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Context-dependent plant–soil regulation of tree water transport in tropical forests

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Abstract

Plant water transport is a key process linking vegetation physiology with soil and atmospheric conditions and regulating ecosystem water and carbon fluxes. Yet, how intraspecific hydraulic strategies vary across heterogeneous tropical environments remains poorly constrained. We investigated hydraulic architecture of *Mangifera sylvatica*, a canopy tree species of South Asian moist tropical forests, across two climatically and edaphically contrasting sites in Bangladesh. Stem and branch xylem anatomical traits were quantified to estimate theoretical hydraulic conductivity and percent loss of conductivity, alongside measurements of tree structural attributes and soil physical and chemical properties. Despite pronounced differences in elevation, soil texture, moisture availability, and stand structure between sites, hydraulic strategies—including conductivity, vessel traits, and safety–efficiency trade-offs—were conserved across forests. In contrast, the mechanisms regulating hydraulic function differed strongly between sites, with crown architecture and soil sand content dominating in the drier site, and sapwood allocation, tree height, and soil bulk density governing hydraulic behavior in the wetter site. These results indicate that similar hydraulic outcomes can emerge from distinct plant–soil–atmosphere interactions across space. Such context-dependent regulation of plant water transport has implications for predicting tropical forest transpiration, drought sensitivity, and land–atmosphere feedbacks under increasing vapor pressure deficit and climate change.

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Short summery

This study investigates how plant–soil interactions regulate tree water transport across contrasting tropical forests in South Asia. Using xylem anatomical traits, hydraulic conductivity estimates, and soil and structural measurements, we show that a tropical canopy tree maintains conserved hydraulic strategies across environments but through different plant–soil regulatory mechanisms. These findings provide process-based insight into vegetation water transport and its role in ecosystem water fluxes under changing climate.

Key words: Xylem hydraulic traits, Safety–efficiency trade-off, Tropical moist forests, *Mangifera sylvatica*, Hydraulic conductivity, Trait–environment relationships, Climate vulnerability

1. Introduction

Water is required to perform tree's biological function, including maintaining stomatal conductance and CO2 uptake during photosynthesis (Gleason et al., 2016). Understanding trees water conducting system is crucial for predicting their survival and function. Xylem vessels in trees conduct water from the soil to the leaves (Sperry et al., 2008) and thus xylem hydraulic traits are critical determinants of plant performance and survival particularly when trees experience higher atmospheric demand under climate change (Choat et al., 2018). These hydraulic traits not only indicate species-level drought tolerance but also represent how trees adapt to fluctuations in climate-driven variables such as temperature, soil moisture, and vapor pressure deficit (VPD)(Anderegg et al., 2016; Brodribb et al., 2020).

As global temperatures rise, the atmospheric vapor pressure deficit (VPD) also increases, which causes water stress and higher rates of tree mortality risks (McDowell et al., 2022). Tropical forests are amongst the vulnerable forest ecosystems to climate change (Rahman et al., 2017; Wright, 2005) . The rise in global temperatures and the corresponding increase in atmospheric VPD can significantly raise the risk of hydraulic failure in tropical tree species (Grossiord et al., 2020). For example, recent studies projected that rising VPD could reduce tropical forest productivity by up to 50% by 2100 (Staal et al., 2020). As VPD increases, plants are forced to balance hydraulic efficiency with safety (Gleason et al., 2016), often resulting in trade-offs in wood anatomy that influence both their growth and survival (Olson et al., 2021).

To cope with climate-driven stressors, tropical trees exhibit diverse hydraulic strategies involving structural, anatomical, and functional adaptations (Chowdhury et al., 2023; Islam et

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al., 2025) . Structural attributes (e.g., tree height, DBH, crown traits etc.) modulate water use efficiency at the stand level (Olson et al., 2021; Rahman et al., 2020). Wood anatomical adaptations, including adjustments in vessel diameter, vessel density, sapwood specific hydraulic conductivity directly influence the safety-efficiency tradeoff (Ferdous et al., 2023; Gleason et al., 2016). Complementary functional traits (e.g., wood density, bark thickness) also regulate hydraulic resilience (Anderegg et al., 2018). However, variation in site-level factors (e.g., elevation, disturbance, slope, soil texture, pH, porosity, bulk density, organic matter, and moisture etc.) might result in diverse hydraulic strategies even within the same species. For instance, contrasting environments may affect how wood reacts anatomically in different ways, which in turn affects the vulnerability or resistance to hydraulic failure (Pfautsch et al., 2016; Schuldt, B., Knutzen, F., Delzon, S., Jansen, S., Müller-Haubold, H., Burlett, R., 2016). Yet, it is still unknown whether species use the same hydraulic strategies in different population structures and growing conditions, especially in tropical biomes that aren't well studied, particularly in South Asian moist tropical forests.

Despite their ecological significance, South Asian moist tropical forests remain understudied in terms of tree hydraulic functioning. There is a lack of research that combines population-level traits, environmental variation, and wood anatomy, which limits our understanding of species resilience in this region (Rahman, Islam, & Bräuning, 2019). This gap is crucial, given that South Aian moist tropical forests particularly those in Bangladesh are increasingly threatened by climate stressors such as more intense monsoons and rising temperatures (Jihan et al., 2025).

M. sylvatica, a canopy tree endemic to these forests, serves as an ideal model to investigate hydraulic responses because of its wide distribution across diverse landscapes. In this study, we examine the xylem hydraulic strategies of *M. sylvatica*, a native tropical tree species, across two moist forest sites in Bangladesh that have different population structures and site characteristics. Specifically, we address two research questions:

(i) Does variation in population structure and site conditions lead to different hydraulic strategies in naturally growing *M. sylvatica* across moist forests?

(ii) Which factors do regulate hydraulic behavior across moist forests with contrasting population structure and growing conditions.

