

## RESEARCH ARTICLE

## Stand structure of Central European forests matters more than climate for transpiration sensitivity to VPD

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## Abstract

1. Temperature rise and more severe and frequent droughts will alter forest transpiration, thereby affecting the global water cycle. Yet, tree responses to increased atmospheric vapour pressure deficit (VPD) and reduced soil water content (SWC) are not fully understood due to long-term tree adjustments to local environmental conditions that modify transpiration responses to short-term VPD and SWC changes.
2. We analysed sap flux density (SFD) of *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris* and *Quercus ilex* from 25 sites across Europe to understand how daily variation in SWC affects the sensitivity of SFD to VPD ( $\beta_{VPD}$ ) and the maximum SFD ( $S_{95}$ ). Furthermore, we tested whether long-term adjustments to site climatic conditions and stand characteristics affect  $\beta_{VPD}$  and  $S_{95}$ .
3. The studied species showed contrasting  $\beta_{VPD}$  and  $S_{95}$  with the largest values in *F. sylvatica*, followed by *Q. ilex*, which surpassed the two conifers that showed low  $\beta_{VPD}$  and low  $S_{95}$ . We observed that  $\beta_{VPD}$  and  $S_{95}$  dropped during days of low SWC in *F. sylvatica*, *P. sylvestris* and *Q. ilex*, but not in *P. abies*. Both  $\beta_{VPD}$  and  $S_{95}$  were driven by tree height, and the temperature and precipitation at the sites. However, stand basal area was the most important driver of  $\beta_{VPD}$  and  $S_{95}$ , explaining 30% of their total variance.
4. *Synthesis and applications:* A future warmer and drier climate will restrict tree transpiration and thereby heavily affect the soil-plant-atmosphere coupling. However, the effect of basal area, being the largest driver of tree transpiration sensitivity to vapour pressure deficit across a broad range of conditions, provides the opportunity to pre-adapt European forests to future climate conditions. While stand thinning can increase the soil water availability for remaining trees, it also increases transpiration sensitivity to high air temperatures and may thereby amplify tree vulnerability to heat and drought.

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## KEYWORDS

basal area, *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, *Quercus ilex*, sap flow, SAPFLUXNET, vapour pressure deficit

## 1 | INTRODUCTION

Forests transpire more than 50% of terrestrial precipitation and thus constitute a key component of the global water cycle (Schlesinger & Jasechko, 2014; Stoy et al., 2019). Air temperatures have recently increased globally, while relative humidity has remained constant (Dai, 2006; McCarthy et al., 2009). As a consequence, the vapour pressure deficit (VPD) of the atmosphere has increased globally (e.g. Ficklin & Novick, 2017), which might lead to higher forest transpiration (Granda, Baumgarten, et al., 2020; Grossiord et al., 2020). At the same time, changes in precipitation patterns, including more frequent droughts, may limit forest transpiration (Grossiord et al., 2019; Liu et al., 2020) and increase the risk of drought-induced forest decline (McDowell et al., 2022). To anticipate future changes in the global water cycle and forest drought responses, we need to better understand the combined effect of higher air temperatures and decreased soil water availability on forest transpiration.

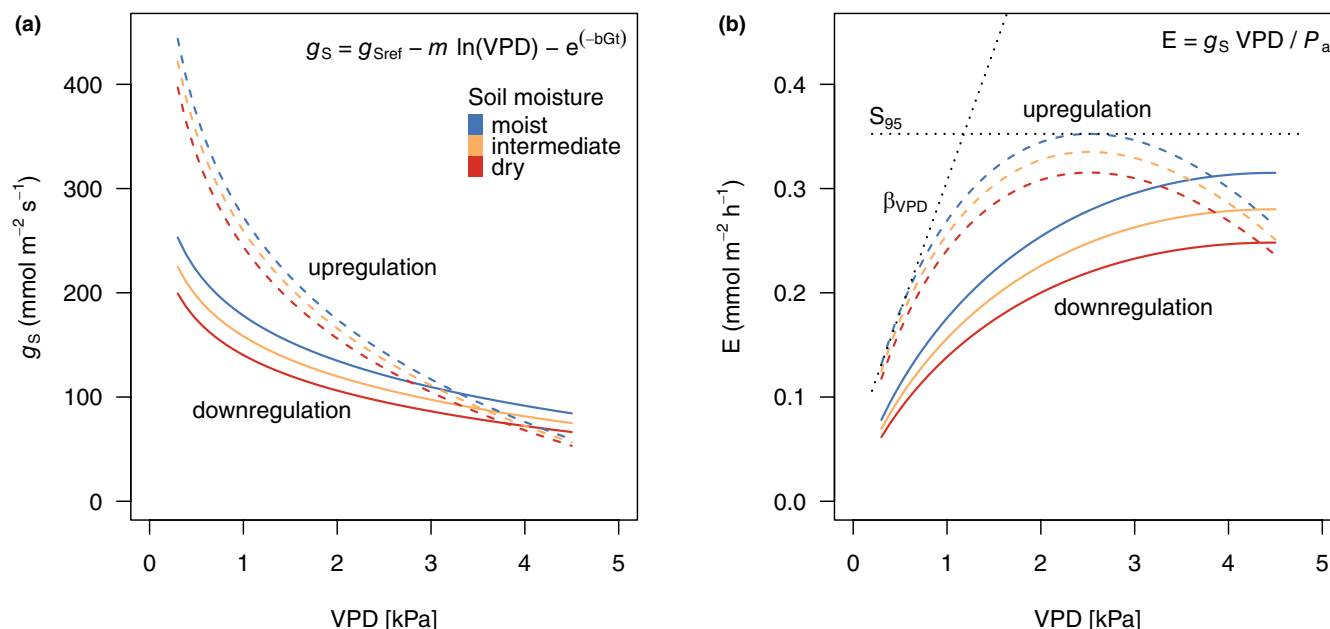
Rising VPD affects tree transpiration in two ways: first, it comes with an increase in the evaporative demand and thus a higher force driving the water loss through stomata, and second, it induces stomatal closure through its effect on leaf water status (Cochard et al., 2002; Monteith, 1995). Therefore, transpiration responses to changes in VPD take a non-linear shape, with an initial increase until a certain threshold where the maximum is reached, after which stomatal closure may result in decreased transpiration (Monteith, 1995). Transpiration regulation in response to changes in VPD is highly species-specific due to differences in hydraulic architecture (Flo et al., 2021; Grossiord et al., 2017; Hassler et al., 2018; Peters et al., 2019). Climate change impacts plants not only through changes in VPD but also soil drought, leading to shifts in the balance between the demand and supply for water (evapotranspiration vs. precipitation; Novick et al., 2016). Drought-stressed trees respond to soil moisture deficit by inducing stomatal closure (Running, 1976), resulting in the reduction of both transpiration and photosynthesis (e.g. Martínez-Vilalta & García-Fórner, 2017; Mencuccini et al., 2015). The sensitivity of stomatal responses to changes in soil water availability largely depends on the plant stomatal behaviour, which ranges along a continuum from isohydric to anisohydric strategy across species (Klein, 2014; Martínez-Vilalta et al., 2014; Martínez-Vilalta & García-Fórner, 2017). Soil water availability and VPD thus co-determine stomatal conductance through their mutual effect on the leaf water potential.

