td>0.52 (0.51 - 0.56)</td>
<td>12.5 (6.8 - 15.1)</td>
<td>15.4 (14.8 - 18.4)</td>
<td>3.6 (1.1 - 14.1)</td>
</tr>
<tr>
<td><em>Luehea speciosa</em> (Willld.)</td>
<td>Malvaceae</td>
<td>0.58 (0.55 - 0.63)</td>
<td>12.1 (8.3 - 13.9)</td>
<td>22.2 (21.9 - 26.5)</td>
<td>0.3 (0.2 - 8.4)</td>
</tr>
<tr>
<td><em>Cordia alliodora</em> (Ruiz &amp; Pav.) Oken</td>
<td>Cordiaceae</td>
<td>0.59 (0.54 - 0.63)</td>
<td>14.4 (11.8 - 16.6)</td>
<td>19.1 (15.0 - 29.2)</td>
<td>2.8 (1.0 - 5.6)</td>
</tr>
<tr>
<td><em>Albizia nigripesdens</em> (Benth.) Burkart</td>
<td>Fabaceae</td>
<td>0.66 (0.60 - 0.77)</td>
<td>14.2 (12.2 - 16.5)</td>
<td>26.3 (21.0 - 36.5)</td>
<td>3.5 (2.1 - 11.1)</td>
</tr>
<tr>
<td><em>Hymenaea courbaril</em> L.</td>
<td>Fabaceae</td>
<td>0.69 (0.66 - 0.76)</td>
<td>24.3 (19.1 - 25.6)</td>
<td>76.2 (52.6 - 91.5)</td>
<td>3.4 (0.8 - 4.3)</td>
</tr>
<tr>
<td><em>Handroanthus impetiginosus</em> (Mart. Ex DC.) Mattos</td>
<td>Bignoniaceae</td>
<td>0.75 (0.71 - 0.80)</td>
<td>14.0 (12.7 - 15.6)</td>
<td>27.4 (23.1 - 34.8)</td>
<td>9.4 (7.0 - 13.2)</td>
</tr>
</tbody>
</table>
3.3. Sap flow measurements

Measurements of radial patterns in sap flux density were performed with the heat field deformation (HFD) method (Nadezhdina et al., 1998, 2012; Nadezhdina, 2018) using a commercially available sensor type (HFD100, ICT International Pty Ltd., Armidale, Australia). During each of four subsequent measurement campaigns of 5–7 days each in October and November 2015, HFD sensors were installed on ten experimental trees. The measurements from two of the trees had to be discarded because of sensor/battery malfunctions, resulting in a final dataset with observations from 38 trees.

To install the sensors, the bark was partially removed and four holes were drilled in pre-defined distances using a drilling template. Then, stainless steel sleeves were inserted into the holes, and the sensors were coated in silicone grease and introduced into the sleeves. Polystyrene spacers of adequate sizes were used to ensure that the first measurement point was situated exactly 5 mm below the cambium in all stems. Each sensor was connected to a 60 Ah battery, and programmed to log sensor temperatures at eight different depths (in 1-cm steps from 0.5 cm to 7.5 cm below the cambium) in intervals of 10 min. To ensure thermal insulation of the sensors, the stem sections containing the sensors were completely covered with insulating mats made of open-cell foam coated with a reflective aluminum layer.

The measured temperature differences between the sensors were used to calculate estimates of sap flow per section (SFS, cm s⁻¹) according to Nadezhdina et al. (1998, 2012) using the Sap Flow Tool software (v1.4, ICT International Pty Ltd., Armidale, Australia), assuming a nominal thermal diffusivity of sapwood of 2.5 × 10⁻³ cm² s⁻¹ (Marshall, 1958). The dataset was then aggregated by calculating daily averages of estimated SFS for all complete measurement days.

The HFD method has recently been criticized due to flaws in the mechanistic derivation of the equation used to calculate sap flux density (Vandegehuchte and Steppe, 2012), a possible underestimation of flux densities of up to 60% (Steppe et al., 2010) and due to the large inter- and intraspecific variability in calibration parameters in empirical calibrations (Fuchs et al., 2017). The thermal properties of the wood of tropical tree species are likely to deviate considerably from the properties of temperate species the method has been tested on. For that reason, absolute values of sap flux density of the studied tropical forest species measured with HFD method should be treated with care unless species-specific calibration data are available. However, relative differences in the radial patterns of sap flux density should not be affected by the above-mentioned problems as long as the within-stem calibration relationship is approximately linear and there are no radial changes in thermal diffusivity. In either case, due to the unanswered question whether SFD can be calculated by dividing SFS by the sapwood depth (cf. Vandegehuchte and Steppe, 2012), we decided to base our model on the raw SFS values.