2. Materials and methods

2.1 Study sites, species, and sampling design

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This research was carried out in two distinct hill forests of Bangladesh: Rema-Kalenga Wildlife Sanctuary (RKWS) and Kaptai National Park (KNP). RKWS lies between 24°06 '-24°14' N and 91°34'-91°41' E with an area of 1,795 hectares, encompassing the Southeastern part of Tarap Hill Reserve of Northeastern Bangladesh. RKWS represents a moist tropical climate with a mean annual temperature of 24.8 °C (highest in August about 33.3 °C and lowest in November about 10.1 °C. The mean annual rainfall is 2363 mm averaged over 1950 to 2020. The monthly average humidity varies from 74% to 89%. The study area consists of hills with a maximum elevation of 100m (a.s.l.) as well as the flood plain valleys. Soil on the hills are sandy loamy, whereas those on the low-lying area are clay loamy. It is tropical evergreen to semi-evergreen hill forest. The sanctuary has a high conservation value due to its unique flora and fauna. Some major tree species are *Dipterocarpus turbinatus, Schima wallichii, Tectona grandis, Chukrasia tabularis, Toona ciliata, Hopea scaphula, Albizia procera, Syzygium grandis,* and *Gmelina arborea.*

KNP is located between 22°29.991′ N and 92°10.722′ E in the hill tracts of Southeastern part of Bangladesh. It encompasses with 5,465 hectares areas zzyyyzz. The region has a tropical monsoon climate, with average maximum temperature is 34°C and average minimum temperature is 18°C. The mean annual rainfall is 2589 mm. This nature reserve consists of tropical ever-green to semi-evergreen forests interspersed with hills, hillocks, and plainlands. Some major species are *Chukrasia tabularis, Artocarpus heterophyllus, Artocarpus chama, Acacia catechu, Acacia mangium, Acacia nilotica, Albizia procera, Toona ciliata, Erythrina variegate, Dipterocarpus turbinatus, Syzygium grande*.

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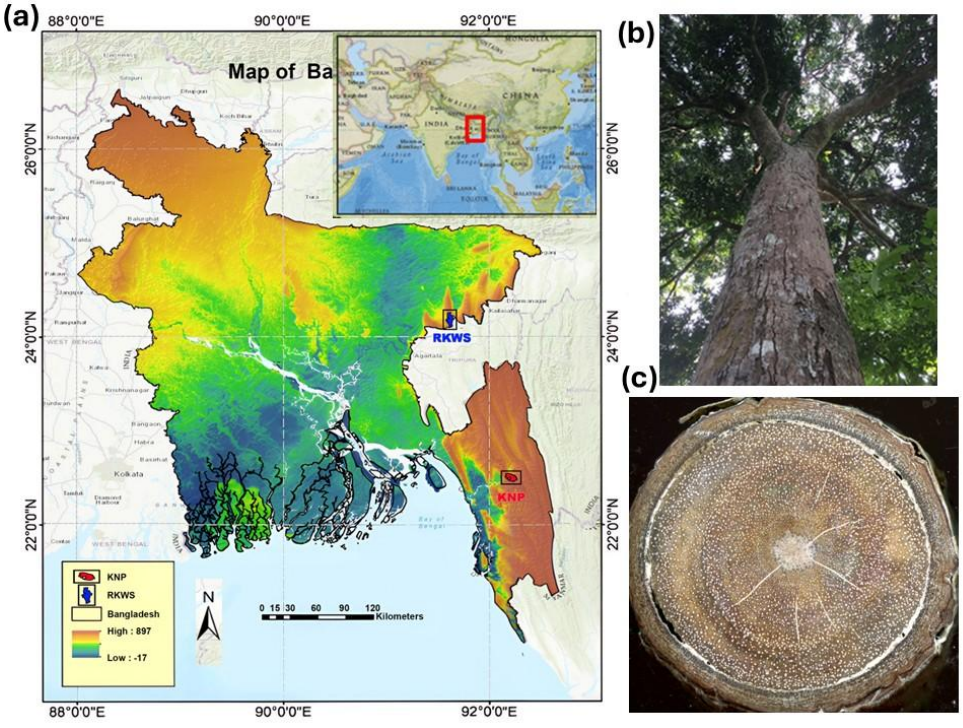

Figure 1. a) Map of Bangladesh showing the study sites: Rema-Kalenga Wildlife Sanctuary (RKWS), and Kaptai National Park (KNP). b) A mature *Mangifera sylvatica* tree. c) a scanned image of the cross-sectional surface of a *M. sylvatica* branch.

We selected *M. sylvatica* as a model tree mainly because this is one of the major native canopy tree species in both study sites and has conservation values since the species has recently been enlisted in the IUCN red list of threatened species (Akhter et al., 2022; Khan et al., 2001). *M. sylvatica* is an evergreen light-demanding tree (Baul et al., 2016), forms annual growth ring boundary (Islam et al., 2018a) and is suitable for wood anatomical measurements.

We established a total of 60 circular plots of 400 m^2 (plot radius 11.3 m) centering an individual of *M. sylvatica* tree in two study sties (RKWS and KNP). Since *M. sylvatica* trees naturally occurred, their distribution is sporadic and therefore a purposive sampling strategy was followed to locate the position of *M. sylvatica* tree and to establish circular plots. Biogeographic and tree demographic data, soil samples, wood samples of both branch and stems, and leaf samples were collected from each plot. Soil samples were collected using a soil auger at 15 cm depth. A total of five soil samples were taken from each plot following the

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sampling criteria described by (Islam et al., 2016). The five soil samples were mixed and made a composite soil sample that was analyzed for soil texture and soil moisture content measurement. Soil samples collected using a soil core were analyzed for soil bulk density and soil organic carbon measurement. A list of variables studied is shown in Table 1.

Table 1. List of biogeographic variables, tree structural attributes and hydraulic traits studied in the present study conducted across two moist forest sites in Bangladesh.

Category	Variables	Abbreviation and unit
Hydraulic traits	Percent loss in theoritical conductivity from stem to branch	$PLC_{(theo.)}$%
	Theoretical stem hydraulic conductivity	$K_{s\text{-}stem}$ ($Kgm^{-1}s^{-1}MPa^{-1}$)
	Hydraulically weighted vessel diameter	DH_{stem} (mm)
	Xylem vulnarability index	Vx
	Stem vessel denstiy	VD_{stem} (mm^2)
	Stem mean vessel area	MVA_{stem}
	Soil bulk density	SBD (gcm^{-3})
Soil variables	Soil Porosity	P (%)
	Soil moisture content	SM (%)
	Soil organic carbon content	SOC (%)
	Soil pH	pH
	Clay content	Clay (%)
	Silt content	Silt (%)
	Sand content	Sand (%)
Biogeographic variables	Elevation	Elevation (m)
	Slope	Slope (degree)
	Disturbance index	DI
	Light interception index	LI
Tree structural attributes	Tree diameter at breast height	DBH (cm)
	Tree height	Height (m)
	Bark thicness	BT (cm)
	Crown surface area	CSA (m)
	Sapwood length	SL (cm)
	Wood density	WD (gcm^{-3})

2.2. Biogeographic and environmental data collection

Biogeographic information, and demographic and environmental data collection were carried out in each plot. Tree diameter at breast height (DBH), tree height, and crown surface area (CSA) were measured for each sampled tree. Tree DBH was measured using a metric diameter tape and tree height was measured using a Suunto clinometer (Suunto PM5/360PC

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Clinometer, Finland). Tree CSA is usually derived from crown radius assuming tree crown as circular shape and thus tree CSA was calculated from the formula of the area of a circle as follows (Pretzsch et al., 2015; Rahman et al., 2021):

$$CSA = \pi r^2, \text{ Where } r = \text{crown radius.}$$

Crown radius is the distance between the center of the trunk and the perimeter of the crown. Crown radii were measured in four directions and averaged to get the mean crown radii (Pretzsch et al., 2015). Similarly, basal area (BA) was calculated from the diameter at breast height (DBH) using the formula of the area of a circle.