While we have a relatively good understanding of the mechanisms of short-term transpiration responses to changes in VPD and soil moisture at the leaf and tree levels, our knowledge of intraspecific variability of transpiration regulation along environmental gradients is

minimal. Some studies observed higher sap flow sensitivity to VPD across species in dry compared to moist sites (e.g. Denham et al., 2021). Moreover, within-species comparisons showed higher sap flow rates and higher sap flow sensitivity to VPD in warmer and soil-drought exposed populations of a species (Maherali & DeLucia, 2001; Poyatos et al., 2007). Such observations of intraspecific variability are consistent with studies showing higher stomatal conductance at high VPD of warm acclimated seedlings (Marchin et al., 2016), which indicates prioritisation of carbon uptake and thermal leaf regulation at the risk of higher transpirational water loss ('upregulation' scenario, Figure 1). However, other studies have reported decreased canopy conductance and lower stomatal sensitivity to VPD under long-term high VPD conditions (Grossiord et al., 2017), indicating long-term downregulation of tree transpiration to maintain hydraulic functioning ('downregulation' scenario, Figure 1).

In addition to adjustments to climatic conditions, soil hydrodynamic properties and stand structure can modulate the physiological responses among populations of a species. Sandy soils have been associated with higher canopy conductance and increased stomatal sensitivity to VPD in *Pinus palustris* compared to loamy soils (Addington et al., 2006). Furthermore, trees in less dense stands tend to have higher transpiration rates per unit sapwood area (Caballé et al., 2016), as typically observed after stand thinning (Gebhardt et al., 2014). However, we do not know how transpiration sensitivity to VPD varies with stand structure and whether these physiological adjustments are related to tree-level water transport properties (Whitehead et al., 1984) for different species, as already observed across *Pinus sylvestris* populations (Poyatos et al., 2007).

We investigated how climate, soil properties and stand characteristics modulate the transpiration sensitivity of trees to VPD and soil water availability by analysing sap flux data on a continental scale. Using the SAPFLUXNET database, we investigated four important European tree species with contrasting water-use strategies, *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris* and *Quercus ilex*, from multiple sites along climatic gradients. We related maximum sap flux density ( $S_{95}$ ) and sap flux sensitivity to VPD ( $\beta_{VPD}$ ) to each site's soil, climate and stand characteristics. We expected that (1) low soil moisture reduces  $S_{95}$  and  $\beta_{VPD}$  of all species and at all sites, but that (2) species with a more isohydric stomatal behaviour (*P. abies* and *P. sylvestris*) exhibit a higher  $\beta_{VPD}$  at a given  $S_{95}$  than more anisohydric species (*Q. ilex* and *F. sylvatica*). We also expect that (3) trees in warmer and drier sites adjust by consistently downregulating  $S_{95}$  and  $\beta_{VPD}$  independently of SWC, that is, they are structurally adapted to low transpiration rates. Lastly, we expected that (4) because of lower soil water competition, less dense stands exhibit higher  $S_{95}$  and higher  $\beta_{VPD}$ .



**FIGURE 1** Schematic representation of (a) stomatal conductance ( $g_s$ ) and (b) transpiration ( $E$ ) in relation to VPD at different soil moisture conditions (moist, intermediate and dry). Populations may adjust to long-term environmental conditions by downregulating (solid lines) the transpiration sensitivity to VPD ( $\beta_{\text{VPD}}$ ) and maximum transpiration ( $S_{95}$ ), whereas other populations under different long-term environmental conditions may upregulate them (dashed lines).  $g_s$  is regulated by the maximum  $g_s$  ( $g_{s\text{ref}}$ ) at low VPD, the stomatal sensitivity to VPD ( $m$ ), the hydraulic conductance of the soil-to-leaf pathway ( $Gt$ ) and the stomatal sensitivity to  $Gt$  ( $b$ ; Meinzer, 2003).  $E$  is driven by  $g_s$ , VPD and air pressure ( $P_a$ ) (Oren et al., 1999).

## 2 | MATERIALS AND METHODS

### 2.1 | Sites and tree species selection

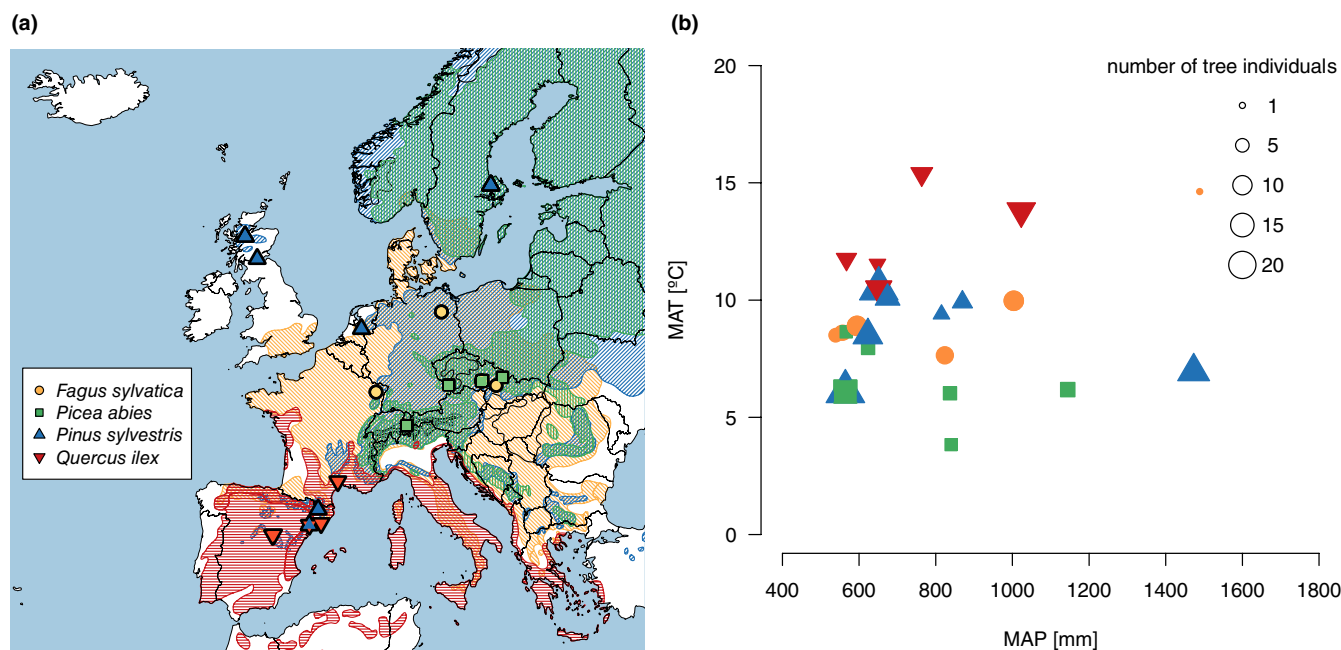
We downloaded the global SAPFLUXNET database, version 0.1.5 (Poyatos et al., 2021), and selected sites where measurements of soil water content (SWC), vapour pressure deficit (VPD) and photosynthetic photon flux density (PPFD) were available concurrently with sap flux density (SFD; sap flow per unit sapwood area). At several sites, SWC was measured manually at low temporal resolution rather than automatically at high resolution. In these cases, data were linearly interpolated to fill gaps no longer than 2 weeks. We excluded sites where experimental manipulations of environmental conditions were applied, such as thinning, N-fertilisation,  $\text{CO}_2$ -fertilisation, rainfall throughfall exclusion or irrigation. We then selected tree species present in at least three sites where three or more dominant, codominant or subdominant tree individuals of the target species were present per site. Four tree species were selected: *Fagus sylvatica* L., *Picea abies* (L.) H. Karst., *Pinus sylvestris* L. and *Quercus ilex* L., which were present in 4, 8, 13 and 5 sites, respectively (Figure 2). At most sites, only one species occurred, but on 5 sites, *P. abies* co-occurred with *P. sylvestris* (Table S1). We obtained measurements from 32, 65, 147 and 52 tree individuals, respectively, amounting to 296 trees from 25 sites (Table S1). To relate SFD to whole-tree functional traits, we obtained measurements of leaf area, sapwood area and Huber values ( $H_v$ ) that were available in the SAPFLUXNET database (*P. abies*, *P. sylvestris* and *Q. ilex*).

