Agricultural and Forest Meteorology 373 (2025) 110738

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Review

Tropical forest transpiration estimates are geographically, ecologically and methodologically biased: a systematic review of sap flow research

Natalia de Aguiar-Campos *, Will Edwards, Susan G. W. Laurance

Centre for Tropical Environmental and Sustainability Science, College of Science and Engineering, James Cook University

ARTICLE INFO

Keywords:
Plant hydraulics
whole-tree water use
Holdridge life zones
heat dissipation
heat pulse
meta-analysis

ABSTRACT

Tropical forest transpiration is essential for the maintenance of the water and carbon cycles and regulation of the global climate. However, recent collective efforts to compile sap flow data, which is the most widely used method for quantifying transpiration in woody stems, have revealed a large data gap in the tropics. Furthermore, accurately upscaling point measurements of sap flow to whole-plant water use (PWU) requires data inputs and corrections that may be difficult to determine in highly diverse tropical forests. This systematic review has two main goals: to assess the methodological limitations of PWU research in tropical forests and to highlight geographical and ecological gaps among current tropical forest PWU research. Our Web of Science search used terms related to 'plant water use' and 'tropical forest' and gathered all peer-reviewed studies that used sap flow sensors and upscaled point measurements to PWU in tropical forests. Based on 72 studies conducted in 85 locations, we found that drier forest types (based on Holdridge life zones) are largely underrepresented in the literature, with more than 75% of the research output concentrated in wetter forest types. We also identified a substantial knowledge gap on liana sap flow, which appeared in less than 6% of the studies. Regarding the methodological limitations, most studies omitted information regarding the number of sensors deployed per plant and the method of zero-flow determination. Other shortcomings specific to each sap flow sensor type are highlighted. Our study underscores the need for standardising key methodological aspects and identifies significant geographical and ecological gaps in tropical forest PWU research. It provides a foundation for further studies to refine estimates of the present and future contributions of tropical forest transpiration to the global water cycle.

1. INTRODUCTION

Plant transpiration is a major component of global evapotranspiration (Schlesinger and Jasechko, 2014). Depending on the methodology applied to calculate its contribution (e.g., land-surface models, remote sensing, isotopic analyses), transpiration is estimated to account for between 57% (Wei et al., 2017) and 90% (Jasechko et al., 2013) of the total water flux from land to the atmosphere. In this context, tropical forest regions contribute disproportionally to the water cycle compared to other vegetation types, with 29-33% of global evapotranspiration estimated to occur in rainforest areas despite covering 14% of the global land surface (FAO, 2020; Schlesinger and Jasechko, 2014). The ground-based data used to validate these estimations are generally sampled from wetter tropical forests, where total annual precipitation exceeds annual potential evapotranspiration (i.e., moist, wet and rain forests *sensu* Holdridge et al., 1971) (Schlesinger and Jasechko, 2014). Conversely, tropical regions where precipitation is less than potential evapotranspiration may harbour drier tropical forests, adapted to highly seasonal water availability (Murphy and Lugo, 1986).

The contrasting moisture conditions experienced by plants in wet and dry ecosystems are reflected in their functional strategies (Aparecido et al., 2020; Apgaua et al., 2022; Lohbeck et al., 2015). Compared to plants in wetter tropical forests, drier forest plants often display deciduousness and tend to have hydraulic traits related to drought avoidance or drought resistance (e.g., more storage tissue, smaller and more connected vessels, higher sapwood density and lower conductivity; Apgaua et al. 2022; Zhu et al., 2017). Although sampling these hydraulic traits is challenging and large-scale data remain limited, some easily measurable functional traits may be linked to species' hydraulic strategies and are well documented (Díaz et al., 2022; Kattge et al., 2020; Zanne et al. 2009). For example, wood density is linked to variations in leaf water potential and potential conductivity in moist

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* Corresponding author.
E-mail address: nataliadeacampos@gmail.com (N. de Aguiar-Campos).

https://doi.org/10.1016/j.agrformet.2025.110738
Received 4 March 2025; Received in revised form 6 June 2025; Accepted 9 July 2025

forests (Meinzer et al., 2008), while combinations of leaf mass per area, wood density and leaf deciduousness are associated with hydraulic vulnerability and stem water storage in dry forest species (Wolfe and Kursar, 2015; Xu et al., 2016). Together, these functional traits offer valuable insights into tropical forest functional variation and can inform tree hydraulic models, ultimately enhancing the predictive power of terrestrial biosphere models (Christoffersen et al., 2016; Xu et al., 2016; Yang et al., 2019). Reliable field measurements of plant water use (PWU) are essential to validate such trait-based hydraulic models.

The choice of method and decisions involved in quantifying PWU in woody plants may introduce uncertainties in the estimates (Flo et al., 2019; Peters et al., 2018). Ground-based PWU estimates are often based on applying heat to the stem and quantifying sap flow at specific points within the sapwood before upscaling these point measurements to whole-plant water use. These heat-based sap flow methods can be divided into broad families depending on their working principles (Flo et al., 2019). The three most widely used families in tropical forests have been *(i)* heat dissipation (Granier, 1985), *(ii)* heat pulse (Burgess et al., 2001; Marshall, 1958) and *(iii)* heat balance (Čermák et al., 1973; Sakuratani, 1981). Heat dissipation and heat pulse sensors involve introducing heater and thermistor probes into the stem and quantifying temperature differences between different parts of the sapwood (details in Table 1). Although heat dissipation sensors measure sap flow density (cm^3 sap cm^{-2} sapwood h^{-1} or equivalent units) and heat pulse sensors measure sap velocity (cm h^{-1} or equivalent units), both methods require multiplying the output by sapwood cross-sectional area to quantify PWU. Conversely, heat balance sensors provide an estimate of sap flow rate and require data processing steps that differ significantly from those required by heat dissipation and heat pulse sensors (Smith and Allen, 1996; Vandegehuchte and Steppe, 2013). Here, our analysis of methodological choices in tropical forest PWU will focus on heat dissipation and heat pulse sensors. We will use the term “sap flow” referring to either “sap flow density” or “sap velocity”, meaning a point measurement that is subsequently upscaled to PWU by multiplying its value by sapwood area (Smith and Allen, 1996).

Despite a few differences between heat pulse and heat dissipation

Table 1

Summary of the sensor families and sensor types used in the sap flow studies covered in the methodological analysis.

Family	Method	General principle	Equations	Inputs	Output	Corrections	References
Heat dissipation	Heat dissipation	Continuous heating is radiated into the stem and the temperature difference between the heated and an unheated upstream point is quantified (ΔT). The temperature difference at which zero flow is assumed needs to be determined (ΔT_0). The temperature difference is then used to calculate sap flux density (J_s) using empirical calibration coefficients (a and b). Measurements are taken at a fine temporal scale (e.g., every 30 seconds) and averaged at pre-defined time intervals (e.g., 10 to 30 minutes). Sap flux can then be multiplied by sapwood area (A_{sw}), yielding whole-plant water use (Q).	$K = \frac{\Delta T_0 - \Delta T}{\Delta T}$ $J_s = a * K^b$ $Q = J_s * A_{sw}$	Calibration coefficients (a and b)	Volume of sap per sapwood area per time Volume of sap per time (if multiplied by sapwood area)	Contact of the probe with nonconducting xylem (i.e., heartwood)	Granier (1985) Granier (1987) Clearwater et al. (1999)
Heat pulse	Heat-ratio method	Heat pulses are radiated into the stem at pre-determined time intervals. Temperature sensors inserted equidistantly above and below the heater (distance $x = 0.5$ or 0.6 cm) record the increases in temperature following the heat pulse (v_d and v_u downstream and upstream, respectively). The thermal diffusivity of the sapwood (k) should be determined beforehand. After determining the heat pulse velocity, sap velocity can be determined by measuring the densities and specific heat capacities of sap (ρ_s and c_s, respectively) and wood in the xylem (ρ_b and c_w, respectively), as well as the water content of the sapwood (m_c) (details in Equation 7 in Burgess et al., 2001).	$V_h = \frac{k}{x}\ln(v_d / v_u) * 3600$ $V_s = \frac{V_h \rho_b (c_w + m_c c_s)}{\rho_s c_s}$ $Q = V_s * A_{sw}$	Thermal properties of the sapwood (k)	Distance travelled by the sap per time Volume of sap per time (if multiplied by sapwood area)	Wound effects Probe misalignment	Marshall (1958) Burgess et al. (2001)
	Compensation heat pulse	Upstream and downstream temperature probes are inserted at equal depths into the sapwood with the heater at an intermediate position. The upstream probe is placed 5 mm (x_u) and the downstream probe 10 mm (x_d) from the heater. After a heat pulse is applied, the temperature of the upstream sensor, which is closer to the heater, becomes higher than that of the downstream sensor due to conduction. After a few more seconds, the stream of moving sap increases the temperature of the downstream sensor. The time taken for the temperatures at the two sensors to become equal (t_0) is used to calculate the velocity of the heat pulse (V_h).	$V_h = \frac{x_d - x_u}{2t_0} * 3600$	-	Distance travelled by the sap per time Volume of sap per time (if multiplied by sapwood area)	Wound effects Probe misalignment	Swanson and Whitfield (1981) Smith and Allen (1996)