Sapwood length and bark thickness were measured immediately after the extraction of increment cores in the field. Sapwood was identified by its light brown color from the dark brown heartwood portion. We did these measurements in the field because the differences in color between sapwood and heartwood become less visible when cores dry. In addition, the attack by stain fungi may further complicate the sapwood and hearth wood identification. We assigned a disturbance index value (1-5) to each sampled tree where 1 = Very low disturbed, 2 = low disturbed, 3 = moderate disturbed, 4 = high disturbed, 5 = very high disturbed. We also assigned a light Interception value (1–5) to each sampled tree following the established protocol as follows: 1 = crown received neither overhead nor lateral light, 2 = crowns received no overhead high but received intermediate lateral light, 3 = crowns received partial light (10–90%) from the vertical direction, 4 = crowns were fully exposed to vertical light (greater than 90%), 5 = crowns were completely exposed to both vertical and lateral light (Clark and Clark, 1992).

2.3. Wood sample collection, processing and surface preparation

A total of 180 increment cores of *M. sylvatica* were extracted from two study sites. All the wood cores were taken at breast height (1.3 m) using a 5.15 mm increment borer. After extraction, the cores were placed in a plastic core holder immediately to prevent them from any mechanical breakdown. The wood cores were airdried for 24 hours to avoid any fungal attack. A total of 60 branch samples were also collected from the two study sites. Branch samples were collected through a sharp wood cutter. After collecting, all the samples were labeled properly and dried accordingly following the same procedure used for increment cores.

The cores were placed on wooden holders and sanded using fine grain papers starting at 120 grit and going up to 2000 grit until the anatomical details of the wood were clearly visible. The dust was cleared using an air blower after sanding with each sandpaper grade. After sanding white chalk was applied on the sanding surface of the core to fill the vessels that

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improves the visibility of the vessels (Islam et al., 2018b). Then, cores were scanned at 2000 dpi by using a flatbed scanner (Epson Perfection V550 scanner, Epson America, Inc. CA). The branches were also sanded following the same methodology but here we used fine grain papers starting at 60 grit due to the coarse anatomical structure of bark portion and going up to 2000 grit until the anatomical details of the wood were clearly visible. Branches were then scanned at 2000 dpi.

The sapwood area was identified on the scanned image of each tree and wood anatomical measurements were made on the sapwood areas using the WinCELL image analysis software (Regent instrument Inc, Quebec Canada). In the sapwood area of each core, three 2mm*2mm analyzed areas were taken for the vessel measurement. Similar measurement protocol was followed for the branch samples. In each branch, three (2mm*2mm) areas were taken from the last five growth rings for the vessel measurement.

2.4. Wood anatomical measurement and calculation of hydraulic traits

Vessel density (VD) and hydraulically weighted vessel diameter (DH) were measured to calculate theoretical hydraulic conductivity (KS) from both stem cores and branches. VD was calculated by counting the number of vessels per unit analyzed area. The radial and tangential diameter of vessels were measured using the WinCELL software. Then, the following equation was used to calculate the Hagen-Poiseuille hydraulically weighted vessel diameter:

$$DH = \sqrt[4]{\frac{1}{n}\sum_{i=1}^{n}\frac{2a^2b^2}{a^2+b^2}};$$ (Tyree and Zimmermann, 2002)

Here, n = Total number of vessels measured, a = Radial axes of vessels (mm), and b= Tangential axes of vessels (mm).

The theoretical hydraulic conductivity (Ks) was measured according to the following formula: (Hagen-Poiseuille's law)

$$Ks = \left(\frac{\pi\rho}{128\eta}\right) * DH^4 * VD;$$ (Fan et al., 2012; Tyree and Zimmermann, 2002)

Here, η= Viscosity of water (1.002×10^{-9} MPa s^{-1}), ρ= Density of water at 20 °C (998.21 kgm^3)

Finally, the Percentage Loss in Hydraulic Conductivity ($PLC_{theo.}$%) from stem to branch was measured using the following formula:

$$PLC_{theo.}\% = (Ks_{stem} - Ks_{Branch}) / Ks_{stem} \times 100$$ (Schönauer et al., 2023)

Here, $Ks_{(stem)}$ = Stem hydraulic conductivity ($Kgm^{-1}s^{-1}MPa^{-1}$), $Ks_{(Branch)}$ = Branch hydraulic conductivity ($Kgm^{-1}s^{-1}MPa^{-1}$).

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2.5. *Measurement of sapwood density*

For the measurement of wood density (WD), an increment core for each tree was oven dried. First, sapwood portion from each core was carefully dissected. The length and diameter of each sapwood sample was measured. Cores were dried using an electric oven for 72 hours at 105º C. The volume of fresh sapwood sample was calculated using the formula of a cylinder as follows:

$$\text{Sapwood volume, V } (cm^3) = \pi r^2 h,$$

Where, r = Radius of the fresh sapwood core sample (cm), h = length of the fresh sapwood sample (cm).

The density of sapwood of each tree was calculated using the following formula:

$$\text{Density } (gm/cm^3) = Dry\ mass\ of\ \text{sapwod}\ (gm)\ /Volume\ of\ fresh\ sapwood\ (cm3)$$

2.6. *Measurement of soil moisture content, bulk density, and porosity*

Soil moisture content was determined using the oven-dry method. Fresh soil samples were weighed to obtain the moist weight (M), oven-dried at 105 °C for 24 h, cooled to approximately 50 °C, and reweighed to determine the dry weight (D). Moisture content (MC) was then calculated as:

$$\text{MC } (\%) = \frac{M - D}{D} \times 100$$

Soil bulk density (SBD) was measured using the core method as described by Cresswell and Hamilton (2002). Soil samples were collected with a cylindrical core of known dimensions, and the core volume (V) was calculated as:

$$V\ (cm^3) = 3.14 \times \text{core radius}^2 \times \text{core height}$$

The oven-dry soil weight was divided by the core volume to obtain soil bulk density:

$$\text{SBD } (gcm^{-3}) = \frac{\text{Dry Soil Weight (g)}}{\text{Soil Volume (cm3)}}$$

Soil porosity, a key physical property influencing soil structure and health, was estimated following Pagliai and Vignozzi (2006). Porosity (P) was calculated as:

$$P\ (\%) = \left(1 - \frac{Bulk\ density}{Particle\ density}\right) \times 100$$

where particle density (PD) was obtained as:

$$PD = \frac{Mass\ of\ soil\ (g)}{Volume\ of\ soil\ particles\ (cm^3)}$$

and the volume of soil particles was computed using:

$$\text{Volume} = \pi r^2 h$$

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All soil samples were oven-dried at 105 °C for 24 h, and weights were measured using a balance with a sensitivity of 0.01 g.