3.4. Measurement of stand microclimate and soil moisture

To track environmental variables relevant for sap flow, we measured vertical gradients in microclimatic variables at three different subsites throughout the entire measurement interval in October and November 2016. To achieve this, we used ropes fixed at high canopy branches to install small loggers (iButton Hygrochron™, Dallas Semiconductor, Dallas, TX) in different heights and recorded air temperature (T) and relative air humidity (RH) in 10-min intervals. The first measurement point was situated at breast height (1.3 m); the following points were installed in 5-m intervals from 5 m height to the canopy level (20 m in two subsites, 15 m in a third subsite). The resulting measurements of T and RH were used to calculate the air vapor pressure deficit (VPD) based on Eq. 11 in Allen et al. (1998). In addition, during each of the four campaigns, soil samples were taken at 10 cm soil depth to measure gravimetric soil water content in all nine subplots of the five sample plots.

3.5. Modeling radial sap flux density profiles

The measured radial sap flux profiles were modeled in a Bayesian hierarchical modeling framework based on the Stan probabilistic programming language (Carpenter et al., 2017) accessed through R v. 3.5.2 (R Core Team, 2018) using rstan v. 2.18.2 (Stan Development Team, 2018).

The observational unit in our model were daily averages of the raw SFS values. The shape of the radial profile was described with the density function of the beta distribution (\(\rho_s\); see Eq. (4)) multiplied with an arbitrary multiplicative constant \(c\) adjusting \(\rho_s\) to the observed absolute values of SFS (see Section 3.6 for the relationship between \(c\) and \(c(t)\)). The observed SFS values were assumed to be distributed normally around their expected value. The parameters \(\mu\) and \(K\) were expressed as linear functions of the predictor variables \(H\), \(WD\) and \(ASI\), using a logit and a natural log link, respectively, and allowed to vary randomly between trees and species. The multiplicative parameter \(c\) was allowed to vary randomly between trees and measurement days within trees, but not assigned a parameter regression, as the absolute value of SFS does not have a mechanistic explanation (see above). The random tree and species effects \(v\) and \(w\) were described with a multivariate normal distribution, while the random day effects were assumed to be drawn from a normal distribution.

For an observation \(i\) on day \(j\) belonging to tree \(k\) of species \(l\), the model could be expressed as:

\[
\begin{align*}
\tilde{SFS}_{ijkl} &= \v c_k \beta_j \rho_k \mu_{ijkl} \mu_{ijkl}^{-1} (1 - \rho_j)^{1 - \mu_{ijkl}} \mu_{ijkl}^{-1} \\
\tilde{SFS}_{ijkl} &\sim \text{Normal} \left( \tilde{SFS}_{ijkl}, \sigma \right)
\end{align*}
\]

(7)

\[
\begin{align*}
\log(\rho_{ijl}) &= \beta_{kijl} + \beta_{kijl} WD_{ij} + \beta_{kijl} H_{ij} + \beta_{kijl} ASI_{ij} + v_{kijl} + w_{kijl} \\
\log(\mu_{ijl}) &= \beta_{kijl} + \beta_{kijl} WD_{ij} + \beta_{kijl} H_{ij} + \beta_{kijl} ASI_{ij} + v_{kijl} + w_{kijl} \\
\log(v_{ij}) &= c_0 + u_r + v_{ij} \\
v_{ij} &\sim \text{MVN}(0, \Sigma_v) \\
w_{ij} &\sim \text{MVN}(0, \Sigma_w) \\
u_r &\sim \text{Normal}(0, \tau_r)
\end{align*}
\]

(8)

(9)

(10)

(11)

(12)

(13)

(14)

where \(\sigma\) is the residual standard error, \(\beta_{kijl}\) and \(\beta_{kijl}\) are the parameters of the tree level regressions of \(\mu\) and \(K\) against \(H\), \(WD\) and \(AGR\), and \(\Sigma_v\), \(\Sigma_w\) and \(\tau_r\) are the covariance matrices/standard deviation of the random effects. In addition to the full model described above, we fitted two simplified models, both of which did not include fixed effects in the parameter regressions for \(\mu\) and \(K\), and one of which additionally assumed \(\mu\) and \(K\) to be constant between trees belonging to the same species.