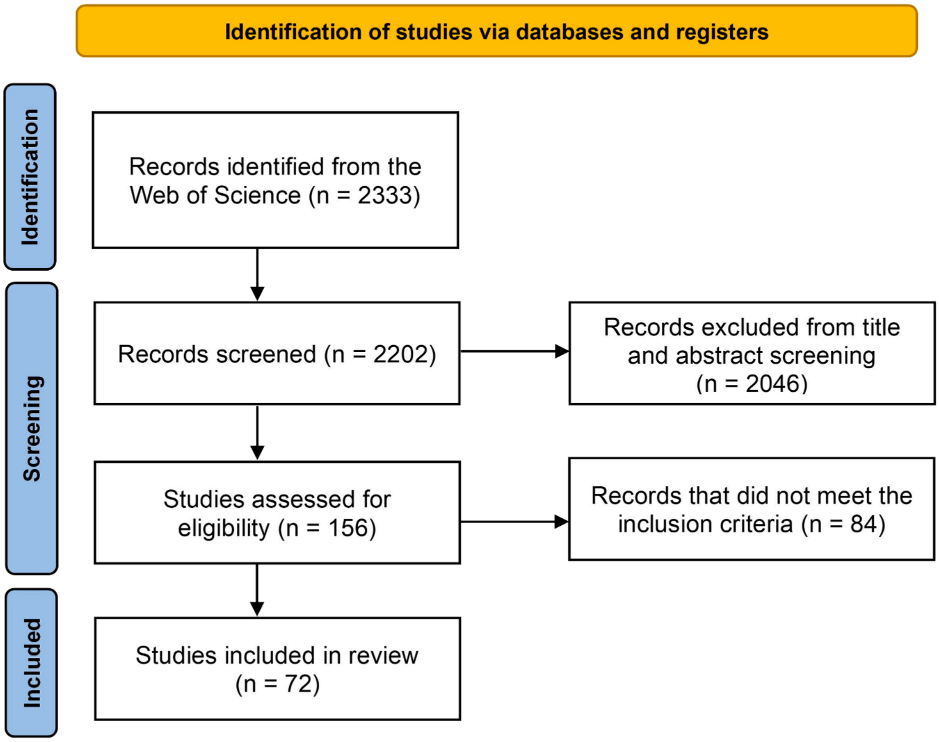

Figure 1. Flow chart describing the screening and appraisal procedure undertaken in the systematic search.

sensors, they share similar pre- and post-data collection requirements for accurate upscaling. For example, the cardinal direction where the sensor is installed (i.e., its azimuthal position) can potentially impact sap flow estimations (Shinohara et al., 2013). The depth of probe insertion within the sapwood also significantly influences the estimates yielded, given the radial profile of sap flow variation (Zhang et al., 2015a). Both sensor families require species-specific preliminary inputs to convert temperature signals to sap flow: while some heat pulse sensors require the determination of the sapwood's thermal properties (Burgess et al., 2001; Green et al., 2003), heat dissipation sensors depend on empirical calibration coefficients (Fuchs et al., 2017). Among post-collection data processing steps, these two sensor families require some form of baselining or determination of zero sap flow (Merlin et al., 2020; Regalado and Ritter, 2007) and the application of correction factors to deal with issues related to wounding (Green et al., 2003), probe misalignment (Burgess et al., 2001) or contact of the sensor needles with the heartwood (Clearwater et al., 1999). The final post-data collection step is the determination of the target plants' sapwood area and the choice of how to deal with the sapwood's radial profile (Zhang et al., 2015a).

Although these methodological requirements are irrespective of the study system, most sap flow research has been developed in relatively homogeneous temperate forest stands (e.g., Kume et al., 2012; Peters et al., 2018; Shinohara et al., 2013). This is evident in the geographical coverage of the SAPFLUXNET database which, despite being the only collective effort for sap flow data compilation on a global scale, still has a large data gap in the tropics (Poyatos et al., 2021). Beyond the methodological challenges already presented, tropical forests' high taxonomic and functional diversity introduce new ones. Their complex vertical structure, heterogeneous tree architecture and diverse array of leaf and wood functional traits linked to hydraulic functioning (Smith-Martin et al., 2023; Xu et al., 2016) warrant further consideration in pre- and post-data collection decisions, particularly regarding sensor calibration. Future research aiming to fill the tropical data gap in SAPFLUXNET could benefit from a comprehensive analysis of methodological shortcomings, geographical biases and ecological gaps in tropical forest sap flow research.

Here, we present a systematic review aiming to assess geographical bias, functional bias and methodological limitations in the global literature on PWU in tropical forests. We assess the global output in tropical forest sap flow research focussing on the studies that upscale point measurements to PWU. First, we ask: is our current knowledge of PWU geographically biased to particular regions within the tropics? For this, we quantify the research output by continent and forest type (*sensu* Holdridge et al., 1971), quantifying how representative current research is in terms of the extant bioclimate envelope suitable to support different tropical forest types. Second, we ask: what is the extent of taxonomic and functional variation included in tropical forest PWU studies? For this, we listed the species included in the studies, classified their growth forms and synthesised key functional traits known to be linked to plant water use. Third, we ask: what are the main sources of uncertainty in upscaling point measurements of sap flow to PWU? We then describe the data-processing steps that lead to estimates of PWU from heat dissipation and heat pulse sensors and highlight persistent shortcomings linked to pre- and post-data collection decisions. Overall, our findings point to multiple biases in current research on tropical forest PWU, allowing us to provide targeted recommendations for future research.

2. MATERIALS AND METHODS

2.1. Search

For the systematic literature review, we constructed a comprehensive Boolean search string with the aid of semi-automated tools, following Grames et al. (2019). To this end, we first performed a naïve search on the Web of Science Core Collection and JSTOR using combinations of the terms “sap flow”, “sap flux”, “tropical”, “dry”, “wet”, “forest*”, “rainforest*” and “tree*” with Boolean operators. We used terms related to sap flow because we intended to focus on the studies that used this approach to upscale to plant water use (PWU). After running text-mining and keyword co-occurrence network analyses with the R package *litsearchr* (Grames et al., 2019), we selected a final combination of 48 key terms combined by Boolean operators: 33 terms that described the variable of interest (i.e., sap flow), 10 terms that described the system of interest (i.e., tropical forest) and 8 terms that described the organisms of interest (i.e., trees, shrubs and lianas) (the full search string can be found in Suppl. Table 1). We used this combination to run a final search on the Web of Science Core Collection, which retrieved 2,333 peer-reviewed journal articles published between 1977 and 2025. This final search was performed on 8 April 2025.

2.2. Study selection

We screened the titles and abstracts of the 2,333 research articles and included those that met the following criteria: *(i)* the study was done in a tropical forest (including seasonally dry forests, mangrove forests, wet forests, and seasonal forests; but not plantations, greenhouse experiments, experimental stands, or other tropical vegetation types), *(ii)* the study measured sap flow in trees and/or shrubs and/or lianas using a heat-based method, *(iii)* the study upscaled point sap flow to PWU, ultimately expressed in mass per unit time or volume per unit time; and *(iv)* the study was the primary source of the information above (i.e., not a literature review or a meta-analysis). After screening, we were left with 72 peer-reviewed journal articles (Fig. 1). In the Suppl. Material, we present an overview of the entire tropical forest sap flow literature as identified by our search (n = 134 studies overall), including the studies that upscaled sap flow to PWU (n = 72, included in the main text) and those that measured sap flow to any other end (n = 62).

2.3. Assessing geographic bias

To identify potential geographical bias in tropical PWU research, we first quantified the number of studies by forest type. Forest type was determined as the combination of latitudinal region, altitudinal belt and life zone as proposed by Holdridge et al. (1971) (e.g., “tropical premontane moist forest”, “tropical lower montane dry forest”). This was achieved based on site elevation, mean annual precipitation (MAP) and mean annual biotemperature (MABT). Unlike mean annual temperature, which was reported in most studies, MABT is not a simple arithmetic mean of monthly average temperatures; rather, it is “the mean of unit-period temperatures with the substitution of zero for all unit-period values below 0 and above 30” (Holdridge et al., 1971). In our study, we used monthly average temperatures (T_{avg}) to calculate MABT, in a process similar to that described by Lugo et al. (1999) and expressed in Equation (1).

$$MABT = \frac{\mathrm{sum}\left(T_{avg}[i]\ if\ 0 < T_{avg}[i] < 30; else\ 0\right)}{12\ \{\mathrm{i} = 1,\ 2 \ldots 12\}} \tag{1}$$

Hence, we extracted the monthly average temperature recorded between 1970 and 2000 for each geographic coordinate from the WorldClim 2.1 database (Fick and Hijmans, 2017), using the finest spatial resolution available (30 arc-seconds or $\sim$1 km^2 per pixel). When a geographic location was reported with error, such as when the point fell in the ocean instead of on land, we corrected the coordinates by *(i)* searching for other studies conducted in the same location in our dataset or *(ii)* searching on Google Earth the name of a reference location reported in the study (e.g., a nearby village).

Although most studies reported MAP values by study site, we decided to extract MAP from the same database from which we drew temperature data. This decision was based on two reasons: *(i)* the MAP values reported in the studies were highly inconsistent, with conflicting values presented for the same location and different periods over which precipitation was averaged; and *(ii)* the Holdridge Life Zone system requires long-term climatic data for a reliable classification (Holdridge et al., 1971). To further standardise our classification, we also drew elevation data from the same database, using the SRTM raster file available. Extracting all environmental variables from an openly available source guarantees the comparability of our results and enables a standardised classification of the sites.

We classified the sites’ forest types into their latitudinal regions, altitudinal belts and life zones. First, we used MAP and MABT to locate the point where the site would fall in Holdridge’s diagram. This provided the site’s life zone (e.g., moist forest) and a preliminary altitudinal belt classification (e.g., montane). Next, we used the site’s elevation to convert MABT to sea-level equivalent biotemperature ($MABT_0$), considering a rate of +6°C for every 1000 metres of altitudinal decrease (Holdridge et al., 1971). The value of $MABT_0$ gave us the site’s latitudinal region classification (e.g., tropical). Moving on, we reassessed the site’s altitudinal belt based on the calculated $MABT_0$. Low-altitude sites would show little difference between MABT and $MABT_0$, resulting in the same classification – that is, lowland (e.g., tropical lowland moist forest). High-altitude sites would have a greater difference between MABT and $MABT_0$, resulting in different classifications. If a site’s $MABT_0$ fell into the lowland category while its actual MABT fell into the montane category, the site would then be classified as montane (e.g., tropical montane moist forest).

Lastly, we compared the research output by forest type with the current bioclimate envelope able to support woody vegetation across the tropical region. For this, we classified the entire global tropics using data from WorldClim 2.1 in a similar approach to the study sites’ classification but using a coarser spatial resolution of 5 arc-minutes (approximately 86 km^2). This analysis allowed us to *(i)* quantify the proportion of the current bioclimate envelope suitable to support different tropical forest types and *(ii)* contrast this bioclimatic suitability to the research efforts in each tropical forest type. Since we were interested in analysing suitability rather than the extant area of tropical forest, we did not quantify the remaining area of different forest types.