2.7. Soil pH and organic carbon measurement

Soil pH was measured using a digital pH meter (Hanna HI2211 pH/ORP meter). For each sample, 5 g of moist soil was placed in a 50 mL test tube, and 10 mL of distilled water was added. The suspension was stirred for 10–15 minutes using an electric shaker, and the pH was recorded directly from the meter display.

Soil organic carbon (SOC) was determined following the Loss on Ignition (LOI) method (Viscarra Rossel et al., 2014). Soil samples were first oven-dried at 105 °C for 24 h to obtain dry weight. A subsample of 10 g of oven-dried soil was placed in pre-weighed crucibles and combusted in a muffle furnace at 550 °C for 4 h. Crucibles were then cooled inside the furnace, and the post-combustion weight was measured. SOC content was estimated as the proportion of weight lost during combustion relative to the oven-dry mass.

2.8. Measurement of soil texture

Soil texture was determined using the hydrometer method (Bouyoucos, 1962), which measures the relative proportions of sand, silt, and clay in soil suspensions. A calibrated hydrometer (ASTM No. 152 H with Bouyoucos scale in g/L) was used to record suspension density at specific time intervals. The corrected hydrometer reading (Rc) was calculated as:

$$Rc = (R\text{-}RL) + (t\text{-}20) \times 0.3$$

where R = hydrometer reading at time t, RL = blank reading in distilled water, and T = suspension temperature (°C).

Particle size fractions were then calculated as:

$$Silt\%+Clay\% = (Rc \text{ at } 40 \text{ sec}/Dry \text{ Weight of sample soil}) \times 100$$

$$Clay\% = (Rc \text{ at } 2 \text{ hrs}/Dry \text{ Weight of sample soil}) \times 100$$

$$Silt\% = (Silt\%+Clay\%) - Clay\%$$

$$Sand\% = 100 - (Silt\%+Clay\%)$$

For each analysis, 40 g of air-dried soil was dispersed in distilled water, pre-treated with 5 mL of 30% hydrogen peroxide when organic matter content exceeded 5%. The suspension was heated on a hot plate for 15 min, cooled, and treated with 100 mL of 5% sodium hexametaphosphate ($Na(PO_3)_6$) as a dispersing agent. The solution was then transferred to a 1000 mL sedimentation cylinder, diluted to volume with distilled water, and stirred mechanically for 3 min. Hydrometer readings were taken at 40 seconds and 2 hours after

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mixing, with concurrent temperature measurements. Blank readings were obtained using the dispersing solution alone.

2.9. Data analysis

The *readxl, dplyr, tidyr,* and *tidyverse* packages were used to organize and clean data. Principal Component Analysis (PCA) was performed using *FactoMineR, factoextra, corrr, corrplot,* and *ggcorrplot* packages to explore the multivariate relationships between hydraulic traits, tree demographics, and soil physical–chemical properties. The loading vectors indicate the relative importance and correlation among variables, where vector length corresponds to correlation strength and the angle between vectors reflects their relationships (acute = positive, obtuse = negative, right angle = no correlation). Independent sample t-test was performed using the *stats* package to compare the population structure and site conditions between two study sites. Similar t-test was also performed to evaluate the differences in hydraulic traits between stem and branch and between two sites. A simple linear regression was performed using *ggpubr* package to test the relationship of hydraulic traits with tree structural attributes, functional traits, and environmental variables. The difference in slope of the linear relationship between two sites was evaluated employing analysis of covariance (ANCOVA) using *car* and *broom* packages. To evaluate the relative importance of each significant variable in predicting hydraulic strategies, we performed linear mixed effect modelling (LMEM) using the *nlme* package, taking tree attributes and environmental variables as fixed factors and tree ID as random factor. Standardized model coefficients and 95% confidence intervals were extracted using *broom.mixed* package. We calculated both conditional and marginal R^2 and used Akaike Information Criterion (AIC) using *MuMIn* package to evaluate the model performance. All analyses were performed in R using the version 4.5.1 (Great Square Root) (R Development Core Team, 2025).

3. Results

3.1. Variation in population structure and growing conditions between sites

The population of *M. sylvatica* in RKWS had significantly higher DBH, height and CSA ($p<0.001$) with lower BT and WD ($p<0.01$) than the population in KNP (Fig. 2). KNP had *M. sylvatica* population at higher elevation (mean elevation 71 m above sea level) compared to RKWS (40 m) ($p<0.001$). The population of *M. sylvatica* in RKWS was grown in soils with higher SM ($p<0.001$), higher SOC($p<0.01$), higher soil porosity ($p<0.001$) and lower

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pH ($p<0.001$) than KNP. In terms of soil texture, RKWS supported *M. sylvatica* population in soils with higher clay content ($p<0.001$) and lower silt ($p<0.01$) content than KNP (Fig. 2). However, there was no significant difference in LI, DI, slope, sand content, SBD, SL, and WD between the two sites inhabiting *M. sylvatica* population (Table S1).