All parameters in the model were assigned weakly informative priors (Gelman, 2006; Gelman et al., 2008). Markov Chain Monte Carlo (MCMC) sampling was performed using Hamiltonian Monte Carlo via Stan’s No-U-Turn-Sampler (Hoffman and Gelman, 2014) using 4 chains with 10,000 iterations each and a burn-in of 5000 samples. To describe the variance explained on different levels in the hierarchy of the model, we calculated the Bayesian \(R^2\) proposed by Gelman et al. (2018) extended to a multi-level modeling approach analogously to Nakagawa and Schielzeth (2013) for each of the parameter regressions, and additionally calculated an overall pseudo-\(R^2\) as a measure of model fit. Model performance was compared between the three alternative model formulations by calculating goodness-of-fit statistics from model predictions to assess precision (correlation between observed and predicted values), trueness (mean signed deviation), and overall accuracy (root mean square error and pseudo-\(R^2\)) when using the model to predict sap flow per section for new measurement days, new trees and new tree species.
A detailed description of our model including details on transformations, prior specification, model fitting and inspection, calculation of explained variance and goodness-of-fit statistics is given in Supplemental Material A.

3.6. Estimates of total sap flow

According to the authors that introduced the HFD method, dividing sap flow per section by the sapwood depth \( L_{SW} \) results in an estimate \( v' \) of sap flux density (Nadezhdina et al., 1998, 2012).

\[
v' = \frac{SFS}{L_{SW}} \tag{15}\]

While there is sufficient evidence that the correlation of this quantity with gravimetrically measured sap flow density is only empirical (Vandegehuchte and Steppe, 2012; Fuchs et al., 2017), we estimated \( v' \) from our sap flux profiles to illustrate how to use our model output to calculate tree water-use.

If the equality in Eq. (15) holds and \( v' \) is indeed an estimate of sap flux density, the multiplicative constant \( c \) in our model equation (Eq. (7)) can be converted to an estimate of stem conductance by dividing it by \( L_{SW} \). If this is the case, the average water-use of a tree can be estimated by

\[
F_i = 2\pi R^2 (1 - \mu_{jk}) \frac{c_k}{L_{SWk}}, \tag{16}\]

where \( c_k \) is the tree-level prediction of \( c \) (i.e., without day-level random effects). As sapwood depth was not measured directly, it was estimated from the model as the depth up to which 90% of flow takes place using the quantile function of the beta distribution with the estimated parameters of the radial profile. We then assessed how the log-transformed posterior mean of tree DWU responded to WD, H and AGR using simple linear mixed effects models with random species effects (Bates et al., 2015) with p-values from Wald z-tests with Satterthwaite’s correction (Kuznetsova et al., 2017). As a species-specific calibration of the HFD sensors was not possible, the outcome of these calculations has to be interpreted with care.

To assess how much our radial profile-based estimates of tree water-use differ from single-sensor measurements with a sensor with a typical sensor length of 2 cm, we calculated a naïve estimate of tree water-use assuming sap flux density to be constant across the sapwood area. We calculated the average sap flux density over a subset of the radial profile ranging from depth \( a \) to depth \( b \) as

\[
F_{\text{naive}} = \frac{1}{b - a} \int_{a/R}^{b/R} \frac{SFS(r)}{r} dr \frac{1}{L_{SW}}. \tag{17}\]

We then used Eq. (1) to calculate the approximate tree water-use based on the average sap flux density in the outermost 2 cm, and calculated the ratio of this quantity to the tree water-use based on radial profiles as

\[
\text{Water use ratio} = \frac{F_{\text{naive}}}{F_i} = \frac{\bar{v}_{\text{naive}} A_i}{F_i} \tag{18}\]

to be able to quantify the degree of over-estimation of single-point measurements with short sensors relative to measurements based on radial sap flux profiles. Based on the propagated MCMC uncertainty of our model, we then tested whether this computed quantity was credibly different from one (i.e., whether there were credible differences in water use estimates).

4. Results

4.1. Microclimatic and hydrologic conditions

According to the soil moisture measurements, gravimetric soil water content was on a lower level during the first campaign (mean ± standard error: 19.0 ± 0.3%) and increased to comparable, somewhat higher values between 23.0 ± 0.3% and 24.2 ± 0.3% during the following three campaigns (Fig. 2a).

The vertical stand microclimate measurement campaign revealed a pronounced increase in evaporative demand with height in the stand during the daytime hours (6:00 am to 6:00 pm), when RH declined by 10.7% from near the forest floor at 1.3 m to the uppermost canopy at 20 m (from 86.1 ± 0.1% to 76.9 ± 0.1%), related to an increase in \( T \) by 1.3 °C (from 27.74 ± 0.03 °C to 29.01 ± 0.04 °C). This resulted in a by
77.1% higher VPD than near the forest floor. During nighttime (6:00 pm to 6:00 am), on the other hand, vertical gradients were neither observed in T (~24 °C in all heights) nor RH (~95% in all heights; Fig. 2b).