Data analysis and forest type classification were done in R version 4.3.1 (R Core Team, 2023). We used the packages *ggplot2* (Wickham, 2016) and *ggsankey* (Sjoberg, 2024) to map and visually display the prevalence of the different forest types used in PWU research. We used the R packages *climenv* (Tsakalos et al., 2023) and *Ternary* (Smith, 2017) to plot Holdridge life zone diagrams.

2.4. Assessing ecological and functional coverage

To assess the ecological and functional coverage of the 72 PWU studies, we first compiled their list of species, when present. We checked species, genus and family nomenclature through the World Flora Online, which had been updated in December 2024 (WFO, 2025). We also extracted from each study the diameter and height of the sampled plants, either directly when explicitly stated or indirectly from scatter plots showing plant diameter and/or height in one of the axes. For this we used the online tool *PlotDigitizer* (https://plotdigitizer.com; accessed April 2025). We classified the plants into their growth forms (trees, shrubs, tree/shrubs and lianas) according to the Global Spectrum Dataset (Díaz et al., 2022, 2015), the World Flora Online (WFO, 2025) and Plants of the World Online (POWO, 2025).

Table 2
Summary of the functional traits extracted for the species sampled for whole-plant water use in tropical forests using heat-based approaches to measure sap flow.

Variable	Tree/shrub	Lianas
Richness sampled	318	23
Median leaf area (mm^2)	5,227.04 (n = 215)	3,327.60 (n = 12)
Median leaf mass per area (g/m^2)	90.12 (n = 209)	69.25 (n = 11)
Median wood density (g/cm^3)	0.58 (n = 238)	0.46 (n = 8)
% leaf phenology	68% evergreen (159 spp.) 32% non-evergreen (75 spp.)	75% evergreen (3 spp.) 25% non-evergreen (1 sp.)

For each sampled species, we obtained four functional traits that can provide insight into the water use strategies of the plants sampled for PWU (detailed description in Appendix 1). We searched in different databases for the trait values of each species or its synonyms, in case the updated nomenclature was not found. As a measure of the species' responses to rainfall seasonality, we extracted leaf phenology type (evergreen vs. non-evergreen) from the TRY database (Kattge et al., 2020). When conflicting phenological classifications were found, we searched in more specific sources to find a consensus (e.g., Atlas of Living Australia, Plants of the World Online, Flora e Funga do Brasil, etc.). We decided to classify non-evergreen plants in this broad category to avoid having to decide whether a species is deciduous, brevideciduous or semideciduous (Eamus, 1999) given the potential lack of data for all the taxa compiled. In addition to phenology, we obtained species-level means of three continuous functional traits: leaf area (LA, mm^2), leaf mass per area (LMA, g.m^{-2}) and wood density (WD, g.cm^{-3}). When available, we extracted species-level means of these traits from the Global Spectrum Dataset (Díaz et al., 2022, 2015). Otherwise, we referred to the TRY database (Kattge et al., 2020) or the Global Wood Density Database (Zanne et al., 2009).

We compared the extent of the functional trait coverage in the studies to the lower and upper boundaries in which these traits appear in tropical forests. To estimate these boundaries, we separately extracted two lists of species from the Global Spectrum Dataset: *(i)* a list of tree/shrub species and *(ii)* a list of liana species. Next, using the *occ* function from the R package *spocc* (Owens et al., 2024), we submitted each separate list to a query in the Biodiversity Information Facility (GBIF, 2025) aiming to extract the geographic locations where these species have been recorded. Based on the occurrence records retrieved (at least 30 per species), we assumed a species had a tropical distribution if at least 15% of its occurrences were recorded between latitudes 23.5 N and 23.5 S (i.e., at least 5 tropical occurrence points). From this filtered 'tropical species dataset', we built a 'tropical functional dataset' by extracting the LA, LMA and WD values of each species from Díaz et al. (2022). Then, we identified the species displaying the highest and lowest values of each functional trait and checked if their native occurrence range included tropical forests by consulting authoritative sources (e.g., World Flora Online, Plants of the World Online, Flora e Funga do Brasil, Atlas of Living Australia, etc.). A more detailed description of the definition of the lower and upper boundaries, as well as further explorations of the 'tropical functional dataset', are provided in Appendix 1.

2.5. *Assessing upscaling uncertainty*

To identify the main sources of uncertainty in upscaling sap flow to PWU, we focussed on heat dissipation and heat pulse studies (Table 1). The data processing steps were separated between pre- and post-data collection decisions that could introduce uncertainty in the water use estimates (details in Suppl. Table 2). Pre-data collection decisions included *(i)* sensor type, *(ii)* whether azimuthal (i.e., circumferential) sap flow variation was considered, *(iii)* depth of probe insertion and *(iv)* whether the study performed sensor-specific calibration. Post-data collection decisions included *(i)* method of zero-flow determination or baselining, *(ii)* sensor-specific data corrections, *(iii)* method of radial integration and *(iv)* method of sapwood area determination.

The four pre-data collection decisions were related to sensor deployment in the field. First, we separated the studies into the sensor families used: *heat dissipation* (HD) or *heat pulse* (HP), excluding heat field deformation and heat balance as explained above. Second, we recorded whether the studies performed sensor-specific calibrations (yes/no/NA), characterised by testing different empirical coefficients (in the case of HD sensors) and using species-specific thermal diffusivity (in the case of some HP sensors, particularly the heat-ratio method). Third, we determined if the study explicitly accounted for azimuthal variation by deploying at least two sensors at different azimuthal positions in the stem (yes/no). Fourth, we observed if the study reported monitoring sap flow at a single depth or multiple depths within the stem (multiple/single/unclear).

The four post-data collection decisions were related to data processing and corrections. First, we recorded if the study explicitly reported the method of zero-flow determination or baselining and whether this was done directly or indirectly (direct/indirect/unclear). Zero-flow determination was considered direct when the study reported cutting the monitored organ and recording the sensor reading for subsequently baselining the previous sap flow data. Zero-flow determination was considered indirect when the study assumed zero flow from specific weather conditions, predawn measurements or by applying statistical approaches such as double regression or moving window. Second, we recorded whether the study explicitly addressed the need for sensor-specific data corrections (yes/no). These included, in the case of HD sensors, checking for contact of the probes with nonconducting xylem (i.e., Clearwater's correction) (Clearwater et al., 1999) and, in the case of HP sensors, accounting for wound effects and checking for probe misalignment. Third, we observed whether the study accounted for radial variation in sap flow (yes/no). A study was considered to account for radial variation if it applied a radial decay function, in the case of a single-depth probe, or if it assigned sap flow recorded at different depths to specific annuli of the sapwood (e.g., Hatton's method) (Hatton et al., 1990). A study was considered to not account for radial variation if it did not explicitly report assigning a radial decay function in the case of single-depth probes or if it averaged multiple-depth probes to a single sap flow value. Fourth, we recorded the method of sapwood area determination (direct/indirect/other). Direct sapwood area determination was characterised by defining the sapwood/heartwood boundary of individual stems by collecting wood core samples or by inserting sensors at multiple depths to observe the region where the xylem becomes inactive. Indirect sapwood area determination was characterised by using a previously developed equation that relates an easily measurable scalar (e.g., diameter at breast height) and sapwood area or sapwood depth.

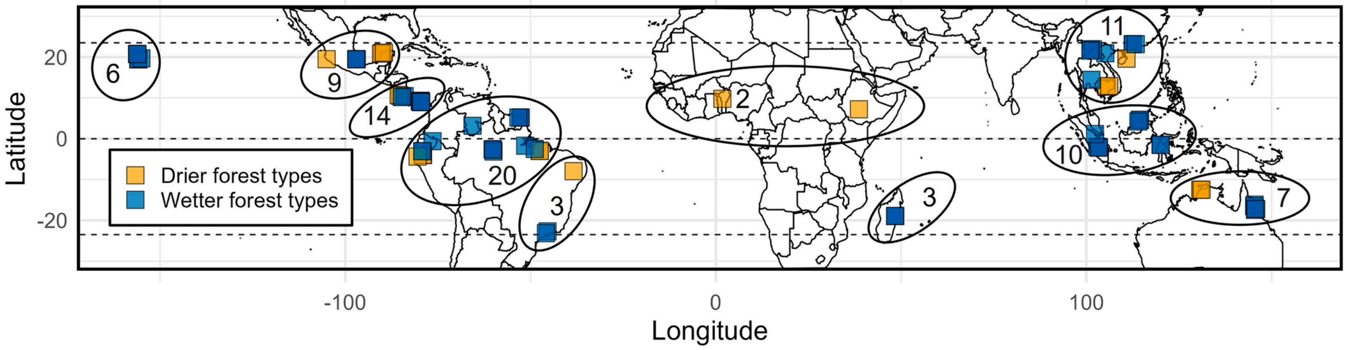

Figure 2. Tropical forest sites where plant water use was estimated using heat pulse and heat dissipation sensors (n = 85 locations from 72 studies).