### 2.2 | Sap flux data processing

From each tree, at each site, we obtained sub-daily (every 10 min or half-hourly) sap flux density (SFD) or sap flow (SF) if the sapwood area ( $A_{\text{SW}}$ ) was not available. The SF data were transformed into SFD by dividing SF values by  $A_{\text{SW}}$  estimated with an allometric approach. For the allometric approach, we used the SAPFLUXNET trees for which the diameter at breast height (DBH) and  $A_{\text{SW}}$  were provided and calculated the species-specific log-log relationship between these two variables (Figure S1). The sub-daily SFD, SWC, VPD and PPFD time series were aggregated, and daytime medians (09:00–16:00) were calculated using the *sfn\_metrics* function from the purposely developed SAPFLUXNET R package (Granda, Poyatos, et al., 2020). Measurements obtained from non-calibrated thermal dissipation sensors were corrected for bias multiplying by 1.405, according to a global synthesis of sap flow calibrations (Flo et al., 2019).

### 2.3 | Sap flux data filtering

To minimise the influence of phenological changes in leaf area index on SFD, we excluded periods with phenological changes during the cold seasons of each species at each site by removing data for periods between 2 weeks (14 days) before the first day with temperatures below  $0^\circ\text{C}$  and 4 weeks (28 days) after the last day with temperatures below  $0^\circ\text{C}$ , similarly to Flo et al. (2021) and Novick et al. (2016). We used temperature thresholds, because the phenological sensitivity to temperature remains relatively stable across



**FIGURE 2** (a) Distribution of the four selected species and location of the 25 SAPFLUXNET sites in Europe that were selected for this study and (b) mean annual temperature (MAT) and mean annual precipitation sum (MAP) at the selected sites. The size of the symbols represents the number of individual trees at each site.

different populations of a species (Vitasse et al., 2009). We also removed days where the average daytime VPD was below 0.1 kPa, and rainy days by filtering out days with precipitation (sum of daily precipitation > 0 mm), where measurements were available. If precipitation measurements were lacking, we filtered out days when SWC increased, assuming that the increase was due to precipitation, similar to the work of Flo et al. (2021). As low light is expected to influence stomatal response to SWC and VPD (Oren et al., 1999), we selected days in which the 24-h average photosynthetic photon flux density (PPFD) was greater than  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , similar to Anderegg et al. (2018).

## 2.4 | Sensitivity to VPD and SWC

To calculate the transpiration sensitivity to VPD under different soil water contents, we split the data into five SWC quantiles at each site and fitted five separate linear regressions for each species at each site. We considered that trees are hydraulically adjusted to site conditions (e.g. rooting depth,  $H_v$ ); therefore, relative changes in SWC instead of absolute differences will drive tree transpiration. Furthermore, by using SWC quintiles, we avoided that extreme values (extremely dry or extremely wet soil) had a too large influence on the regression. We chose to use five quantiles in order to be comparable to existing literature (Denham et al., 2021; Novick et al., 2016), to be able to identify both linear and non-linear (e.g. quadratic) relationships, and to have sufficient datapoints in each quintile for robust regressions.

We applied mixed-effects zero-intercept regression models (LMM) with SFD as the dependent variable, the log-transformed

VPD as a fixed factor, and the tree individuals at each site as random slopes. We selected a log-linear regression, as we did not observe a decrease in SFD as VPD increased in the daytime-aggregated data, so they followed a log-linear shape. The VPD was log-transformed to ensure normal distribution of residuals. The LMMs were fitted using the *lmer* function from the *LME4* package (Bates et al., 2014). We obtained the SFD sensitivity to VPD ( $\beta_{\text{VPD}}$ ) model coefficient for each SWC quintile of each species and site. In addition, for each site and SWC quintile, we calculated the maximum SFD ( $S_{95}$ ), as the 95% percentile of the SFD distribution, and the relative SFD sensitivity to VPD ( $\beta_{\text{VPD}}/S_{95}$ ). The effect of SWC on  $\beta_{\text{VPD}}$ ,  $S_{95}$  and  $\beta_{\text{VPD}}/S_{95}$  was tested separately for each species with a mixed-effects model, where the SWC quintile was treated as an ordered factor and used as a fixed effect, and the site was considered a random effect. To compare the effect of SWC on  $\beta_{\text{VPD}}$ ,  $S_{95}$  and  $\beta_{\text{VPD}}/S_{95}$  between species, we used the same mixed-effect model, but for all species combined, and added the species as a fixed effect together with SWC, and the site as random effect. Differences in the SWC effects between species and sites were calculated with the *lstrends* function from the *EMMEANS* package.