### 4.2. Model of radial sap flow profiles

The predictions of our model described the observed radial patterns in SFS very well for the large majority of trees (Figure B.1). In total, the day-specific predictions of the full model explained 96% of the variance in the observed SFS. A plot of the radial profiles predicted by the full model is shown in Fig. 3 (for tree-level plots, see Figure B.2 in the supplementary material).

All parameters in the model had a value of $R^2$ well below 1.1 (average $R^2$: 1.00007, maximum $R^2$: 1.00180), which indicates that the chains had fully converged after the burn-in period of 5000 iterations. The effective sample size was 17,097 on average, and did not reach less than 20% of the total sample size except for three parameters associated with the covariance matrices of the random effects and less than 10% for none of the parameters.

### 4.3. Model comparison

The accuracy of the predictions of the three different models is shown in Table 2. The predictions of the model with average profile depth $\mu$ and concentration parameter $K$ fixed on the species level performed worst in precision (Corr.) and overall accuracy (RMSE, pseudo-$R^2$) on all three levels of predictions, and only scored best in trueness (lowest MSD) for the day-level predictions. The average predictions for new days by both the tree-level models with and without parameter regressions performed almost identically in terms of bias, precision and overall accuracy. However, when generalizing to new trees and new species, the model that incorporated information about tree size, wood density and growth achieved a much better fit, with the average predictions for new trees explaining 69.0% and the predictions for new species still explaining 66.6% of the variance in the dataset compared to 62.1% and 55.1%, respectively, for the model without parameter

### Table 2

Predictive accuracy of the three fitted models on three levels of generalization (average predictions for new measurement days, new trees and new tree species). Model A: constant radial profile within species, no parameter regressions; Model B: tree effects, but no parameter regressions; Model C: full model. Given are the root mean square error (RMSE), mean squared deviation (MSD), Pearson correlation between observed and predicted values (Corr.) and explained variance (pseudo-$R^2$).

<table>
<thead>
<tr>
<th>Level</th>
<th>Model</th>
<th>MAE</th>
<th>RMSE</th>
<th>Bias</th>
<th>Corr.</th>
<th>pseudo-$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>New day</td>
<td>Model A</td>
<td>3.977</td>
<td>6.517</td>
<td>−0.024</td>
<td>0.888</td>
<td>0.786</td>
</tr>
<tr>
<td></td>
<td>Model B</td>
<td>2.346</td>
<td>4.041</td>
<td>−0.139</td>
<td>0.959</td>
<td>0.919</td>
</tr>
<tr>
<td></td>
<td>Model C</td>
<td>2.351</td>
<td>4.049</td>
<td>−0.125</td>
<td>0.958</td>
<td>0.918</td>
</tr>
<tr>
<td>New tree</td>
<td>Model A</td>
<td>5.325</td>
<td>10.409</td>
<td>−0.879</td>
<td>0.716</td>
<td>0.621</td>
</tr>
<tr>
<td></td>
<td>Model B</td>
<td>4.880</td>
<td>9.187</td>
<td>−0.551</td>
<td>0.784</td>
<td>0.690</td>
</tr>
<tr>
<td></td>
<td>Model C</td>
<td>4.885</td>
<td>9.280</td>
<td>−0.885</td>
<td>0.772</td>
<td>0.666</td>
</tr>
<tr>
<td>New species</td>
<td>Model A</td>
<td>6.046</td>
<td>10.804</td>
<td>−2.122</td>
<td>0.671</td>
<td>0.508</td>
</tr>
<tr>
<td></td>
<td>Model B</td>
<td>6.221</td>
<td>11.664</td>
<td>−1.665</td>
<td>0.638</td>
<td>0.551</td>
</tr>
<tr>
<td></td>
<td>Model C</td>
<td>5.158</td>
<td>9.320</td>
<td>−0.885</td>
<td>0.772</td>
<td>0.666</td>
</tr>
</tbody>
</table>
regressions. While it is notable that the models had a tendency to underpredict the true values (negative MSD), this is likely partially an artefact caused by smoothing out the curvature of the predicted profile when marginalizing over a large set of possible parameter values.

4.4. Parameter models

The predictor variables explained a considerable part of the variance in both the estimated concentration parameter $K$ and the expected relative profile depth $\mu$. On the scale of the linear predictor, the fixed effects for $H$, $WD$ and $ASI$ explained 46.3% of the variance in the average profile depth $\mu$, while only 6.7% of the variance was explained by random species and 47.0% by random tree differences. For the concentration parameter $K$, on the scale of the linear predictor, 43.2% of the variance was explained by the fixed effects, while species-level random effects explained 27.0% and random tree effects 29.8% of the variance, respectively.