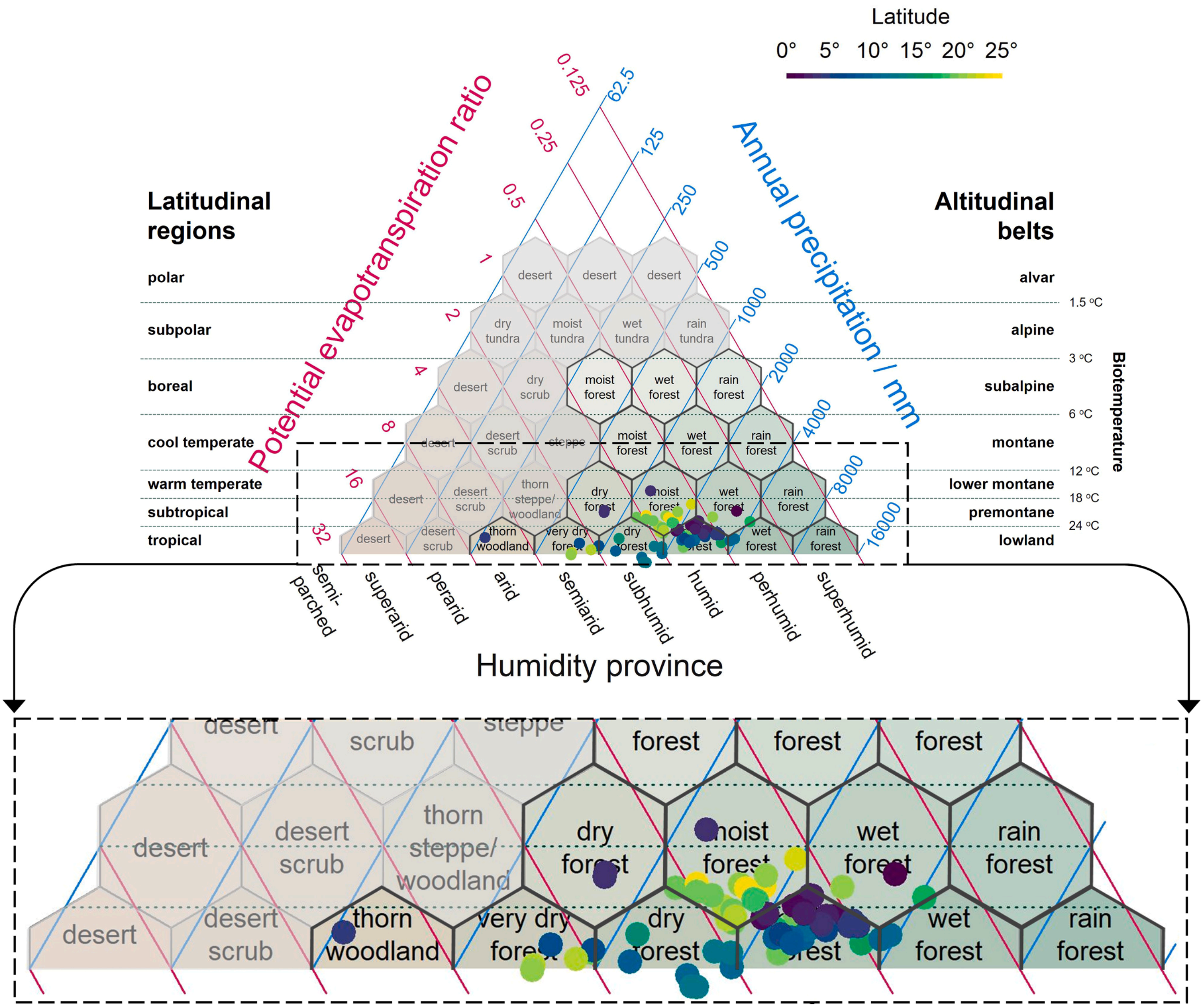

Figure 3. Holdridge life zone classification of 85 study sites where whole-plant water use was quantified in tropical forests.

3. RESULTS

The systematic literature review examined 72 studies conducted in 85 sites that used heat-based methods to estimate whole-plant water use (PWU) in native tropical forests (Fig. 2). First, we report a significant geographic bias in the research output, with an overrepresentation of Central and South America and very little research on the African continent. We also show that this locational-biased research has been mostly focused on wetter compared to drier forest types. Second, we reveal a significant data gap on liana sap flow (< 6% of studies) and a focus on canopy trees. Third, we show multiple shortcomings in the reporting of pre- and post-data collection decisions, particularly related to the lack of sensor-specific calibration and reporting of zero-flow determination. We have also added to the Appendix further information gathered from the sap flow literature (n = 135 studies) regarding geographical biases and temporal trends, although we do not delve into detail on these additional results here.

3.1. Geographic bias

The research output on tropical forest plant water use (PWU) is mostly concentrated in tropical lowland moist forests (Fig. 3, Fig. 4a-d). Based on Holdridge life zones, 89% of the sites were classified as tropical and 11% as subtropical. The sites' altitudinal belts were mostly lowland (61%), followed by premontane (22%), lower montane (14%) and montane (2%). Lastly, we found that most sites investigated were moist forests (64%), followed by dry forests (16%) and wet forests (13%). The study sites were largely concentrated in the Americas (54%) and the Asia/Pacific (40%), with very little output in the African continent (6%) (Fig. 2).

While the latitudinal region coverage in our dataset adhered to the actual bioclimate envelope for tropical woody vegetation (~90% tropical, ~10% subtropical) (Fig. 4b), research was biased towards wetter and higher-altitude sites. For instance, the proportion of research done in lower montane forests (14% of studies) is much greater than the proportion of potentially suitable areas to support them (3% of the area) (Fig. 4c). A similar bias is true for the humidity gradient: although 52% of the tropical bioclimatic envelope is suitable for sub-humid, semi-arid or arid woody vegetation, only 23.5% of PWU studies have been conducted in these forest types (dry forests, very dry forests and thorn woodland) (Fig. 4d). Consequently, PWU research disproportionately represents humid or wetter vegetation types (moist forests, wet forests and rain forests) (76.5%), which could potentially occupy less than half of the global bioclimatic envelope (48%, Fig. 4d).

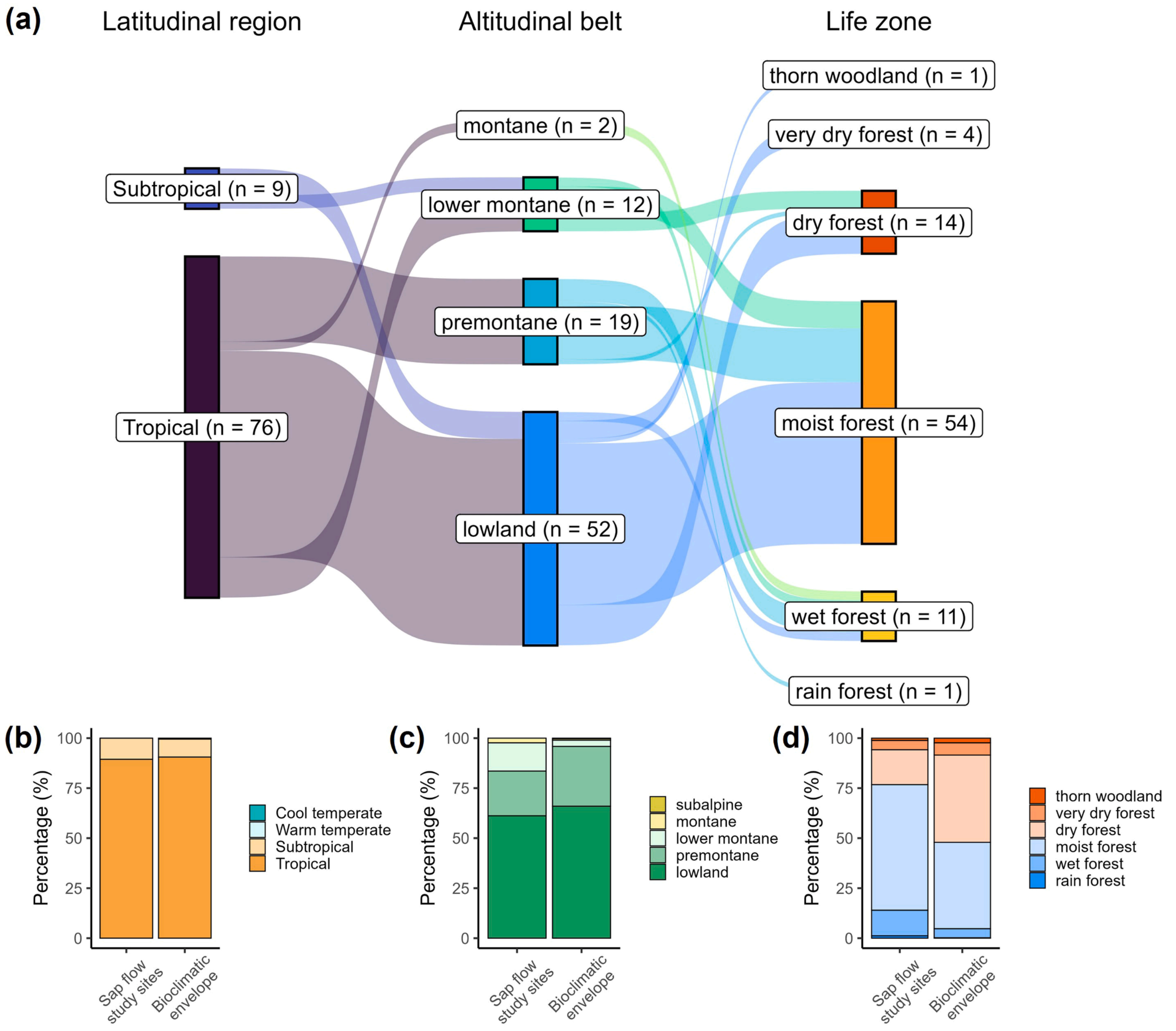

Figure 4. Latitudinal regions, altitudinal belts and life zones of the study sites (a) compared to the classification of the global bioclimate envelope able to support each of them (b-d).

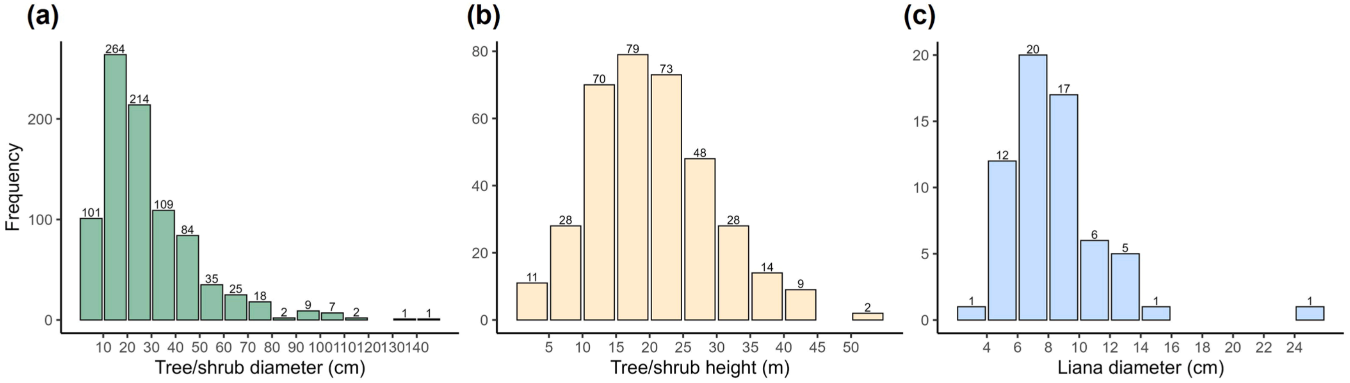

Figure 5. Size distribution of plants instrumented with heat-based sap flow sensors for estimation of whole-plant water use in 72 studies conducted in tropical forests. (a) Tree/shrub diameters (n = 872), (b) tree/shrub heights (n = 362) and (c) liana diameters (n = 63).