## 2.5 | Effect of site soil, climatic and stand characteristics on sap flux

We tested the effect of several site-specific soil and climate variables and stand characteristics on tree-level  $\beta_{\text{VPD}}$  and  $S_{95}$ , as well as  $\beta_{\text{VPD}}/S_{95}$  across all five SWC quintiles of all the species with multiple linear regression models. The assumptions of homoscedasticity were assessed visually and were met in all cases. In particular,

we tested how mean annual temperature (MAT), mean annual precipitation sum (MAP), mean annual precipitation over potential evapotranspiration (P:PET), precipitation seasonality (standard deviation of the monthly deviation from the annual average) and annual temperature range, as well as stand-level basal area, leaf area index (LAI), mean tree height, clay and sand content of the soil, affect  $\beta_{VPD}$  and  $S_{95}$ . All long-term means of climatic variables were obtained from the interpolated climate data set CHELSA that covers a time period from 1979–2013 (Karger et al., 2017), whereas basal area, LAI, tree height, clay and sand content are available in the SAPFLUXNET database and were provided by the site managers. We tested the combined effects of the site characteristics by including all variables in a multiple linear regression model and treating the species as random effect. We excluded average tree age from the explanatory variables, as it was too highly correlated with other stand characteristics (e.g. stand height). We then performed a model selection based on the Akaike information criterion (AIC) using the *step* function in R (R Core Team, 2016) to retrieve the most influential variables. To determine the relative importance of the selected variables in explaining  $\beta_{VPD}$  and  $S_{95}$ , we performed variance partitioning using the *YHAT* package, which can separate contributions to explained variance in the presence of multicollinearity (Ray-Mukherjee et al., 2014). The ability to correct multicollinearity effects on variance partitioning was particularly important for calculating the explained variance of MAP, MAT and P:PET, because the latter is calculated from the former two and thereby not fully independent. In addition to the analysis across SWC quintiles, we selected the driest and wettest SWC quintiles from all sites and repeated the procedure to identify if the same climatic and stand characteristics drive  $\beta_{VPD}$  and  $S_{95}$  during days where soils are dry or wet.

### 3 | RESULTS

#### 3.1 | Transpiration response to VPD and SWC changes across species

VPD is a strong driver of transpiration, explaining on average 60.3%, 76.5%, 63.6% and 54.6% of the variance (marginal  $R^2$ ) of the averaged daytime SFD of *F. sylvatica*, *P. abies*, *P. sylvestris* and *Q. ilex*, respectively. SFD increased with higher VPD in all species and SWC quintiles (positive  $\beta_{VPD}$ , Figure 3). The tree species differed in  $\beta_{VPD}$ , with *F. sylvatica* generally having the highest  $\beta_{VPD}$  (Figure 3,  $p < 0.001$ ). The  $\beta_{VPD}$  significantly increased with the SWC quintile in *F. sylvatica*, *P. sylvestris* and *Q. ilex* ( $p = 0.010$ ,  $p = 0.005$  and  $p < 0.001$ , respectively; Figure 3, Table 1), while for *P. abies*, SWC quintile showed no effect on  $\beta_{VPD}$  ( $p = 0.515$ ). Pairwise comparisons between species showed that SWC quintile had a more pronounced effect on  $\beta_{VPD}$  (i.e. steeper linear relationship) in *F. sylvatica* and *Q. ilex* than *P. abies* and *P. sylvestris* (Table 2). Pairwise comparisons between sites showed a consistent SWC effect, with the exception of *P. abies* at SWE\_NOR\_ST5\_REF that showed a significantly stronger

SWC effect on  $\beta_{VPD}$  compared to other sites, and *P. sylvestris* at GBR\_DEV\_CON where SWC had a negative effect on  $\beta_{VPD}$ .

The maximum SFD ( $S_{95}$ ) reached on average 27.1, 8.9, 7.3 and 18.3  $\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$  across all SWC quintiles and sites for *F. sylvatica*, *P. abies*, *P. sylvestris* and *Q. ilex*, respectively. Similarly, as with  $\beta_{VPD}$ ,  $S_{95}$  significantly increased with SWC quintile in *F. sylvatica*, *P. sylvestris* and *Q. ilex* ( $p < 0.001$ ,  $p = 0.010$  and  $p = 0.002$ , respectively; Figure 3, Table 1), but not in *P. abies* ( $p = 0.476$ ). Pairwise comparisons between sites showed also a consistent WSC effect on  $S_{95}$  except for *P. abies* at SWE\_NOR\_ST4\_BEf where SWC had a negative effect on  $S_{95}$ .  $\beta_{VPD}$  and  $S_{95}$  were positively correlated among populations of the same species ( $p < 0.001$ ), independently of SWC quintiles ( $p > 0.05$ ; Figure 4). The slope between  $\beta_{VPD}$  and  $S_{95}$  differed between species, with *P. sylvestris* having the steepest slope, followed by *P. abies*, *F. sylvatica*, and *Q. ilex*. All slopes differed significantly ( $p < 0.05$ ), except *P. abies*, which was not different from *P. sylvestris* and *F. sylvatica*. Leaf area and  $H_v$  did not affect  $\beta_{VPD}$  and  $S_{95}$  across species and populations (Figure S2).

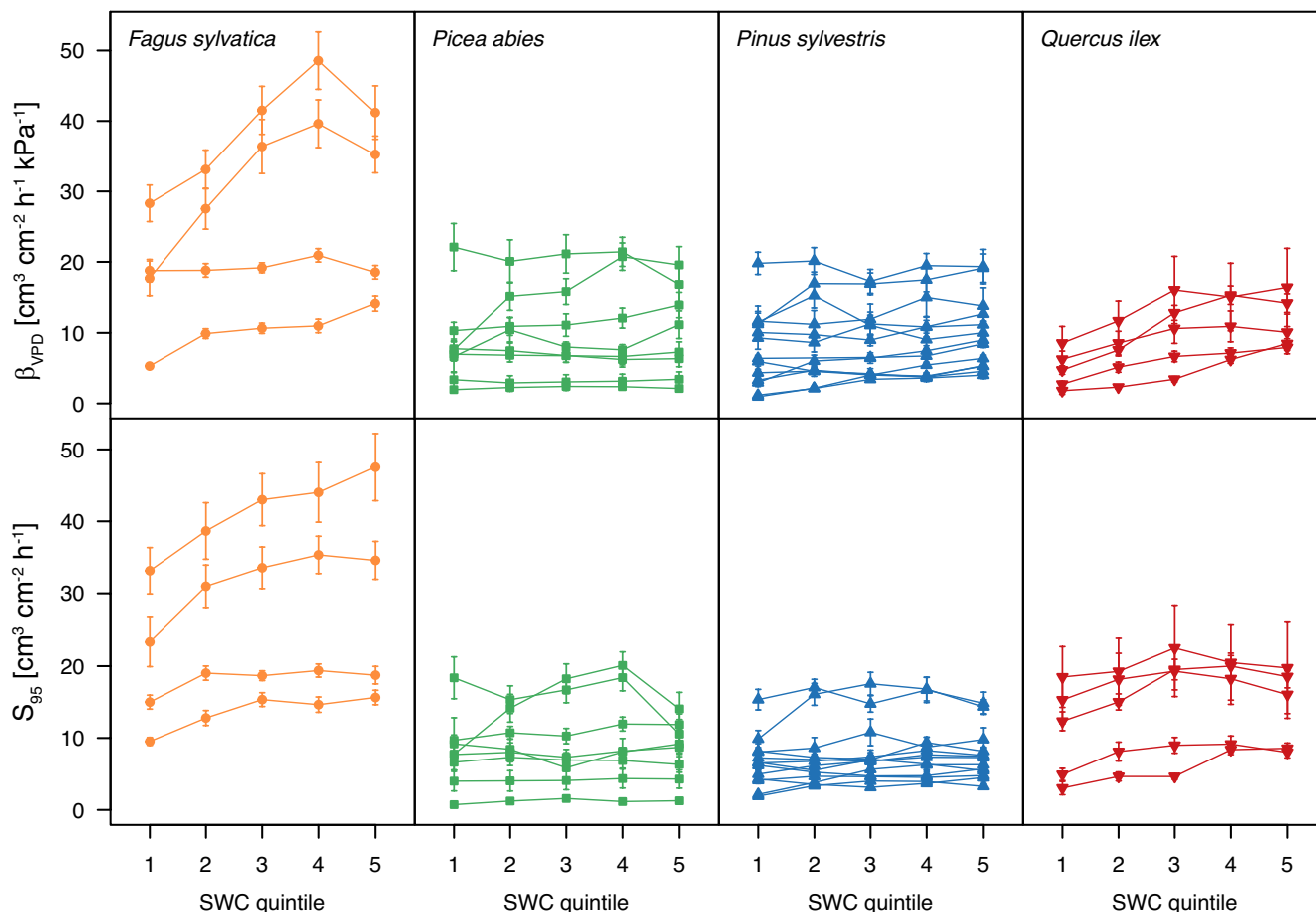
#### 3.2 | Climate, stand characteristics and soil properties influence tree transpiration regulation across populations