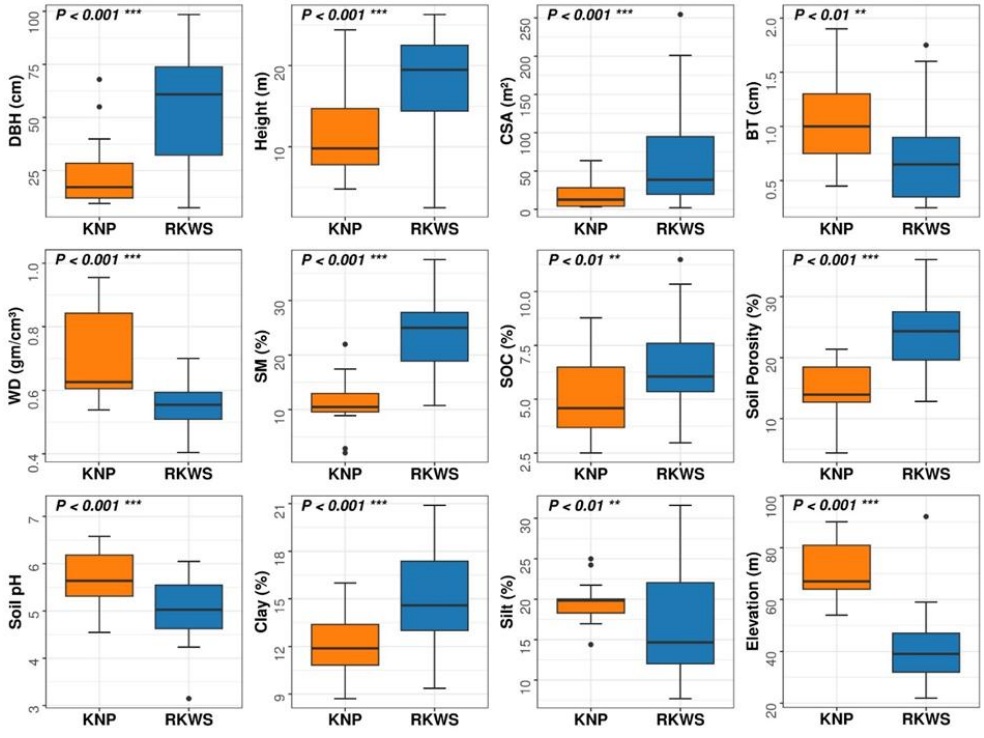

Figure 2. Comparing population structure and growing conditions of *Mangifera sylvatica* across two moist forest sites in Bangladesh.

3.2. Hydraulic strategies of M. sylvatica across sites

The independent sample t-test revealed no significant difference in Ks, VD, and $PLC_{(theo.)}$% of *M. sylvatica* population between two sites (Fig. 3). However, within a site, stem Ks was significantly higher than branch in the *M. sylvatica* population of KNP ($t=-14.1$, $p<0.001$). Likewise, a significantly higher Ks was found in stem than in branch at RKWS ($t=16.7$, $p<0.001$) . In contrast, VD was higher in branch than in stem in both sites ($p<0.001$) (Fig. 3). At KNP, Ks decreased by **72.4%** from from Stem to Branch which is slightly lower than RKWS with a decrease of 76 %.

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We observed a significant trade-off between stem DH and VD in both sites with slightly higher slope in RKWS (R^2=0.63, p<0.001) than in KNP (R^2=0.49, p<0.001) albeit the difference in slope of the linear relationship between two sites was not significant as revealed by the ANCOVA test (Table S2). This site level vessel diameter and density trade-off also existed when we analyzed data from two sites together (R^2=0.61, p<0.001) (Fig. 4). Thus the *M. sylvatica* populations from two sites followed the same hydraulic strategies though they experienced different growing conditions and had different population structures.

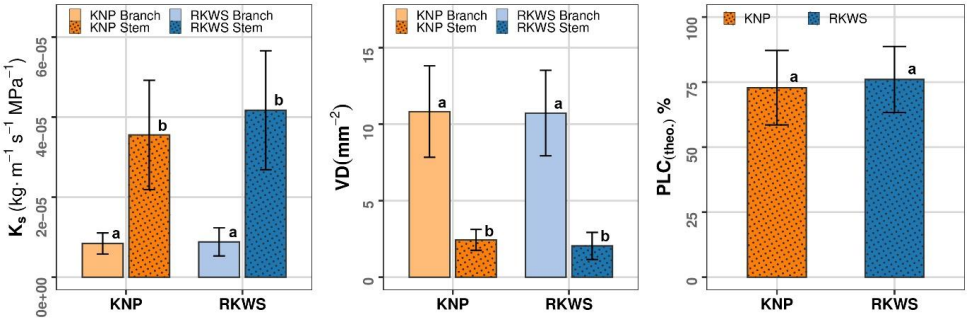

Figure 3. Comparison of stem and branch xylem hydraulic traits of M. sylvatica across two moist forest sites in Bangladesh.

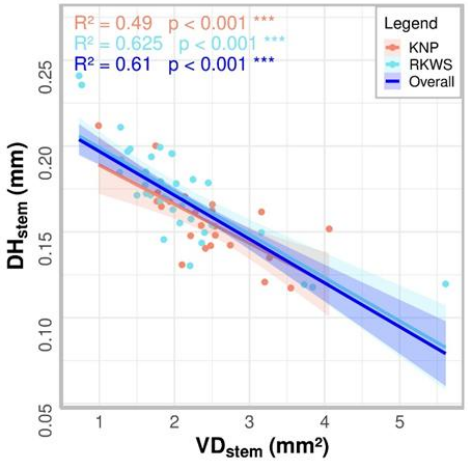

Figure 4. Trade-off between hydraulically weighted vessel diameter, Dh (Hydraulic efficiency) and vessel density, VD (hydraulic safety) in *Mangifera sylvatica* at two moist forest sites in Bangladesh.

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3.3. Association between hydraulic traits, structural and functional attributes and site factors

In KNP, the first two principal components explained nearly 80 % of the total variance (PC1=62.3%, PC2=17.4%). PC1 was primarily influenced by DH, MVA, Vx, CSA, tree Height, DBH, and SL. These vectors are closely aligned, indicating strong positive interrelationships among these wood hydraulic traits and size metrics. In RKWS, PC1 and PC2 explained a total of 61.6% of the variance (PC1 = 43.9%, PC2 = 17.7%). Here, PC1 was most strongly associated with CSA, DBH, Height, DH, MVA, and $PLC_{(theo.)}$%, indicating that in this site, larger, wider vessels and bigger trees are strongly linked to greater conductivity loss (Fig 5).

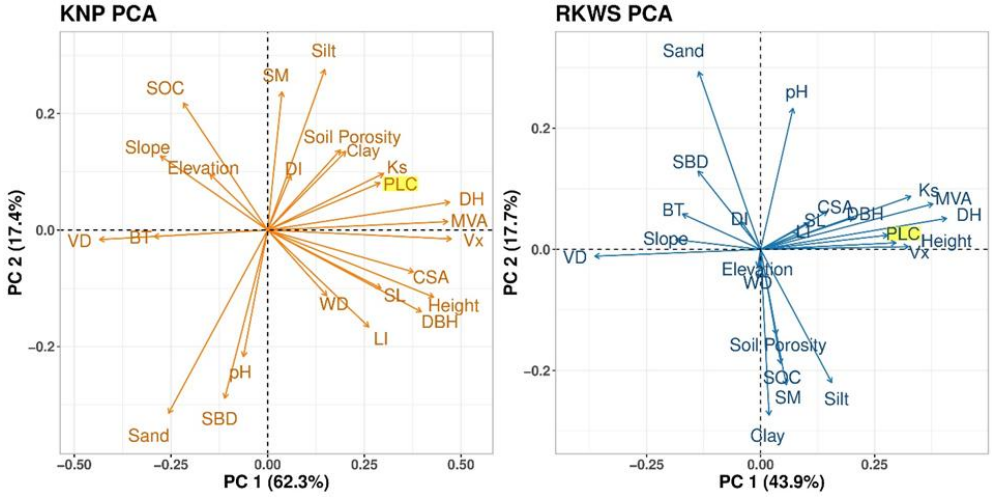

Figure 5. Principal Component Analysis (PCA) results showing the association between site factors, hydraulic traits, structural and functional attributes of *Mangifera sylvatica* across two moist forest sites in Bangladesh. For variable names please refer to Table 1.