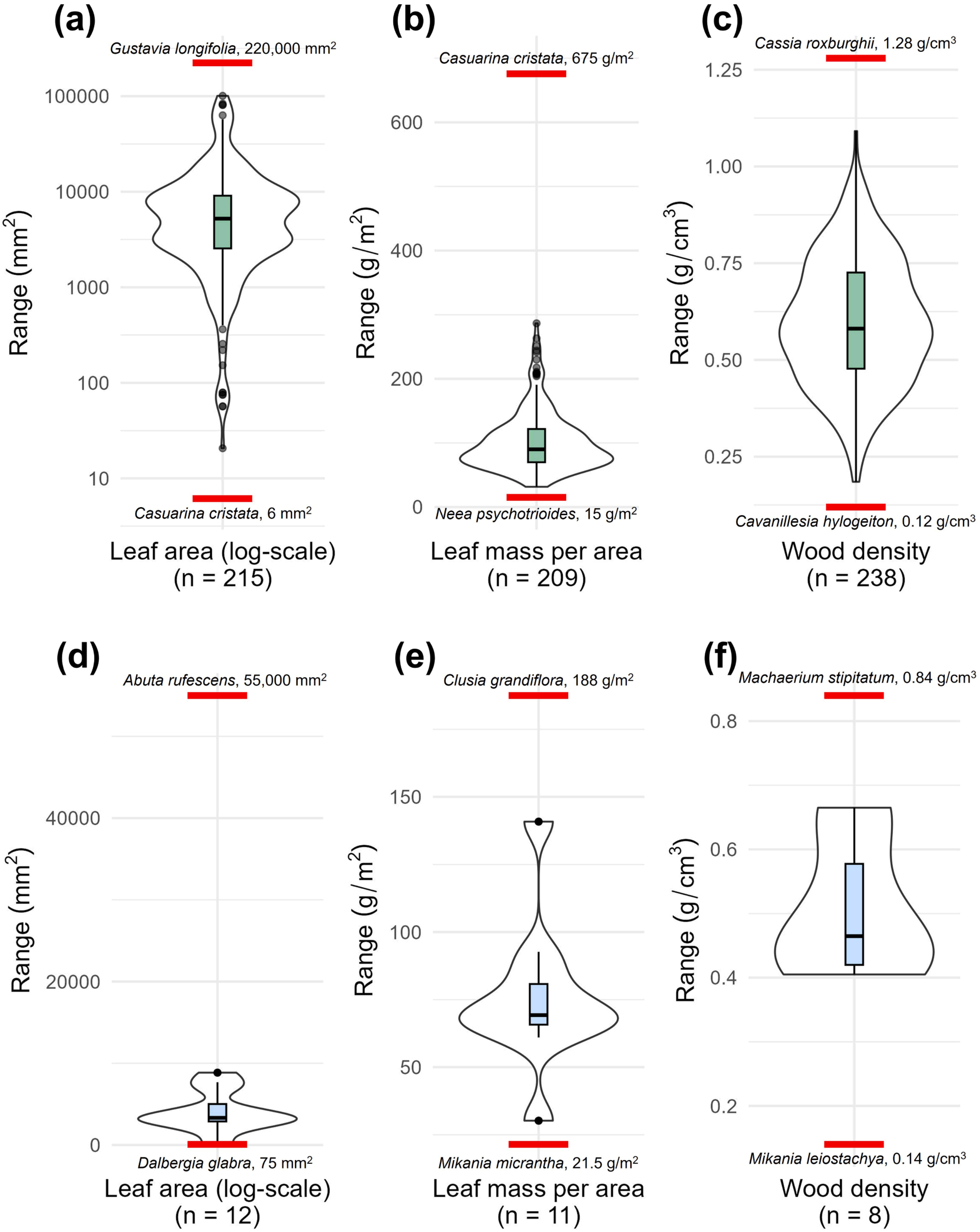

Figure 6. Distribution of functional traits of the trees (a-c, green) and lianas (d-f, blue) included in whole-plant water use studies along with the upper and lower extremes recorded within tropical forests based on data retrieved from the Global Spectrum Dataset. Details on the determination of lower and upper extremes are provided in Appendix 1. Leaf area is on a log-scale, while leaf mass per area and wood density are on a linear scale.

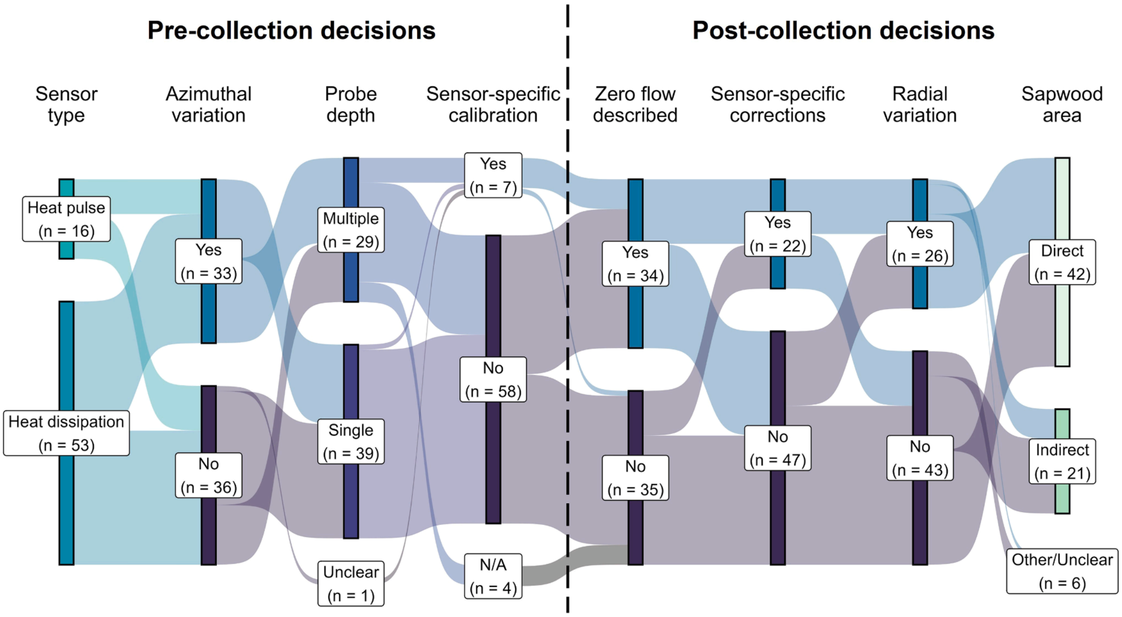

Figure 7. Sankey diagram with pre- and post-data collection decisions regarding sap flow device deployment and data processing steps to convert sap flow data to whole-tree water use (TWU). Displayed are only the studies that used heat dissipation and heat pulse devices and upscaled point sap flow to TWU. Details on the assignment of each study to each category can be found in Suppl. Table 2.

3.2. Ecological and functional coverage

The 72 studies included in our review measured whole-plant water use (PWU) in at least 1275 individuals belonging to 362 morphospecies (342 identified to the species level), 261 genera and 98 families (Suppl. Table 3). From this total, 318 species were classified as tree, shrub or tree/shrub (93%), 23 were lianas (7%) and 1 was a fern (< 0.3%). Since only eight species were classified as "shrub" and 25 were classified as "shrub or tree", we decided to pool trees and shrubs together in this section due to the high degree of phenotypic plasticity amongst some of the taxa, which make it hard to establish rigid boundaries between these classifications, especially in large-scale studies such as this. Below, we focus on the tree/shrub and liana components of the vegetation (Table 2).

From the 318 tree/shrub species, we were able to extract leaf area - LA for 215 species (68%), leaf mass per area - LMA for 209 species (66%), wood density - WD for 238 species (75%) and leaf phenology for 234 species (74%). While 68% of the tree/shrub species have an evergreen habit, the remaining 32% present some form of deciduousness. The leaf-level traits indicate a predominance of large and soft leaves (median LA = 5,227.04 mm^2, median LMA = 90.12 g/m^2) (Table 2, Fig. 6a-b, Fig. A.1). On the other hand, the wood density coverage was broad among the tree/shrubs (median WD = 0.58 g/cm^3), with most species moderately heavy-wooded and a few soft-wooded pioneers (<0.30 g/cm^3) (Table 2, Fig. 6c, Fig. A.1).

From the 23 liana species, we obtained LA for 12 species (52%), LMA for 11 species (49%), WD for 8 species (35%) and leaf phenology for 4 species (18%). The small sample of lianas points to a significant knowledge gap on the transpiratory behaviour of this growth form in tropical forests. As such, the summary statistics on liana functional traits are barely informative but are nonetheless presented (Table 2).

To illustrate the extent of the functional variation represented by the sampled species, in Appendix 1 we compare it with the functional variation recorded among tropical species in general (Fig. A.1). Although this graphical analysis is meant as a reference and not as a definitive comparison, it underscores the greater representation of tropical tree/shrubs and poor representation of lianas in PWU studies relative to the functional trait extent of these growth forms in the tropics.

Although species identity, sample size, diameter and height were not always clearly presented in the studies, we were able to extract the diameter and height for the following number of individuals: diameter for 872 tree/shrubs, height for 362 tree/shrubs and diameter for 63 lianas (Fig. 5). Tree/shrub diameters had a log-normal distribution with a geometric mean and standard deviation of 22.5 ± 2 cm, whereas tree/shrub heights followed an approximately normal distribution, with mean 20.6 ± 9.1 metres.