Partial residual plots displaying the response of the estimated parameters to each of the predictor variables while controlling for the effect of other predictors are provided in Fig. 4. While the effect of wood density and stem increment was not credibly different from zero neither for average profile depth nor for the concentration parameter (Fig. 4, Table 3), both parameters responded strongly to tree height, with radial profiles reaching up to a lower relative depth and being more concentrated around their expected value for higher trees (Fig. 4, Table 3).

4.5. Estimated tree water-use

While there was considerable within-species variability in the estimated daily water-use ($DWU$), clear species patterns were visible (Fig. 5a), with species averages of $DWU$ spanning more than one order of magnitude. The approximate $DWU$ did not respond significantly to wood density and stem increment, but was strongly positively associated with tree height ($t = 56.98, \text{edf} = 33.5, p < 0.001$; cf. Fig. 5b-d).

On average, estimates of $DWU$ based on short sensors were 26% higher than the radial-profile-based estimates used as a baseline, with a range of $-41\%$ to $+113\%$. Credible underpredictions only occurred for two trees with strongly hump-shaped radial profiles (cf. Fig. 6). The average $DWU$ predictions from short sensors were credibly larger than the profile-based predictions for all but one species (Handroanthus impetiginosus).

5. Discussion

5.1. Modeling results

Our results indicate that our model was well able to capture the shape of the observed radial sap flux profiles, with the day-wise predictions of the full model explaining a total of 96.0% of the variance in sap flow per section. However, a large part of the variance in the dataset was associated with sources of random variability acting on higher levels in the hierarchy of the data, resulting in considerably larger uncertainty when predicting to new trees and new species. Due to differences in the scale of the response, we cannot directly compare our model fit to the model of Berdanier et al. (2016), to our knowledge the
only other authors who modeled radial sap flow profile based on Bayesian hierarchical models. However, Figure B.1 suggests at least a similar fit to that of those authors (cf. Fig. 1a-d in Berdanier et al., 2016). The better performance of the models that allowed for within-species variation in the parameters describing the shape of the radial profile indicates the magnitude of the observed intraspecific differences, and questions the assumption of Caylor and Dragoni (2009) that the relative radial component of sap flux density should be