3.4. Driving factors of hydraulic behavior

The Ks of *M. Sylvatica* population in KNP showed a significant positive relationship with CSA (R^2= 0.26, p<0.05), and tree height (R^2= 0.20, p<0.05), and a negative significant relationship with sand content in soil (R^2= 0.174, p<0.05) (Fig. 6) but no significant relationship with SL (R^2=0.005, p=0.76) and other variables. In RKWS, Ks of *M. sylvatica* population showed a significant positive relationship with tree Height (R^2= 0.21, p<0.01), CSA

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(R^2=0.21, p<0.01), and SL (R^2=0.19, p<0.01) but no significant relationship with soil sand content (R^2=0.006, p=0.64) and other variables.

The $PLC_{(theo.)}$ of *M. Sylvatica* population in KNP showed a significant positive relationship with CSA (R^2= 0.22, p<0.05) but no significant relationship with tree height (R^2= 0.13, p=0.10), SL (R^2= 09, p=0.93), and SBD (R^2= 0.07, p=0.21) and other variables. In contrast, the $PLC_{(theo.)}$ of *M. sylvatica* population in RKWS showed a significant positive relation with tree height (R^2= 0.21, p<0.01), SL (R^2=11, p<0.05), and SBD (R^2=0.12, p<0.05) but but no significant relationships with CSA (R^2= 0.03, p=0.32) and other variables.

The VD of *M. Sylvatica* population in KNP showed a significant negative relationship with tree height (R^2= 0.25, p<0.05), DBH (R^2= 0.32, p<0.01), CSA (R^2= 0.18, p<0.05), SL (R^2= 0.18, p<0.05) and significant postive relationship with slope (R^2= 0.19, p<0.05), soil sand content (R^2= 0.181, p<0.05), and BT (R^2= 0.385, p<0.01). In RKWS, the VD of *M. sylvatica* population showed negative significant relationship with tree height (R^2= 0.27, p<0.001), and DBH (R^2=0.19, p<0.01), but no significant relationship with any other variables (Fig 6).

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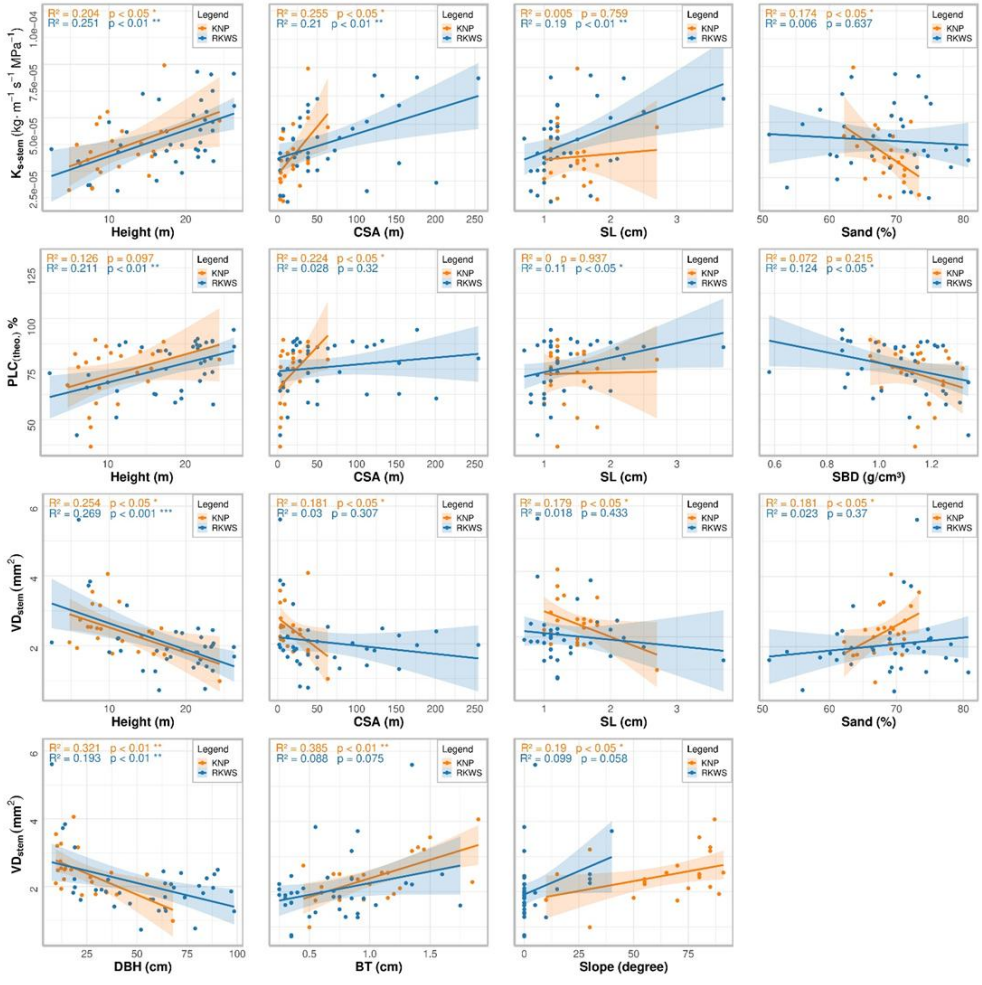

Figure 6. Driving factors of hydraulic behavior in *Mangifera sylvatica* across two moist forest sites in Bangladesh.

Linear mixed effect modelling with significantly correlated variables as fixed factors and tree species identity as the random factors revealed the relative importance of each factor in predicting Ks, PLC($_{theo.}$), and VD in KNP and RKWS. The outputs of mixed effect models are shown in Table 2.

Table 2. Linear mixed effect modeling results for predicting Ks, VD, and PLC ($_{theo.}$) in two moist forest sites in Bangladesh.