3.3. Upscaling approaches

Here, we focus on the upscaling approaches presented in the studies that used heat dissipation and heat pulse sensors in tropical forests. We found that 100% of these studies reported tree sap flow, 4% shrub sap flow and 3% liana sap flow. Although some of the sampled species may satisfy either 'tree' or 'shrub' categories – as presented in the section '3.2 Ecological and functional coverage' –, the literature is largely focussed on 'trees' as a plant functional group. Hence, the results presented in this section mostly apply to tree water use (TWU) estimations.

That said, we found multiple issues and a few positive trends in TWU upscaling (Fig. 7). The studies included sap flow monitoring in tree branches and/or tree trunks using custom-built (32/69) or commercial sensors (Suppl. Table 4). Only two studies estimated TWU from branch-level sap flow (Cerón-Aguilera et al., 2025; Feild and Holbrook, 2000), while nine other studies used both branch- and stem-level sap flow to investigate the hydraulic coordination between different plant compartments (e.g., Andrade et al., 1998; Meinzer et al., 2004, 2003) (Suppl. Table 4).

Among pre-collection decisions, all studies clearly described the type of sensor used, yet they often omitted the number of sensors deployed per tree. Less than half of the studies (33/69) clearly described whether (and how) they dealt with the effects of potential azimuthal variation in sap flow readings. None but one study conducted with heat dissipation devices (52/53) described calibrating the device readings. Instead, nearly all studies used the empirical coefficients originally proposed by Granier (1985), which were devised using log fragments with diameters between 4 and 5 cm of three temperate tree species (Douglas fir, black pine and pedunculate oak).

Among post-collection decisions, we found that more than half of the studies (35/69) did not state the method of zero-flow determination. As for sensor-specific data corrections, heat dissipation studies rarely addressed the issue of probe contact with inactive xylem. Of the 50 studies conducted after Clearwater et al. (1999) proposed a correction for this problem, only 7 mentioned assessing the need for this correction. Lastly, regarding the depth of probe insertion and consideration of the sapwood's radial profile, we found that most studies either did not describe how they dealt with the sapwood's radial profile or considered it uniform. Other than these limitations, we also found some positive trends in the literature. For example, all studies that employed heat pulse devices to detect sap flow (16/69) applied corrections for wounding effects and/or probe misalignment. As the last step between data collection and TWU quantification, we also found that sap flow researchers often make an extra effort to directly determine sapwood area, which increases confidence in the estimates (42/69). The study-by-study assessment of each pre- and post-data collection decision can be found in Suppl. Table 4.

4. DISCUSSION

This review of 72 tropical forest studies found that whole-plant water use (PWU) estimates were geographically and ecologically biased and often methodologically inconsistent or unclear. Wetter forests are overrepresented in the literature, while drier forests, which comprise a significant proportion of tropical woody vegetation (Murphy and Lugo, 1986, Pennington et al., 2018), were largely underrepresented. This was reflected in the analysis of functional coverage, which showed that the pool of sampled species consists of predominantly evergreen species with large and soft leaves. We also identified a predominant focus on tree/shrub sap flow, and a substantial knowledge gap on liana sap flow. The methodological limitations identified mostly apply to tree water use estimations (TWU), given the disproportionate representation of canopy trees compared to lianas and understory tree/shrubs in the literature. While we found sensor-independent limitations, such as poorly reported zero-flow determination, we found specific issues pertaining to heat dissipation studies and predominantly good practices among heat pulse studies. We also found most researchers strived to directly observe tree sapwood depth in the field, which increases the confidence in TWU estimations. Below, we discuss each aspect separately and, finally, propose directions for future PWU and, more specifically, TWU research in tropical forests.

4.1. Geographic, ecological and functional coverage

Most of our knowledge of tropical forests PWU is based on observations done in the Americas (42/72) and the Asia/Pacific (26/72), with very little output in the African continent (4/72) (Fig. 2, Suppl. Fig. 1). Overall, most studies were performed in sites classified as wetter tropical forests based on Holdridge life zones (i.e., where total annual precipitation exceeds annual potential evapotranspiration). Recent evidence suggests that American and Asia/Pacific wetter tropical forests are more vulnerable to climate change than their African counterparts. For example, Neotropical wetter forests have experienced increases in dry season length and intensity in the past few decades (Fu et al., 2013; Passel et al., 2024), including repeated extreme drought events. Given that Neotropical plant species distributions are limited by drought sensitivity (Engelbrecht et al., 2007), forest composition has been shifting toward increasing recruitment of dry-affiliated taxa (Esquivel-Muelbert et al., 2019). Similarly, studies have shown significant negative effects of extreme drought events in the carbon sink of Southeast Asian tropical wetter forests due to high tree mortality as a response to drought (Qie et al., 2017; Slik, 2004).

Conversely, African wetter forests have shown higher resistance and resilience to repeated droughts (Bennett et al., 2021; Hubau et al., 2020; Tao et al., 2022). For example, following one of the strongest El Niño Southern Oscillation events on record (2015-2016), the largest trees across African wetter forests experienced a non-significant increase in tree mortality (Bennett et al. 2021), contrary to South American wetter forests, where the largest trees represented the most mortality-prone size class after the same event (Bennett et al., 2023). This resilience, translated into the survival of the largest trees in this example, may be partially attributed to Africa's biogeographic history, which has favoured the persistence of drought-adapted rainforest species in response to past climatic fluctuations (Parmentier et al. 2007). Moreover, although an extensive assessment of tree hydraulic functioning is still lacking in Central African rainforests, studies have suggested some leaf-level adaptations to rising temperatures and CO_2 fertilisation, such as decreased stomatal density (Bauters et al., 2020; Hatangi et al., 2023). However, conflicting evidence also indicates a decrease in intrinsic water use efficiency among African rain forest species (Bauters et al., 2020), which warrants further studies. Overall, more research is needed in the hydraulic adaptations of the trees inhabiting the second-largest rainforest in the world. A deeper understanding of the hydraulic strategies of these resilient African forests could *(i)* refine predictions of water and carbon cycles, *(ii)* reveal successful plant strategies for coping with extreme drought events, and *(iii)* potentially guide functional trait-based restoration efforts.

Despite these geographically defined knowledge gaps among tropical wetter forests, drier forests have, overall, received even less attention in PWU studies (see also Suppl. Fig. 2). This is observed in other areas of research and conservation initiatives (Pennington et al., 2018). While we acknowledge that the geographical bias toward wetter forests could be justified by their disproportional contribution to atmospheric moisture via evapotranspiration (Eltahir and Bras, 1994; Zemp et al., 2014), changes in global climate will increase the pressure on these ecosystems due to increasing temperatures and atmospheric water stress (Bauman et al., 2022; Zhang et al., 2015b). Coupled with unpredictable rainfall patterns, this could lead to compositional changes in wetter forests toward a greater functional similarity with drier forests (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2019). Despite this, the lower functional diversity and functional redundancy observed in drier tropical forests on a global scale put them more at risk than wetter forests (Aguirre-Gutiérrez et al., 2022). In fact, drier forests have already been responding to intense drought events with functional homogenisation, with an increase in leaf deciduousness (Aguirre-Gutiérrez et al., 2020, 2019). A broader understanding of the ecophysiological strategies of trees inhabiting drier tropical forests could help us understand their future and also that of wetter forests.

The diameter distribution of the trees and shrubs sampled for sap flow generally resembled tropical forest expectations, whereas their height distribution deviated from these expectations. Tree/shrub diameters followed a log-normal distribution, which has been shown to best describe the maximum diameter attained by tropical forest trees (Poorter et al., 2008). Taking only diameter into account, this suggests that the trees/shrubs sampled may provide insight into the transpiration potential of tropical forests. For instance, we found that the abundance of very large trees (i.e., above 70 cm in diameter) was double what is typically recorded in tropical wet and dry forests: 5.2% in the sap flow literature, compared to 2-2.5% in tropical forests (Bradford and Murphy, 2019; Clark and Clark, 1996; Lanuza et al., 2023). The effort to estimate transpiration from these very large trees is justified, considering their disproportionate contribution to stand-level transpiration (Berry et al., 2018). In terms of height, the trees sampled exhibited a normal distribution, with a mean height of 20.6 metres. This differs from the typical height distribution expected in tropical forests, where a negative exponential pattern is often observed for trees above 10 cm in diameter (e.g., Paijmans, 1970), highlighting a focus on transpiration of canopy and emergent trees. Taken together, these results reveal a focus on large canopy trees with less emphasis on understorey trees and shrubs.

We found very few studies measuring liana sap flow (4/72), highlighting a clear knowledge gap in liana hydraulic functioning. This is especially pressing given the documented increase in liana abundance and biomass in tropical seasonal forests (Phillips et al., 2002) and overall competitive advantages of lianas over co-occurring trees. For instance, the competition for water resources of lianas on neighbouring or host trees is greater than that of saplings with similar biomass (Tobin et al., 2012). Despite greater leaf area relative to basal area compared to trees (Eltahir and Bras, 1994) and greater exposure to atmospheric evaporative demand due to their top-heavy architecture (Chen et al., 2017), lianas can maintain high productivity during seasonal droughts largely due to efficient stomatal control (Chen et al., 2015, 2017). However, evidence is conflicting as to whether lianas exhibit generally higher sap flow density than trees of similar diameters (e.g., Chen et al., 2015; Restom and Nepstad, 2001) or comparable density (e.g., Andrade et al., 2005), and whether they are able (e.g., Chen et al., 2015) or unable (e.g., Andrade et al., 2005; De Deurwaerder et al., 2018) to access water from deeper soil layers than trees. As for the contribution of lianas to stand-level transpiration in tropical forests, the only evidence to our knowledge comes from a secondary Amazonian forest, where lianas were estimated to contribute 9-12% of transpiration despite representing 5.5% of total basal area (Restom and Nepstad, 2001). Overall, the conflicting evidence on liana sap flow rates, soil water extraction and contributions to stand-level transpiration highlight the urgent need for elucidating their transpiratory behaviour. Filling this knowledge gap could greatly improve model predictions of the carbon and water cycles (Verbeeck and Kearsley, 2016), especially given their increasing presence in tropical forests.