Across all SWC quintiles,  $\beta_{VPD}$  was related to several site climatic variables and stand characteristics (Figure 5). Basal area explained the largest fraction of variability in  $\beta_{VPD}$  with 29.9%, whereas the other site characteristics (mean tree height, MAT, P:PET) explained less than 3% each. In contrast, MAP, precipitation seasonality, annual temperature range, LAI, clay and sand soil content had no significant effect on  $\beta_{VPD}$ . Most notably,  $\beta_{VPD}$  strongly decreased with higher basal area and the average tree height across species and sites. MAT and P:PET also negatively affected  $\beta_{VPD}$ , indicating that a higher temperature and mean annual water availability reduced the SFD sensitivity to VPD (Table 3). For  $S_{95}$ , we observed very similar effects, with the basal area and mean height having a large negative effect on  $S_{95}$  across species and populations (Figure 5). In contrast to  $\beta_{VPD}$ , we found strong evidence that the annual temperature range positively affects  $S_{95}$ . Again, basal area explained the largest fraction of variance with 30.7%, whereas mean height and annual temperature range explained 5.6 and 9.5% of the variance, respectively (Table 3). The relative sap flux density ( $\beta_{VPD}/S_{95}$ ) was not affected by basal area but decreased with annual temperature range (28.7%), increased with tree height (21.6%) and LAI (5.9% explained variance; Figure S3).

#### 3.3 | SFD during wettest and driest SWC quintiles in relation to site characteristics

During the 20% wettest days,  $\beta_{VPD}$  was related to the same site characteristics across all SWC quintiles (Table 4). Basal area was the most influential driver of  $\beta_{VPD}$  (28.2%), followed by MAT (6.2%), P:PET (2.3%) and mean height (1.3%). Similarly,  $S_{95}$  was related to the basal





**FIGURE 3** Sap flux density (SFD) sensitivity to VPD ( $\beta_{VPD}$ ) and maximum SFD ( $S_{95}$ ) in relation to the soil water content (SWC) quintiles at each site for the four species. Error bars represent the standard error of the linear regressions of SFD in relation to VPD of each site and SWC quintile.

**TABLE 1** Linear mixed model effects of SWC quintiles on SFD sensitivity to VPD ( $\beta_{VPD}$ ) and maximum SFD ( $S_{95}$ ) of the four species. Sites were treated as random effects.

Dependent variable	Species	Mean Sq	Num df	Den df	F-value	p-value
$\beta_{VPD}$	<i>F. sylvatica</i>	97.066	4	12	5.382	0.010
	<i>P. abies</i>	3.969	4	28	0.835	0.515
	<i>P. sylvestris</i>	9.471	4	47	4.275	0.005
	<i>Q. ilex</i>	39.362	4	16	18.527	<0.001
$S_{95}$	<i>F. sylvatica</i>	51.283	4	12	12.066	<0.001
	<i>P. abies</i>	4.175	4	28	0.903	0.476
	<i>P. sylvestris</i>	4.005	4	47	2.718	0.041
	<i>Q. ilex</i>	16.314	4	16	7.471	0.001

area, mean height and annual temperature range. In addition to the analysis across SWC quintiles, the soil's clay fraction was an additional factor driving  $S_{95}$ . During the 20% driest days,  $\beta_{VPD}$  and  $S_{95}$  strongly decreased with soil clay and sand fractions (Table 4). While in both cases, the negative effect of basal area remained the most critical driver of SFD responses ( $\beta_{VPD}$ : 25.9%,  $S_{95}$ : 35.2%), the two soil characteristics explained a considerable fraction of the variance ( $\beta_{VPD}$ : 11.9% and 14.1% for clay and sand;  $S_{95}$ : 8.2% and 14.8% for clay and sand). Maximum SFD was also marginally related to precipitation seasonality ( $p = 0.05$ ), which explained 17.2% of  $S_{95}$  during the driest 20% of days.

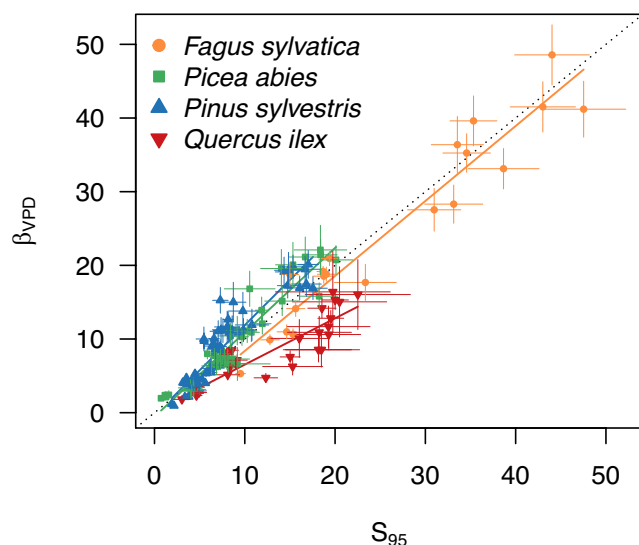
## 4 | DISCUSSION

### 4.1 | Transpiration responses to VPD vary with SWC across species

SFD sensitivity to VPD ( $\beta_{VPD}$ ) was strongly related to the soil water availability in *F. sylvatica*, *Q. ilex* and to a lesser degree in *P. sylvestris* (Table 1, Figure 3). As hypothesized, days with lower SWC reduced  $\beta_{VPD}$  and maximum SFD ( $S_{95}$ ) in these species (Figure 3). These findings confirm that water demand and supply co-determine tree

Species	<i>Picea abies</i>	<i>Pinus sylvestris</i>	<i>Quercus ilex</i>
<i>Fagus sylvatica</i>	2.320; $p < 0.001$	2.214; $p < 0.001$	1.014; $p = 0.169$
<i>Picea abies</i>		-0.106; $p = 0.988$	-1.305; $p = 0.012$
<i>Pinus sylvestris</i>			-1.200; $p = 0.012$

**TABLE 2** Pairwise comparison of the effect of SWC quintiles on  $\beta_{VPD}$  between species. Coefficients are differences in slope parameters, where significantly positive differences indicate that in the species in the first column, the SWC quintile had a larger impact on  $\beta_{VPD}$  than in species shown in the top row, and vice versa.