Response Variable	Study Site	Fixed Factors	AIC	Marginal R^2	Conditional R^2	P-values

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Ks	KNP	Height + CSA + Sand	-343.7282	0.3458081	0.9193462	<.0001
	RKWS	Height + CSA + SL	-620.4492	0.4367171	0.9305542	<.0001
$PLC_{(theo.)}$	KNP	CSA	186.8223	0.2160646	0.9033504	0.0225
	RKWS	Height + SL + SBD	276.3645	0.3086773	0.9147684	<.0001
VD	KNP	Height + CSA + Sand + SL + BT + Slope + DBH	80.27306	0.582859	0.9485717	0.1112
	RKWS	Height + DBH	107.9036	0.3010927	0.9138333	0.5895

Our mixed effect models revealed that CSA was the most important variable in predicting K_s and $PLC_{(theo.)}$ of *M. Sylvatica* population in KNP (Fig 7). The dominant factors that drove VD of *M. Sylvatica* population in KNP were mostly the structural attributes of trees including tree height, DBH, CSA, and BT. However, the highest contribution in explaining VD variation in *M. Sylvatica* population in KNP was made by tree height and bark thickness as indicated by the higher standardized coefficient (effect size) (Fig. 7). In RKWS, tree height, DBH, and SL played significant rule in regulating Ks of *M. sylvatica* population with highest contribution by SL followed by tree height and CSA (Fig. 7). Tree height also played the most important role in determining $PLC_{(theo.)}$ of *M. Sylvatica* population in RKWS. The VD variation in *M. Sylvatica* population in RKWS was explained by tree two most important tree structural attributes: tree height and DBH, with tree height as the most dominating factor (Fig. 7).

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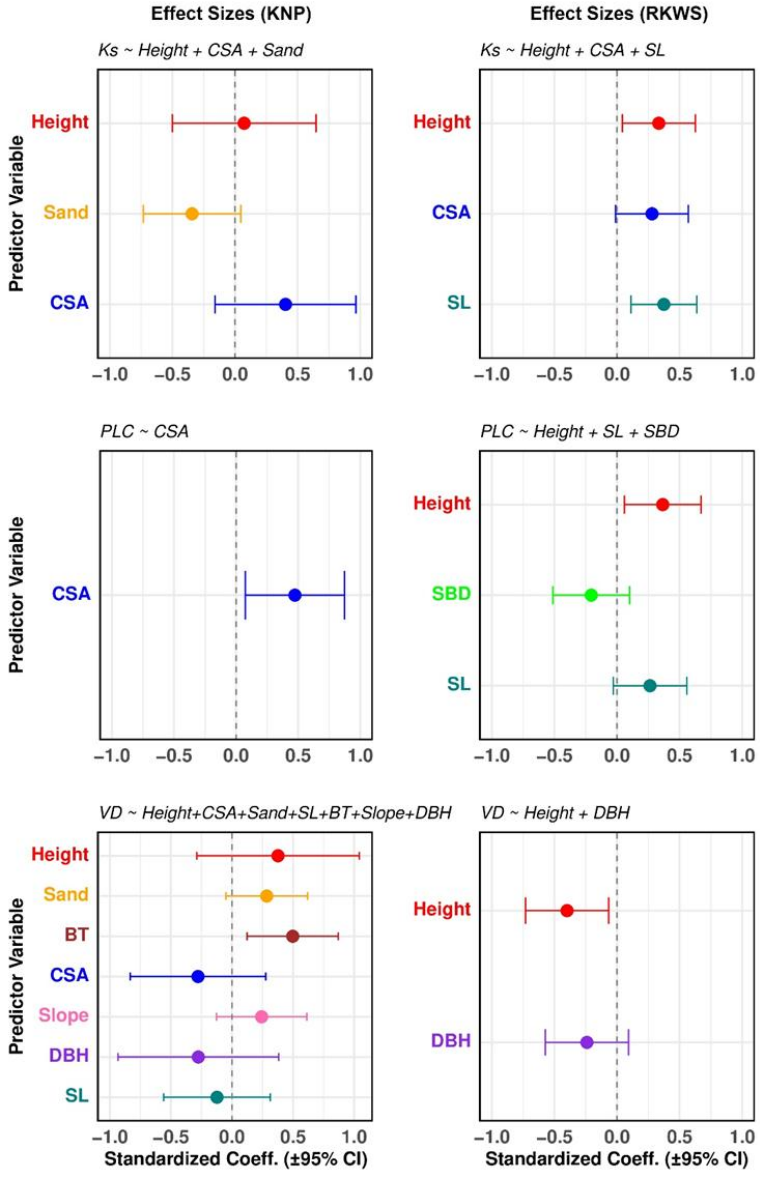

Figure 7. Standardized effect size derived from linear mixed-effect models for predicting site- specific hydraulic behavior across moist tropical forests in Bangladesh.

4. Discussion

4.1. Population structure and environmental variation shaping local contexts

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Our study revealed pronounced differences in population structure and growing conditions of *Mangifera sylvatica* across RKWS and KNP. Trees in RKWS were notably larger—with higher DBH, greater height, and larger crown surface area—than those in KNP, and grew in soils with higher moisture, greater porosity, higher organic carbon, and more clay. Such structural divergence is typical of tropical forests where topography, soil formation, disturbance history, and microclimate combine to generate steep ecological gradients over relatively small spatial scales (Feroz et al., 2014; Islam et al., 2016). These factors influence resource availability, below-ground water storage, rooting depth, and nutrient cycling, all of which directly or indirectly affect hydraulic architecture.

The contrasting soil textures between sites are particularly noteworthy. Clay-rich soils in RKWS likely retain moisture for longer periods and exhibit greater water-holding capacity but may impose higher mechanical resistance to root penetration. In contrast, the sandier soils of KNP drain rapidly and often create drier rooting zones, especially during dry seasons. Soil moisture and textural variability are known to influence xylem anatomy by modulating water availability and tension gradients within the hydraulic pathway (Pfautsch et al., 2016). Yet, despite these strong environmental contrasts, *M. sylvatica* maintained statistically similar hydraulic traits across sites—a striking indication of hydraulic trait stability.

The absence of site-level differences in wood density, sapwood length, and many other functional traits further suggests that *M. sylvatica* possesses a conserved structural strategy that may reflect evolutionary stability in its hydraulic architecture. Many tropical species exhibit such trait conservatism, particularly those occupying relatively stable climatic ranges (Gleason et al. 2016). However, the divergence in tree size, soil characteristics, and microclimate between sites indicates that populations of the same species can experience significantly different hydraulic challenges, making it crucial to understand how conserved hydraulic strategies are maintained across such varied environments.

4.2. Hydraulic strategies remain conserved despite ecological contrasts

Across both sites, we observed remarkably similar hydraulic strategies, as evidenced by comparable values of hydraulic conductivity (Ks), vessel density (VD), and theoretical percent loss of conductivity (PLC). This finding strongly supports our hypothesis that *M. sylvatica* maintains a consistent safety–efficiency balance regardless of local environmental variations. Such conservatism is widely documented in tropical species and often emerges from

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evolutionary constraints on xylem anatomy, which limits the extent to which hydraulic traits can shift in response to local conditions (Brodribb et al., 2020; Gleason et al., 2016).