4.2. *Sources of uncertainty in upscaling*

We identified major issues in the reporting of sap flow upscaling across the literature. Since 100% of the studies included in this section measured sap flow in trees, 6% in shrubs and 3% in lianas, this discussion mostly applies to tree water use (TWU) estimations. Some of these issues were specific to heat dissipation sensors, while others were universal in TWU studies. Among pre-data collection decisions, the main problems identified were the lack of consideration for azimuthal variation in sap flow (sensor-independent) and lacking efforts to test or develop species-specific calibration coefficients in the case of heat dissipation sensors. Among post-data collection decisions, the main problem identified was the unclear reporting of zero sap flow determination (sensor-independent) and a disregard for the contact of needle probes with heartwood in the case of heat dissipation sensors (i.e., Clearwater's correction). Most of these observations agree with those made by Peters et al. (2018), who quantified the influence of multiple methodological decisions on TWU estimations done with the heat dissipation method, shown by us to be the most methodologically inconsistent when applied in tropical forests, compared to heat pulse sensors. Importantly, heat dissipation sensors are the most used in the tropical forest sap flow literature as a whole (Suppl. Fig. 2).

Conversely, we also found some positive trends in the literature that indicate general efforts to overcome part of the limitations imposed by tropical forest heterogeneity in tree traits. The main positive aspect identified was that researchers frequently quantify sapwood depth or sapwood area in situ and, when not possible, develop and apply scaling equations that are species- and/or site-specific. This also translates into attempting to apply radial decay functions to account for radial variations across the sapwood profile, even if sensors are limited to calculating sap flow at the outermost sapwood layer. In the case of heat pulse sensors, we found that the application of data corrections is well accepted and generally applied in the literature. All these positive steps are taken after data collection, which suggests that researchers attempt to compensate for pre-collection limitations linked to sensor design, to more accurately quantify TWU.

4.2.1. *Pre-collection decisions*

Most studies were unclear about the number of sensors used and the azimuthal position where sensors were installed in the tree (i.e., the cardinal direction towards which the installed sensor points). Although azimuthal variation in the stem is often mentioned as a source of within-tree sap flow variability in many studies, it has seldom been directly measured in tropical forest trees and, even when reported, it is often incidentally mentioned without delving into its main implications for tree- and stand-level transpiration estimates. Even among the studies that acknowledged azimuthal sap flow variation in our review, very few reported the size of the difference between sides. The ones that did report it showed within-tree variations due to sensor position that ranged between 2% and 100% in a Panamanian tropical seasonal forest (Goldstein et al., 1998; James et al., 2002) and up to 150% in large dipterocarp trees in Borneo (Becker, 1996). Similar variability has also been documented in temperate and subtropical forests, where within-tree coefficients of variation of sap flow estimated from multiple aspects (N, S, E, W) may reach up to 47.2% and 62.5% in Japanese cedars (Shinohara et al., 2013), 45.5% in black locust and 44.8% in oak trees (Kume et al. 2012). While this has been shown to introduce substantial errors in stand-level water use estimates in these sites (e.g., 9-20% in Japanese cedar forests and 16-21% in black locust plantations and native oak forests in China), a targeted assessment of azimuthal variation on upscaled stand-level transpiration is still lacking in tropical forests.

We also found that sensor calibration is a specific issue with heat dissipation sensors. Almost all the heat dissipation studies (98%) used the empirical coefficients originally proposed by Granier (1985). This included 100% of the studies using custom-built heat dissipation sensors (Suppl. Table 4). When tested against species-specific calibration coefficients or others drawn from the literature, Granier's calibration has been shown to underestimate individual and plot-level transpiration by 37-60% across tropical dry forests (Iida et al., 2020), temperate conifer forest (Peters et al., 2018) and laboratory experiments with American beech (Steppe et al., 2010). The same calibration coefficients have also been used in sensors constructed with probes of variable length (James et al., 2002), an approach deemed adequate by early empirical tests involving tropical forest saplings (McCulloh et al., 2007), but questioned in a more recent study with a more comprehensive sample (although of temperate species), which found underestimations ranging between 23 and 45% for probes with deviating design (Fuchs et al., 2017). This finding is consistent with another review which found that only ~5% of studies incorporating sap flow data published between 2010 and 2018 documented the performance of calibrations on sap flow sensors (Dix and Aubrey, 2021).

4.2.2. *Post-collection decisions*

The method used to determine zero sap flow is often omitted in tropical forest TWU research. Among the studies that reported the method of zero flow determination, 5/35 directly observed it in situ by cutting the organ of the plant being monitored and interrupting the flow of sap (e.g., Berry et al., 2018; Eller et al., 2015; Gotsch et al., 2014). Since this approach may not be justifiable or feasible in most field research, and especially in native forests, many studies assume zero flow from specific weather conditions, predawn sap flow measurements or statistical approaches. However, indirect baselining is unable to account for important physiological processes that occur at night. For instance, positive or upward nocturnal sap flow can indicate nocturnal transpiration or refilling of stem water storage tissues (Alvarado-Barrientos et al., 2015), while nocturnal negative or downward sap flow, if identified in branches, can indicate foliar water uptake (Binks et al., 2019; Eller et al., 2013), and if identified in roots hydraulic redistribution as a response to drought (Oliveira et al., 2005). This observation is particularly relevant given that heat dissipation sensors, which composed the majority of the studies, have limitations in distinguishing low from zero flows and are unable to identify reverse sap flow (Vandegehuchte and Steppe, 2013). Zero-flow determination is generally not considered an issue among the heat pulse family, but in practice, small misalignments of the probes due to wounding or installation errors may lead to offsets in the zero-flow measured by the sensors (Burgess and Downey, 2014; Merlin et al., 2020), rendering baselining an important data processing step.

The sensor-specific corrections evaluated were mainly a problem with heat dissipation sensors. One of the main issues with sap flow collected with heat dissipation sensors is contact of the probes with inactive xylem (Clearwater et al., 1999). Although in some cases applying this correction does not result in important changes (Shinohara et al., 2013), in other cases, it can significantly improve the quality of sap flow estimations (Clearwater et al., 1999). The absence of this correction can even hamper the application of calibration coefficients (Paudel et al., 2013). On the other hand, correction for wound effects is well accepted among studies with heat pulse sensors, but this has yet to be incorporated in studies done with heat dissipation sensors. No study in our dataset that used heat dissipation devices accounted for wound effects, but in recent years the need for developing and applying wound correction approaches in these measurements has been underscored (Peters et al., 2018; Wiedemann et al., 2016). While wound healing corrections in heat dissipation studies have mostly been applied on forest plantations and orchards in recent years (e.g., Bodo & Arain, 2022; Bringhenti et al., 2025; Ferrara et al., 2024), it has only rarely been applied to native forests, even in the subtropical and temperate regions (e.g., Moreno et al., 2021).

Another limitation with heat dissipation sensors was the depth of probe insertion, which was generally restricted to the outer 20 mm of sapwood (i.e., Granier's design). Although it is usually assumed that the outermost layers of sapwood should display the bulk of sap flow (Zhang et al., 2015a), it has been shown that the curve of sap flow against the radial profile greatly varies in uneven-aged tropical moist and tropical dry forests (James et al., 2002; Link et al., 2020). Moreover, the contribution of inner sapwood to daily water use can vary depending on the period and environmental conditions at the time of observation (Poyatos et al., 2007). In this context, directly determining the area of sapwood and considering the radial decay of sap flow across the sapwood from outer to inner layers (James et al., 2003) greatly improves the accuracy of TWU estimations (Zhang et al., 2015a). We found that indeed, despite limitations in pre-collection steps, such as depth of probe insertion, most studies attempted to directly determine sapwood area, either by coring or by preliminarily testing sap flow with long probes, such as those with heat field deformation devices (e.g., Ghimire et al., 2022). In the cases where coring was not possible due to the protection of the trees or for the trees being located in a long-term monitoring plot, the studies often applied site- or species-specific equations relating an easily measurable scalar (such as DBH) to sapwood depth or sapwood area (e.g., Alvarado-Barrientos et al., 2015; Horna et al., 2011; Kunert et al., 2017).

5. FUTURE RESEARCH

In this review, we showed that tropical forest plant water use (PWU) research is geographically biased toward Neotropical and Asian wetter forests. Given the ongoing changes to global climate, this observation leads us to make two recommendations. The first is to investigate PWU and hydraulic functioning in African wetter forests, shown to be more resistant and resilient to extreme droughts (Bennett et al., 2021; Hubau et al., 2020; Tao et al., 2022). This could enhance carbon and water cycle predictions and potentially provide insight into functional trait-based approaches for forest restoration. The second recommendation is to dedicate more efforts to quantifying PWU in drier tropical forests. This could improve ecophysiological models and enhance predictions of plant-atmosphere feedback. Furthermore, understanding the strategies and behaviour of drier forest types could inform us about the future of wetter forests under an increasingly hot and dry climate.

Our review also revealed a substantial knowledge gap on liana sap flow. Despite their increasing abundance (Phillips et al., 2002) and competitive dominance over water resources (Chen et al., 2015), lianas remain underrepresented in the literature, with only a handful of studies quantifying their sap flow. This gap limits our understand of how lianas contribute to forest-level water use, especially considering their acquisitive water-use strategies and potentially significant contributions to stand-level transpiration (Restom and Nepstad, 2001). Future research should therefore prioritize integrating lianas into sap flow studies, not only to clarify their physiological responses and competitive interactions but also to refine global vegetation models under changing climatic conditions (Verbeeck and Kearsley, 2016).

We also showed that tropical forest PWU research is methodologically biased and, often, poorly reported. Most methodological issues identified were related to the use of heat dissipation sensors and equally distributed between pre- and post-data collection stages. Although these methodological shortcomings are irrespective of the study system, their implications are particularly critical in tropical forests, which are the primary contributors to the global water cycle. Addressing these issues will not only strengthen PWU research but also enhance the coverage and reliability of global databases such as SAPFLUXNET (Poyatos et al., 2016). As collaborative efforts in the Earth sciences become increasingly essential in the face of climate change, we strongly advocate for standardising sap flow methodologies and improving reporting practices to facilitate large-scale synthesis and predictive model development.