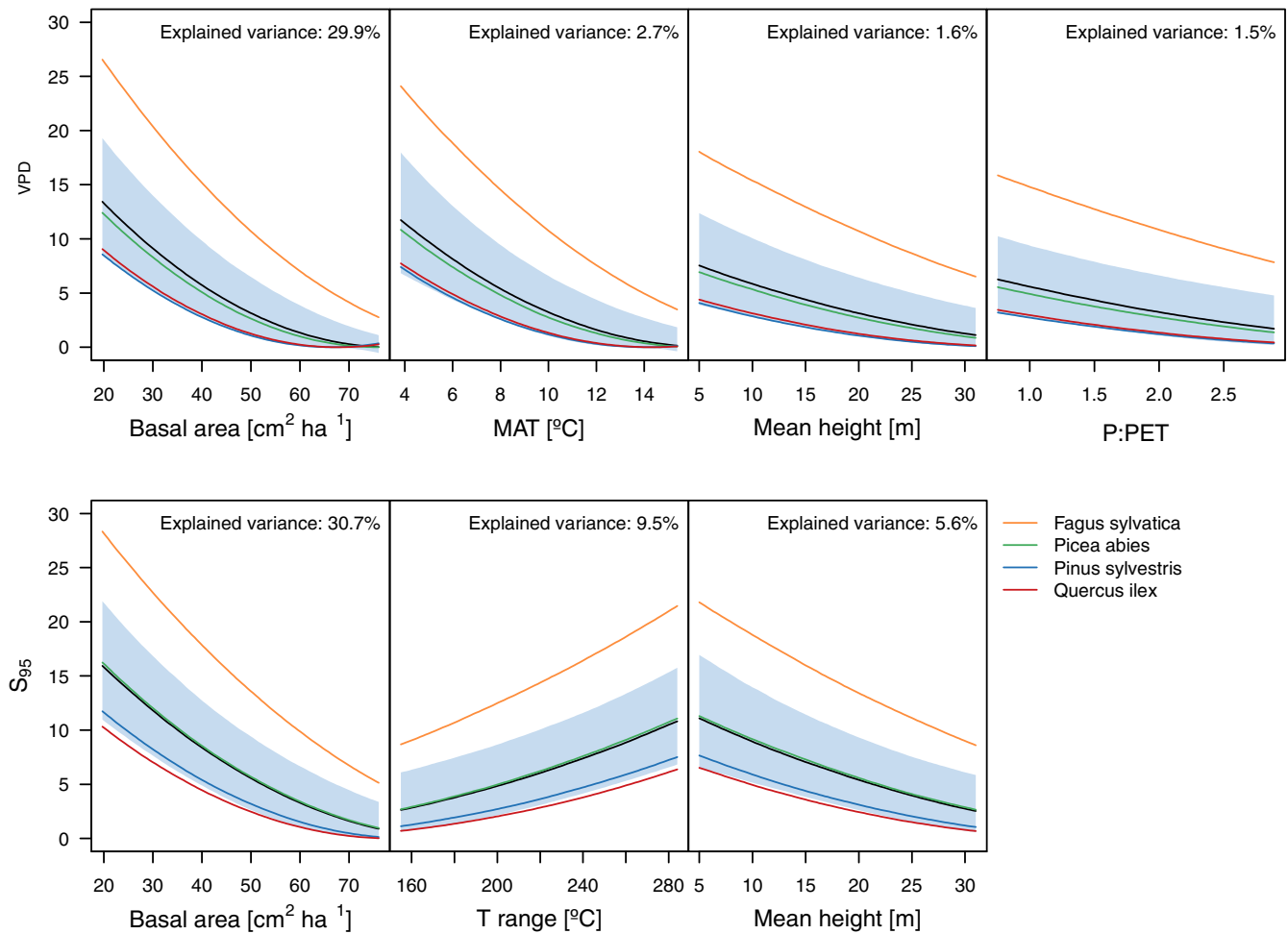
**FIGURE 4** Sap flux density sensitivity to VPD ( $\beta_{VPD}$ ) in relation to the maximum sap flux density ( $S_{95}$ ) of the four species at each site and in all SWC quintiles. Error bars represent the standard error of the linear regressions of SFD in relation to VPD of each site and SWC quintile.

transpiration and that SWC strongly modulates stomatal sensitivity to VPD (e.g. Grossiord et al., 2018). Despite the wide range of absolute soil water contents, the relationship between  $\beta_{VPD}$  and  $S_{95}$  and the SWC quintiles was consistent across sites (Figure 3), with the exception of three sites, where *P. abies* and *P. sylvestris* showed stronger or contrasting SWC effects. The consistent SWC effect indicates that relative, not absolute changes in soil moisture was determining the transpiration of the locally adjusted trees. Thus, using SWC quintiles, instead of absolute values of SWC proved to be beneficial in tracking tree transpiration responses to soil moisture. In addition to these general patterns, we observed large species-specific differences in the transpiration responses to VPD and SWC, with evergreen species showing overall lower  $S_{95}$  and  $\beta_{VPD}$  compared to the deciduous *F. sylvatica* (Figure 3). While  $\beta_{VPD}$  and  $S_{95}$  of the two broadleaves were strongly co-determined by SWC, the two conifers showed no, or only a weak response to SWC (Figure 3). The large species-specific differences were expected due to their affiliation to different functional types and hydraulic traits (Flo et al., 2021; Grossiord et al., 2018; Hassler et al., 2018; Peters et al., 2019). By relating  $\beta_{VPD}$  to  $S_{95}$ , we observed that the two conifers showed higher sensitivity at a given  $S_{95}$  than the broadleaves (Figure 4). The relative sap flux sensitivity to VPD ( $\beta_{VPD}/S_{95}$ ) was positively related to the

SWC quintile for *P. sylvestris* and *Q. ilex* ( $p < 0.05$ ) but not for the other two species (Figure S4). The differences in relative sensitivities can be explained by contrasting stomatal regulation in response to water potential, as indicated by the leaf water potential at the turgor loss point ( $\Psi_{TLP}$ ). Accordingly, the least sensitive species, *Q. ilex*, has the lowest  $\Psi_{TLP}$  (-3.2 MPa), followed by *F. sylvatica* (-2.5 MPa), *P. abies* (-2.5 MPa) and *P. sylvestris* (-2.1 MPa; Martin-StPaul et al., 2017). Similarly, their isohydricity aligns along the same order (hydroscape area; Fu & Meinzer, 2018) with *Q. ilex* (3.18) as the most anisohydric species having the lowest  $\beta_{VPD}$  at a given  $S_{95}$ , followed by *F. sylvatica* (2.49), *P. abies* (2.11) and *P. sylvestris* (1.95). Hence, in contrast to recent findings where similar responses of several tree species to VPD were found along an isohydric range (Denham et al., 2021), we observed a strong species effect consistent with hydraulic traits.