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean ± SE</th>
<th>SD</th>
<th>2.5%</th>
<th>25%</th>
<th>50%</th>
<th>75%</th>
<th>97.5%</th>
<th>n_eff</th>
<th>R̂</th>
</tr>
</thead>
<tbody>
<tr>
<td>βμ: Intercept</td>
<td>−1.557 ± 0.000</td>
<td>0.029</td>
<td>−1.613</td>
<td>−1.576</td>
<td>−1.557</td>
<td>−1.538</td>
<td>−1.499</td>
<td>11,192.3</td>
<td>1.0001</td>
</tr>
<tr>
<td>βμ: WD</td>
<td>−0.002 ± 0.001</td>
<td>0.111</td>
<td>−0.230</td>
<td>−0.071</td>
<td>0.000</td>
<td>0.071</td>
<td>0.212</td>
<td>6695.9</td>
<td>1.0006</td>
</tr>
<tr>
<td>βμ: H</td>
<td>−0.491 ± 0.002</td>
<td>0.108</td>
<td>−0.714</td>
<td>−0.559</td>
<td>−0.488</td>
<td>−0.420</td>
<td>−0.286</td>
<td>4954.5</td>
<td>1.0001</td>
</tr>
<tr>
<td>βμ: ASI</td>
<td>−0.133 ± 0.002</td>
<td>0.101</td>
<td>−0.327</td>
<td>−0.202</td>
<td>−0.133</td>
<td>−0.066</td>
<td>0.072</td>
<td>4095.4</td>
<td>1.0004</td>
</tr>
<tr>
<td>c0</td>
<td>1.788 ± 0.000</td>
<td>0.023</td>
<td>1.745</td>
<td>1.773</td>
<td>1.797</td>
<td>1.802</td>
<td>1.833</td>
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</tr>
<tr>
<td>σ</td>
<td>2.857 ± 0.000</td>
<td>0.057</td>
<td>2.748</td>
<td>2.818</td>
<td>2.856</td>
<td>2.896</td>
<td>2.972</td>
<td>17,691.8</td>
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<tr>
<td>τu</td>
<td>0.174 ± 0.000</td>
<td>0.009</td>
<td>0.157</td>
<td>0.168</td>
<td>0.174</td>
<td>0.18</td>
<td>0.193</td>
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<tr>
<td>τc: μ</td>
<td>0.583 ± 0.001</td>
<td>0.056</td>
<td>0.478</td>
<td>0.545</td>
<td>0.583</td>
<td>0.619</td>
<td>0.697</td>
<td>4737.2</td>
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<tr>
<td>τc: K</td>
<td>0.504 ± 0.001</td>
<td>0.075</td>
<td>0.376</td>
<td>0.451</td>
<td>0.498</td>
<td>0.550</td>
<td>0.668</td>
<td>5732.6</td>
<td>1.0010</td>
</tr>
<tr>
<td>τc: c0</td>
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<td>0.681</td>
<td>0.723</td>
<td>0.771</td>
<td>0.886</td>
<td>7533.2</td>
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<tr>
<td>τw: μ</td>
<td>0.197 ± 0.002</td>
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<td>0.010</td>
<td>0.100</td>
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<td>0.277</td>
<td>0.454</td>
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<tr>
<td>τw: K</td>
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<td>0.172</td>
<td>0.369</td>
<td>0.456</td>
<td>0.546</td>
<td>0.776</td>
<td>5383.9</td>
<td>1.0001</td>
</tr>
<tr>
<td>Ωv: cor(μ, K)</td>
<td>−0.724 ± 0.002</td>
<td>0.13</td>
<td>−0.900</td>
<td>−0.818</td>
<td>−0.749</td>
<td>−0.658</td>
<td>−0.399</td>
<td>5520.7</td>
<td>1.0004</td>
</tr>
<tr>
<td>Ωv: cor(μ, C0)</td>
<td>0.649 ± 0.002</td>
<td>0.11</td>
<td>0.388</td>
<td>0.589</td>
<td>0.666</td>
<td>0.729</td>
<td>0.812</td>
<td>4991.4</td>
<td>1.0009</td>
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<tr>
<td>Ωv: cor(K, C0)</td>
<td>−0.724 ± 0.002</td>
<td>0.130</td>
<td>−0.900</td>
<td>−0.818</td>
<td>−0.749</td>
<td>−0.658</td>
<td>−0.399</td>
<td>5520.7</td>
<td>1.0004</td>
</tr>
<tr>
<td>Ωv: cor(μ, K)</td>
<td>−0.123 ± 0.005</td>
<td>0.376</td>
<td>−0.762</td>
<td>−0.412</td>
<td>−0.148</td>
<td>0.142</td>
<td>0.650</td>
<td>6968.7</td>
<td>1.0000</td>
</tr>
<tr>
<td>A</td>
<td>0.563 ± 0.002</td>
<td>0.319</td>
<td>0.181</td>
<td>0.353</td>
<td>0.491</td>
<td>0.684</td>
<td>1.374</td>
<td>20,700.0</td>
<td>0.9999</td>
</tr>
</tbody>
</table>

![Fig. 5. Estimated daily water-use (posterior mean ± 95% CI on a log10 scale) vs. a) species, b) wood density, c) tree height and d) annual stem increment. Regression lines in b)-d) from mixed effects models with random species effects based on the posterior mean predictions with bootstrapped 95% confidence bounds.](image-url)
approximately constant within species. In either case, it should be noted that the exact amount of between-tree variability cannot be determined from our data as we only could install one HFD sensor per tree due to technical limitations, which makes it impossible to separate between-stem and azimuthal variation. A sizeable part of the observed within-tree variability along the azimuthal dimension, which is known to significantly affect sap flux estimates (Reyes-Acosta and Lubczynski, 2014; Molina et al., 2016).

In contrast to Berdanier et al. (2016) who reported a poor performance of models based on relative depth, we were able to model sap flux with good accuracy based on relative distance from the cambium using a reparameterized beta distribution. While the shape of radial profiles certainly can be described with models based on absolute depth with equal accuracy as with our model, models based on relative depth have a number of clear advantages. Working with relative depth ensures that the function for the radial component of sap flux integrates to one over the tree radius without further corrections, which facilitates the decomposition of the sap flux signal into a radial and time-varying component. Moreover, due to our reparameterization (cf. Fig. 1), the average profile depth is directly estimated as a model parameter, which greatly simplifies integrating over the cross-section of a tree to estimate whole-tree water-use. In addition, in experimental model runs with different equations for the radial profile, we found the beta-based model to achieve similar accuracy while having much better convergence properties in our case than the reparameterized gamma probability density function that performed best in the study of Berdanier et al. (2016) (results not shown).