The universal decline in hydraulic efficiency from stem to branch (72–76%) across both RKWS and KNP reflects a consistent within-tree hydraulic hierarchy. Branches exhibited higher vessel density and smaller vessel diameters—suggests that increase hydraulic safety, reduce cavitation risk, and ensure maintenance of water supply to leaves under fluctuating atmospheric demand (Olson et al., 2021). Similar patterns have been widely observed in tropical and temperate trees where distal organs act as hydraulic bottlenecks to enhance safety margins (Sperry et al., 2008; Trifilo et al., 2014).

The strong trade-off between vessel diameter and vessel density in both sites provides further evidence of this consistency. A larger Dh is associated with higher hydraulic efficiency but increased vulnerability to embolism. Conversely, higher vessel density enhances safety by making sure that some vessels remain functional while some vessels become blocked by cavitation or embolism (Venturas, M.D., Sperry, J.S., Hacke, 2017). The slope and strength of this trade-off were nearly identical between RKWS and KNP indicating that *M. sylvatica* follows a fixed architectural strategy to balance risk and performance, likely reflecting constraints imposed by its phylogeny and ecological niche (Fan et al., 2012).

The absence of site-level variation in hydraulic trait suggests that environmental differences did not induce anatomical divergence. This pattern could arise from (i) stabilizing selection maintaining optimal xylem design, (ii) developmental canalization limiting the plasticity of xylem traits, or (iii) species-level adaptation to broad climatic envelopes rather than local microhabitats. Together, these results provide strong evidence that *M. sylvatica* is hydraulically conservative across the diverse moist forests in Bangladesh.

4.3. Divergent trait–environment associations reveal site-specific mechanisms

Although hydraulic traits remained consistent across sites, the multivariate patterns revealed by PCA and regression suggest that different structural and environmental variables regulate hydraulic function at each site. This finding reflects an important ecological nuance: the strategy is uniform, but the pathways that sustain the strategy differ according to local contexts.

In KNP, hydraulic efficiency aligned strongly with structural variables such as crown surface area, DBH, tree height, and sapwood length. These results imply that in a drier, sandier environment—where soil moisture is more limited—tree architecture plays a crucial role in

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determining hydraulic performance. Larger crowns and taller stems demand greater water transport capacity, explaining the strong association of Ks and Dh with crown traits. Similar patterns have been documented in moisture-limited tropical forests where canopy architecture influences water balance more than soil traits (Anderegg et al., 2018; Grossiord et al., 2020). By contrast, in RKWS, hydraulic traits aligned most closely with tree height, sapwood length, and soil bulk density. Clay-rich soils with higher porosity may create mesic but mechanically challenging rooting environments, where sapwood allocation becomes more critical for ensuring efficient water transport. Sapwood depth is known to buffer against water stress and contributes significantly to the total conductive area (Chave et al., 2009; Meinzer et al., 2003). The strong influence of sapwood length on hydraulic traits in RKWS therefore reflects the increased role of internal water storage and radial conductivity in wetter, denser soils.

Moreover, PLC in RKWS was associated with soil bulk density and tree height, whereas in KNP it was primarily linked to crown surface area. These divergent patterns reflect how site-specific constraints—soil structure versus evaporative demand—shape conductivity loss along the flow path. Together, these findings highlight that although hydraulic architecture is conserved, *M. sylvatica* fine-tunes its structural and environmental relationships differently at each site, demonstrating functional plasticity in the drivers but not in the outcome.

4.4. Drivers of hydraulic behaviour vary across sites

Mixed-effect modelling provided clearer insight into the relative contributions of different drivers. In KNP, crown surface area was the dominant predictor of both Ks and PLC, emphasizing the strong influence of canopy architecture in environments characterized by higher evaporative demand and coarser soil texture. This suggests that trees in KNP adjust water transport capacity to match transpirational demand imposed by crown size—a pattern typical of trees in moisture-limited or seasonally dry conditions.

Conversely, in RKWS, sapwood length and tree height were the strongest drivers of Ks and PLC, reflecting that water transport capacity in this wetter, clay-rich environment may be more related to internal xylem allocation than canopy-driven demand. The importance of sapwood variables in RKWS also suggests that trees in wetter sites rely on structural redundancy and internal buffering to regulate hydraulic efficiency, which aligns with previous studies showing that sapwood allocation increases in mesic environments where mechanical resistance is higher (Schuldt, B., Knutzen, F., Delzon, S., Jansen, S., Müller-Haubold, H., Burlett, R., 2016). Vessel density exhibited strong associations with structural and

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environmental factors in KNP but was primarily regulated by tree height and DBH in RKWS. This again suggests that hydraulic safety is shaped more by environmental stressors in KNP but by ontogenetic scaling in RKWS.

The divergence in drivers across sites suggests that *M. sylvatica* uses different functional mechanisms to maintain a stable hydraulic balance in different environments. This flexibility in trait–environment relationships may underpin the species' ability to persist across diverse South Asian moist forest ecosystems.

4.5. Ecological and conservation implications under climate change

The resilience of *M. sylvatica* under future climate conditions will depend on the interaction between its conserved hydraulic architecture and its flexibility in structural and functional drivers. Rising temperatures and increased atmospheric VPD are expected to intensify hydraulic stress, particularly in tropical forests already near their physiological thresholds (Choat et al. 2018; McDowell et al. 2022). Populations in KNP—where hydraulic function relies heavily on crown traits and is sensitive to soil sand content—may become especially vulnerable under scenarios of declining soil moisture. In contrast, RKWS populations may be more buffered by sapwood allocation but could face limitations if rising VPD exceeds the compensatory capacity of internal hydraulic storage.

Because *M. sylvatica* is listed as a threatened species, identifying populations most vulnerable to water stress will be crucial for conservation planning. Our results suggest that management strategies should be site specific: protecting soil moisture and reducing disturbances in KNP, and maintaining stand structure and soil integrity in RKWS. The stability of hydraulic traits across contrasting environments is encouraging, as it suggests a degree of resilience to climatic variability. However, the limited plasticity in core hydraulic architecture implies that the species' adaptive capacity may rely more on structural adjustments (crown architecture, sapwood depth) than on modifications to xylem anatomy.

Conflict of interest statement

The authors declare no conflicts of interest.

Data availability statement

All data supporting the manuscript can be found in the supplementary materials.

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Author contributions

MI, MM, and MR conceptualized the study; MI, MR, MASA, FS, MM planned the field campaign; MM, MSIS, SHC performed the measurements and laboratory analysis; MI, MR, MM analyzed the data; MI and FS acquired funding; MR, MASA performed the validation of analysis and results; MI MM wrote the first manuscript draft with important contribution from MR; All authors contributed to the revision and editing of the manuscript.

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