#### 4.2 | Adjustment to climate modifies VPD and SWC effects on transpiration

Across species, adjustment to climate led to lower  $\beta_{VPD}$  in trees growing in warmer and moister sites (higher P:PET), whereas a larger annual temperature range, that is, a higher continentality of the site, increased  $S_{95}$  (Figure 5). Consequently, the relative sap flux sensitivity to VPD ( $\beta_{VPD}/S_{95}$ ) was lower in more continental sites (Figure S3). The observed adjustment to warm temperatures is consistent with previous work where *Pinus edulis* and *Juniperus monosperma* acclimated to warmer climate by reducing the sensitivity of SFD to VPD even under high soil moisture (Grossiord et al., 2018). These findings indicate a long-term downregulation of tree-level transpiration under warmer climate to maintain hydraulic functioning ('downregulation' scenario, Figure 1). Reduced  $\beta_{VPD}$  at moister sites (higher P:PET) is contrary to our third hypothesis, as we expected a downregulation combined with reduced sensitivity at xeric sites. However, it supports observations of a long-term irrigation experiment with *P. sylvestris* that showed lower tree transpiration sensitivity to VPD of trees acclimated to humid soils (Schönbeck et al., 2022). Furthermore, it is consistent with a recent study by Denham et al. (2021), who found higher transpiration sensitivity to VPD of trees in xeric compared to mesic sites. At first glance, this contradicts the observation that days with lower SWC reduced  $\beta_{VPD}$  (Figure 3). We observed, however, that only during times of high water availability (Q5)  $\beta_{VPD}$  was reduced by a high P:PET (Table 4), which implies a more competitive strategy of tree water use in these conditions. As soils dry out (Q1)  $\beta_{VPD}$  becomes similar across the



**FIGURE 5** Partial regression of sap flux sensitivity to VPD ( $\beta_{VPD}$ ) and maximum sap flux density ( $S_{95}$ ) in relation to climatic and stand characteristics of all sites, across the four species and the five SWC quintiles (black lines). Species-specific regressions were obtained from the random intercepts. Only the climatic and stand characteristics that were significant in the multiple regression model are shown (see Table 3). The blue bands show the prediction intervals of the fixed effects.

**TABLE 3** Linear mixed model effects of stand characteristics and climate on SFD sensitivity to VPD ( $\beta_{VPD}$ ) and maximum SFD ( $S_{95}$ ) across all SWC quintiles. Species were treated as random effects.

Dependent variable	Explanatory variable	Estimate	Standard error	df	T-value	p-value	Explained variance
$\beta_{VPD}$	Basal area	-0.062	0.009	19.329	-7.259	<0.001	0.299
	Mean height	-0.065	0.019	19.323	-3.432	0.003	0.016
	MAT	-0.264	0.068	20.468	-3.869	0.001	0.027
	P:PET	-0.557	0.186	19.065	-2.996	0.007	0.015
$S_{95}$	Basal area	-0.054	0.010	20.513	-5.208	<0.001	0.307
	Mean height	-0.067	0.021	21.609	-3.136	0.005	0.056
	Temp range	0.013	0.004	20.275	3.701	0.001	0.095
$\beta_{VPD}/S_{95}$	Temp range	-0.007	0.001	18.282	-4.890	<0.001	0.287
	Mean height	0.023	0.006	9.414	3.826	0.004	0.216
	LAI	0.073	0.031	14.337	2.394	0.031	0.059

P:PET gradient. Our observations are partly in contrast with Novick et al. (2016), who found a positive effect of site soil dryness on stand-level transpiration sensitivity to VPD, however, mainly in savannahs and grasslands, while forests showed no clear adjustments

to soil humidity. Our observations also contrast with Poyatos et al. (2007), who showed increased sap flow sensitivity to VPD and SWC in *P. sylvestris* in warmer sites with drier soils, although no hot and dry sites were included (Sus et al., 2014).



**TABLE 4** Linear mixed model effects of stand characteristics and climate on SFD sensitivity to VPD ( $\beta_{VPD}$ ) and maximum SFD ( $S_{95}$ ) during driest (Q1) and moistest (Q5) quintiles of SWC of each site. Species were treated as random effects.

SWC quintile	Dependent variable	Explanatory variable	Estimate	Standard error	df	T-value	p-value	Explained variance
Driest (Q1)	$\beta_{VPD}$	Basal area	-0.061	0.010	14.6	-5.840	<0.001	0.259
		Clay %	-0.276	0.062	5.4	-4.454	0.006	0.119
		Sand %	-0.127	0.029	5.5	-4.407	0.005	0.141
	$S_{95}$	Basal area	-0.055	0.010	20.0	-5.766	<0.001	0.352
		Clay %	-0.210	0.053	11.6	-3.959	0.002	0.082
		Sand %	-0.113	0.025	10.6	-4.594	0.001	0.148
		Precip seasonality	-0.035	0.017	21.7	-2.079	0.050	0.172
	$\beta_{VPD}/S_{95}$	MAT	-0.105	0.030	24	-3.491	0.002	0.279
		Temp range	-0.004	0.002	24	-2.168	0.040	0.079
Moistest (Q5)	$\beta_{VPD}$	Basal area	-0.055	0.008	19.3	-7.030	<0.001	0.282
		Mean height	-0.095	0.017	19.3	-5.446	<0.001	0.013
		MAT	-0.275	0.063	20.2	-4.391	<0.001	0.062
		P:PET	-0.649	0.170	19.1	-3.814	0.001	0.023
	$S_{95}$	Basal area	-0.036	0.009	19.5	-3.821	0.001	0.276
		Mean height	-0.085	0.021	19.4	-4.113	0.001	0.051
		Temp range	0.017	0.004	19.2	3.988	0.001	0.048
		Clay %	-0.047	0.022	20.0	-2.158	0.043	0.079
	$\beta_{VPD}/S_{95}$	MAT	-0.044	0.019	24	-2.364	0.027	0.11
		Temp range	-0.004	0.001	24	-3.019	0.006	0.21