5.2. Determinants of the shape of radial sap flow profiles

The pronounced intraspecific variability in the shapes of the observed radial profiles is evident from the data at first glance (compare Fig. 3). While up to a certain degree this might be a masked effect of azimuthal variation (see above), the highly different shapes of the curves make it likely that between-tree variability plays a significant role. The variance decomposition of the parameter regressions indicates that also after including functional traits as regressors, random tree effects still explained 47.0% of the variance in the average relative profile depth $\mu$ and 29.3% of the variance in the concentration parameter $K$. In contrast, especially for $\mu$, the contribution of random species differences to the total variance was comparatively low (cf. Fig. 1 for the interpretation of the parameters).

As the predictor variables tree height, wood density and growth rate vary considerably between species (cf. Table 1), a certain part of the interspecific variability was likely explained by the fixed effects, thus shrinking the variance of the random species component. This is illustrated by the better performance of the model that included parameter regressions when marginalizing out random species- and tree-effects (Table 2). Nonetheless, the outcome of our study underlines the need to account for within-species differences in radial profiles in order to reliably propagate uncertainty when scaling up water-use estimates.

The radial profiles of the observed species can be grouped into three types: a) species with consistently monotonously declining profiles (Albizia niopoides, Bursera simaruba and Machaerium bivolatum), b) species with predominantly hump-shaped profiles (Hymenaea courbaril, Handroanthus impetiginosus) and c) species without clear patterns and with large intraspecific variability in profiles (Cordia alliodora, Cordia panamensis and Luehea speciosa). Notably, while the species in the first group share few common traits, the second group comprises the two most hard-wooded species in the dataset (Table 1), and the third consists only of small early-successional species. The fact that in the latter group some individuals were found to have the maximum of sap flux density close to the center of the trunk is not surprising, as due to their small size their wood was likely conductive over the entire cross-section.

In our model, the only predictor that had a credible effect on the parameters of the radial profiles was tree height. For taller trees, the bulk of flow occurred closer to the cambium (i.e., lower average profile depth $\mu$) and the profile was more narrowly centered around its average value (i.e. higher concentration parameter $K$; cf. Fig. 1). This is in accordance with the results of Zhang et al. (2018), who found tree height to be a major driver of the shape of radial profiles of trees in a Chinese subtropical evergreen forest, and described hump-shaped profiles for lower canopy species, while upper canopy species tended to have a maximum of flow close to the cambium. A similar pattern was also reported by Delzon et al. (2004), who found steeper radial profiles for trees with larger diameters. The large height effect on the shape of the radial profile likely reflects the fact that the relative fraction of sapwood in the cross-sectional area of a tree tends to decrease with tree size, a pattern that has repeatedly been described for Neotropical seasonally-dry forest species (Meinzer et al., 2005; Reyes-Garcia et al., 2012). This may be exacerbated by the fact that in order to make up for the longer flow path, taller trees need wider vessels (Ryan and Yoder, 1997; Ryan et al., 2006; Olson et al., 2018), which can be expected to increase the contribution of the outermost xylem layers to total water transport.

5.3. Upscaled estimates of whole-tree water-use

The approximate estimates of tree daily water-use differed considerably between species, and were positively associated with tree height. The higher water-use observed in tall trees is in line with theoretical expectations based on allometric scaling models (West et al., 1999; Enquist, 2002; Meinzer et al., 2005) and is likely related to an increased transpirational demand (cf. Horna et al., 2011). This is corroborated by our microclimatic measurements, which indicated VPD during daytime to be on average 77.1% higher in tree crowns at a height of 20 m than at the position of the sensors close to the forest floor (Fig. 2b). Similar vertical microclimatic patterns have been observed in Paleotropical perhumid forests, where VPD doubled from the forest floor to the uppermost canopy (Schuldt et al., 2011). While increased rainfall after the first measurement campaign led to increased soil water content in the following campaigns (Fig. 2a), the estimated average sap flux densities during a measurement campaign were not associated with the soil water content and did not change systematically between
campaigns (Figure B.3). This indicates that soil water supply did not limit tree transpiration during the measurement interval.