CRediT authorship contribution statement

Natalia de Aguiar-Campos: Writing – original draft, Formal analysis, Conceptualization, Writing – review & editing, Investigation, Data curation. **Will Edwards:** Supervision, Writing – review & editing. **Susan G. W. Laurance:** Writing – review & editing, Conceptualization, Supervision.

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.

ACKNOWLEDGEMENTS

The authors thank James Cook University for a JCU Postgraduate Research Scholarship granted to NdAC and the Australian Research Council for the funds awarded to SL (DP200103100).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2025.110738.

APPENDIX 1: Detailed description of the functional coverage analysis

Categorical functional traits

The only categorical variable included in our functional coverage analysis – leaf phenology type – was obtained from the TRY database (Kattge et al., 2020). We classified a species' phenology based on the number of records of it contained in the database. For example, we considered it a reliable classification when a species contained 5 or more records of a single type of phenology – e.g., *Garcinia cowa* had 9 entries into the database, all describing it as an evergreen species; hence, *Garcinia cowa* was classified as evergreen. Conversely, when the number of observations was smaller than 5 or when the records were conflicting, we searched in specialised websites, such as Atlas of Living Australia, Flora e Funga do Brasil, Kew Herbarium Online, among others. An example of this case is the species *Corymbia porrecta*, which had 5 entries describing it as deciduous and 8 entries describing it as evergreen, but which after a search in the Atlas of Living Australia, we decided could be classified as facultative deciduous, hence, non-evergreen.

Continuous functional traits

For the continuous trait data (leaf area, LA in mm^2; leaf mass per area, LMA in $g.m^{-2}$; wood density, WD $mg.mm^3$), we used a hierarchical approach. We first searched for species-level values of that trait in the Global Spectrum Dataset, which we considered as a reference due to the rigour in the collective efforts for the assembly of the data (Díaz et al., 2022, 2015). When a trait was not present in the Global Spectrum Dataset for a particular species or its synonyms, we extracted from the TRY database all entries satisfying our search. In the case of WD, if not present in the Global Spectrum Dataset, we extracted from the TRY database only basic wood density values (dry mass divided by green volume). If not present in either of the mentioned sources, we searched for the species' WD in the Global Wood Density Database (Zanne et al., 2009).

To ensure the reliability of the data extracted from the TRY database, we followed a series of steps before averaging the observations into species-level trait means. To avoid duplicates, we filtered the data to contain only distinct values once contributor name was excluded from the dataset. We then filtered out all values with an Error Risk above 4 – i.e., more than 4 standard deviations away from the calculated means of its assigned species-, genus-, family or, in case the amount of data in the previous categories were insufficient, the mean for all vascular plant species (details in Kattge et al. 2020 and Díaz et al. 2022). Since the continuous traits were shown to sample from a log-normal distribution, we calculated their geometric means (Díaz et al., 2022).

Comparing the extent of continuous functional traits to the observed in tropical forests

On the main text (Fig. 5), we presented the extent of LA, LMA and WD covered in the studies relative to the upper and lower boundaries of each trait found in tropical forests. Below is a step-by-step description of our approach for the tree/shrub and liana species:

(1) We filtered the Global Spectrum Dataset (doi: 10.1038/s41597-022-01774-9; available as an Excel spreadsheet) to contain only *woody terrestrial shrubs* and *woody terrestrial trees* and, separately, to contain only *woody terrestrial climbers* (i.e., tree/shrubs and lianas, respectively).
(2) We submitted the list of tree/shrub species (12,864 species) and, separately, liana species (956 species), to a query at the Global Biodiversity Information Facility (GBIF) using the function *occ*, from the R package *spocc* (Owens et al., 2024). We employed the following criteria:

a. Even if a species had >50 occurrence points, we retrieved only 50 occurrence points, aiming to optimise the search and decrease computing time.
b. If a species had fewer than 30 occurrence points, we removed it from the analysis.
c. In the end, the number of occurrence points per remaining species in the dataset was between 30 and 50.

(3) After removing duplicates, we quantified for each remaining species the total number of occurrences in the tropical region by quantifying the points between latitudes 23.5 N and 23.5 S (i.e., the tropical region).
(4) We filtered the resulting dataset to keep only the species that had at least 15% of observations recorded within the tropical region. We called this the 'tropical species dataset', which is a list of:

a. 5,160 tree/shrub species,
b. 453 liana species.

(5) From the Global Spectrum Dataset (Díaz et al., 2022), we extracted the LA, LMA and WD values for the species present in the 'tropical species dataset'. This we called the 'tropical functional dataset', whereby:

a. LA was found for 2,134 tree/shrub species and 272 liana species,
b. LMA was found for 1,672 tree/shrub species and 107 liana species,
c. WD was found for 3,270 tree/shrub species and 67 liana species.

(6) We filtered the 'tropical functional dataset' so as to display the highest and lowest value of each trait, separately.
(7) Next, we checked if the species displaying these extreme values indeed occurred in tropical forests (i.e., not exclusively occurring in other tropical vegetation types, such as savannas), by consulting authoritative sources such as WFO (2025) and POWO (2025).
(8) We considered these extreme values from the dataset as the upper and lower boundaries at which these traits occur in tropical forests worldwide (Fig. 5).

In addition, we present in the Appendix (Fig. A.1) the distribution of functional traits from the species included in the review along with the distribution of traits from the 'tropical functional dataset' that we described above. The results depicted in Fig. A.1 should be interpreted with caution, since some of the species included could have a distribution outside tropical forests. This is meant as a visual reference to illustrate the extent of functional variation covered by the sap flow studies. For instance, the large functional gap in lianas is highlighted, while the focus on trees and tree/shrub species is clear, since it more closely follows the variation found all throughout the tropics.

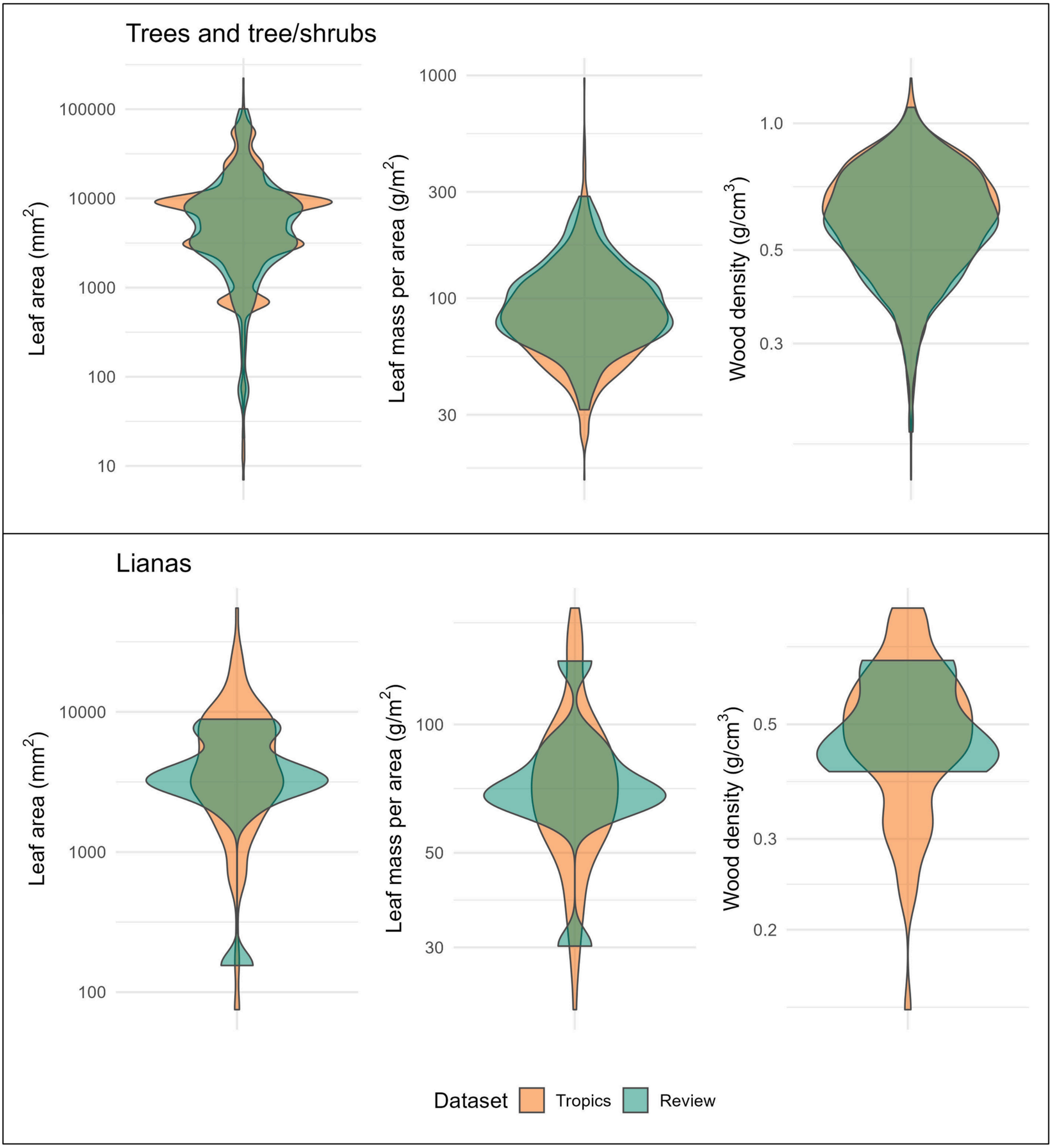

Figure A.1. Distribution of leaf area (log-scale), leaf mass per area (log-scale) and wood density for the species included in the review along with the species with a tropical occurrence according to our search at the GBIF (i.e., at least 15% of occurrences within the tropics and at least 30 occurrence points recorded overall). The top panel depicts tree/shrub species, while the bottom panel depicts liana species. These results should be carefully interpreted, since the distribution of the species included in the "Tropics" dataset is not confirmed to extend into tropical forests – i.e., some could be exclusive to savannas or other tropical vegetation types. This figure is to serve as a general depiction of the functional trait space covered by studies that upscaled sap flow to PWU in tropical forests.

Data availability

The data used are in the Suppl. Material.

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