Across species, the sensitivity to VPD is related to hydraulic traits, such as vulnerability to embolism,  $H_v$ , hydraulic conductivity, turgor-loss point, rooting depth and leaf size (Flo et al., 2021). Similarly, within a single species, Poyatos et al. (2007) found a significant effect of tree-level  $H_v$  on sensitivity parameters of transpiration to VPD. While detailed plant trait measurements were lacking for most sites, we obtained leaf area, sapwood area and  $H_v$  for *P. abies*, *P. sylvestris* and *Q. ilex*. We found, however, no effect of leaf area and  $H_v$  on  $\beta_{VPD}$  and  $S_{95}$  across species and populations (Figure S2), whereas the relative sap flux sensitivity to VPD was positively related to leaf area across species and populations ( $p = 0.018$ ). Overall, our findings partly validate our third hypothesis: populations from warmer sites adjusted to higher temperatures by downregulating their transpiration sensitivity to VPD, indicating that they are structurally adjusted for reduced transpiration rates. However, in contrast to our third hypothesis, lower climatic water availability, which could translate to higher soil drought, had a slightly positive effect on transpiration rates. The different adjustments of VPD sensitivity to long-term soil water and air temperature therefore call for further in-depth analysis of the adjustment mechanisms to soil vs atmospheric droughts. Furthermore, earlier cross-species analyses of climate adjustments could not incorporate species-specific responses due to data scarcity. Therefore, whether adjustments to environmental gradients and stand characteristics vary from species to species could not be ascertained.

### 4.3 | Stand structure drives transpiration responses to VPD and SWCI

We observed that across species  $\beta_{VPD}$  and  $S_{95}$  were mainly driven by stand basal area, which explained around 30% of their variability across soil moisture levels and during days with dry and wet soils (Tables 3 and 4). We excluded experimentally thinned plots to avoid measuring short-term responses of tree transpiration to changes in stand characteristics. Nevertheless, studies assessing thinning effects might help identify the mechanisms underlying stand structure effects on transpiration responses to the environment as they assess the impact of stand density and basal area reductions under a given climate and soil type. Thinning induces changes in light availability, airflow within the canopy, and soil water availability through reduced water consumption and interception by the canopy (Gebhardt et al., 2014; Moore et al., 2004). Thus, changes in stand structure affect tree water relations in two ways: through changes in the above-ground microclimate and changes in belowground water availability and competition (Hassler et al., 2018). The higher  $\beta_{VPD}$  and  $S_{95}$  of trees growing in stands with lower basal area are most likely related to these effects. The effect of access to extractable soil water was evident during days with low soil moisture, where high clay and sand contents (and correspondingly a low silt content) were reducing  $\beta_{VPD}$  and  $S_{95}$  (Table 4). This confirms previous observations on the importance of soil type on tree transpiration (Hassler et al., 2018; Tromp-van Meerveld & McDonnell, 2006). Canopy microclimate further strongly impacted transpiration as

indicated by a strong effect of basal area on  $\beta_{VPD}$  when soil water access was not limiting (Table 4). In stands with higher basal area, the water exchange from the leaf to the atmosphere is hampered because the atmosphere around leaves in the canopy is not well coupled to the atmosphere above the forest stand (Paul-Limoges et al., 2017; Zhang et al., 2016). This lowers transpirational water loss of individual trees, resulting in a microclimate with lower VPD at the bottom canopy layers than the canopy top (Bachofen et al., 2020). Consequently, the sensitivity of stomata to changes in VPD is dampened in high basal area stands compared to low basal area stands (Song et al., 2020; Zhang et al., 2016). Correspondingly, trees in low-basal area forests exhibit a higher VPD sensitivity, which might increase their susceptibility to extremely hot conditions and soil drought (Song et al., 2020). Stand basal area can also be correlated with the ontogenetic state of the forest and, thus, be partly confounded with tree height and stand LAI (Figure S5). By including these variables in the linear mixed model, we are confident that stand basal area was the most important driver of tree transpiration sensitivity to VPD. The average tree age of the forest stands was highly correlated with other stand characteristics, particularly stand height, thus specific age effects could not be disentangled from the effects of basal area, height and LAI. Tree height and LAI were also important drivers of the relative SFD sensitivity to VPD ( $\beta_{VPD}/S_{95}$ ; Figure S3), indicating that multiple site characteristics drive tree transpiration in conjunction. In addition, low stand basal area can be related to high sapwood area per tree, which has been shown to result in a higher canopy transpiration, and a pronounced transpiration sensitivity to climate and soil drought (Chen et al., 2020). Hence, our work suggests that tree transpiration response to VPD can be effectively regulated by controlling stand basal area. The beneficial effect of an open stand on soil moisture contrasts with the effect it has on the susceptibility to hot conditions and soil drought. Therefore, the advantages and disadvantages of low-basal area stands need to be evaluated locally by considering the major limitations of tree transpiration.

#### 4.4 | Conclusions and implications for forest management

We observed that tree transpiration is sensitive to changes in soil and atmospheric water availability that happen on a short timescale (daily), and that trees adjust to site climatic and edaphic conditions that vary on a longer timescale (decades). The consistent observations of a downregulation of transpiration and its sensitivity to VPD with higher air temperatures have important implications on the global water cycle because of the role of tree transpiration on global water exchange (Schlesinger & Jasechko, 2014). Regional forest transpiration can be directly linked with precipitation in the vicinity, creating a positive feedback between transpiration and precipitation (Spracklen et al., 2012; Staal et al., 2018). Thus, transpiration downregulation under a warmer climate could reduce water exchange with the atmosphere (Grossiord et al., 2019), leading to negative feedback and lower precipitation. Basal area was the main driver of maximum tree transpiration and the sensitivity of tree transpiration to VPD. Hence, forest management practices can

tremendously impact tree transpiration. In Europe, land-use changes since the 1950s, including the abandonment of agroforestry practices, have led to nearly doubling stand densities (Fuchs et al., 2013; Gold et al., 2006). Consequently, resource competition among trees increased (Giuggiola et al., 2018). Stand thinning can generally increase the water availability for the remaining trees (Flathers et al., 2016; Giuggiola et al., 2016), but it might also increase the susceptibility of remaining trees to heat and soil drought events (Song et al., 2020) with contrasting responses of tree species according to their transpiration responses to VPD and soil water conditions (Figure 3). Any interventions in stand structure thus need to be considered in the specific context, including the climatic and edaphic conditions.

#### AUTHOR CONTRIBUTION

The study was conceived and designed by Christoph Bachofen, Charlotte Grossiord, Rafael Poyatos, Jordi Martínez-Vilalta, Víctor Flo and Maurizio Mencuccini. Víctor Flo, Víctor Granda and Rafael Poyatos set the database. Christoph Bachofen carried out the statistical analyses with support from Charlotte Grossiord and Rafael Poyatos and led the writing of the manuscript. All authors contributed critically to the draft and approved publishing the final version.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest or personal relationships that could have influenced this work.

#### DATA AVAILABILITY STATEMENT

All data of the SAPFLUXNET (version 0.1.5) are freely available from the Zenodo Repository at <https://doi.org/10.5281/zenodo.3971689> (Poyatos et al., 2020).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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