Our results further highlight the importance of accounting for radial profiles to obtain correct estimates of whole-tree daily water use. We found single-point estimates of water-use based on the average flux density over the first 2 cm of the profile to overestimate tree water-use by on average 26.0% compared to water-use estimates based on radial profiles, with a large variability in the ratio both within and between species. As our own measurements of radial profiles are limited by the maximum measurement depth of 7.5 cm permitted by the installed sensor system, it is possible that the actual amount of bias is even larger. While it has often been reported that ignoring radial variation most likely leads to an overestimation of sap flow (Nadezhdina et al., 2002; Reyes-Acosta and Lubczynski, 2014; Zhang et al., 2015), many transpiration estimations are still based on uncorrected single-point measurements (see review in Berdani et al., 2016). Our results show that, in addition to the overall positive bias of on average 26% resulting from the use of short-sensor probes, ignoring radial gradients in sap flux density induces a species-specific bias depending on the prevailing shapes of radial profiles that may obscure comparisons of water-use between trees of different species.

5.4. Measuring radial profiles with HFD sensors

The heat field deformation method for sap flow measurement has the advantage of being able to continuously monitor the radial distribution of sap flux density with a single sensor installation at high temporal and spatial resolution (Nadezhdina et al., 2012; Nadezhdina, 2016). The availability of commercial stand-alone HFD sensor systems makes the application of the method relatively easy. However, it has repeatedly been reported that the HFD method is likely to result in biased estimates without species-specific calibration (Steppe et al., 2010; Vandeguchte and Steppe, 2012; Fuchs et al., 2017), which can hardly be accomplished in species-rich tropical forests (cf. Section 3.3). Additionally, commercial HFD probes are comparatively costly, and their use in remote sites is complicated by the relatively high energy use. Notwithstanding these limitations, the high radial resolution of HFD sensors makes them a valuable tool for studies that scale up water-use, especially when using the framework of Caylor and Dragni (2009) to decompose sap flow into a radial component and an overall stem conductance. In this setting, HFD sensors can be used to track radial profiles for a subsample of trees, which can then be used to more accurately estimate the water-use of a larger sample of trees equipped with more economical single-point sensors, e.g. thermal dissipation probes (TDP, Granier, 1985) or heat-ratio-method (HRM, Burgess et al., 2001) sensors by applying a correction as detailed by Eq. 11–15 in Caylor and Dragoni (2009). Examples for the use of HFD sensors in conjunction with TDP sensors can be found in Poyatos et al. (2007), Reyes-Acosta and Lubczynski (2013; 2014) and Pinto et al. (2014), while Fan et al. (2018) show the parallel use of HFD and HRM sensors in a laboratory setting. However, none of these studies explicitly adopted the aforementioned framework.

5.5. Temporal changes in radial profiles

While our model operates under the simplifying assumption that the radial component of sap flow is time-invariant, it should be mentioned that there is substantial evidence that this is not always the case. Radial sap flow profiles have been reported to change both diurnally (Ford et al., 2004a; Fiora and Cescatti, 2006; Poyatos et al., 2007; Hernandez-Santana et al., 2016) and seasonally (Ford et al., 2004a; Fiora and Cescatti, 2006; Nadezhdina et al., 2007; Poyatos et al., 2007; Chiu et al., 2016), with suspected links to soil water content (Ford et al., 2004a; Nadezhdina et al., 2007), light availability (Fiora and Cescatti, 2006) and stomatal conductance (Hernandez-Santana et al., 2016). When scaling up sap flux density measurements to tree level water-use, aggregating data as daily averages is a simple procedure to at least reduce the effect of diurnal changes in the profile. Dealing with seasonal changes in radial profiles is considerably more complicated, as they can only be detected with long-term monitoring settings and averaging them out to avoid biased estimates of tree transpiration is difficult. However, Chiu et al. (2016) found the magnitude of seasonal changes in both radial profiles and azimuthal gradients in sap flux density to be much smaller than seasonal tree-to-tree variation, which indicates that to improve up-scaled water-use estimates with limited resources, it may be more beneficial to increase the number of trees equipped with easier-to-operate single-point sensors.

6. Conclusions

In this study, we have demonstrated how measurements of sap flux per xylem section measured with the heat field deformation method can be used to estimate radial gradients in sap flux density using a Bayesian hierarchical modeling approach. Extending on the framework of Caylor and Dragni (2009), we have shown how the output of these models can be integrated with sap flux measurements of single-probe sensors to obtain more accurate estimates of tree water-use, and how to improve model predictions onto additional species by incorporating functional traits as predictors of the shape of radial sap flow profiles. Building upon the model code provided in the digital supplement, it is possible to predict radial profiles for new trees with similar wood properties. In addition, our model lends itself to extension e.g. by including observations covering a wider range of tree functional types, by incorporating a submodel for azimuthal flow variation, by using more adequate predictor variables or by allowing the parameters of radial profiles to vary as a function of time.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary material


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Caylor, K.K., Dragni, D., 2009. Decoupling structural and environmental determinants of


