1 Title page

3 (i) Title

4 **Contrasting stomatal sensitivity to temperature and soil drought in mature alpine conifers**

5 **Short title:** Sensitivity of stomatal conductance in conifers

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(v) Abstract

Conifers growing at high elevations need to optimize their stomatal conductance (g_s) for maximizing photosynthetic yield while minimizing water loss under less favourable thermal conditions. Yet, the ability of high-elevation conifers to adjust their g_s sensitivity to environmental drivers remains largely unexplored.

We used four years of sap flow measurements to elucidate intra- and inter-specific variability of g_s in *Larix decidua* Mill. and *Picea abies* (L.) Karst along an elevational gradient and contrasting soil moisture conditions. Site- and species-specific g_s response to main environmental drivers were examined, including vapour pressure deficit, air temperature, solar irradiance and soil water potential.

Our results indicate that maximum g_s of *L. decidua* is >2 times higher, shows a more plastic response to temperature, and downregulates g_s stronger during atmospheric drought compared to *P. abies*. These differences allow *L. decidua* to exert more efficient water use, adjust to site-specific thermal conditions, and reduce water loss during drought episodes.

The stronger plasticity of g_s sensitivity to temperature and higher conductance of *L. decidua* compared to *P. abies* provide new insights into species-specific water-use strategies, which affect species' performance and should be considered when predicting terrestrial water dynamics under future climatic change.

(vi) Keywords

conifers; high-elevation forests; hydraulic plasticity; inter- and intra-specific variability; *Larix decidua*; *Picea abies*; sap flow; stomatal conductance; transpiration.

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Summary statement

Regulation of stomatal conductance to changing environmental conditions is crucial for optimizing tree water use. We found contrasting water-use strategies, where the pioneer *Larix decidua* is more plastic in adjusting stomatal conductance to temperature-limiting conditions compared to late-successional *Picea abies*.

Main text

Introduction

The biogeographical distribution of coniferous trees extends across a wide range of contrasting environmental conditions, from the Arctic Circle to the equator and Southern Hemisphere (Farjon & Filer 2013). Although many factors affect the distribution of tree species (see Zimmermann *et al.* 2010; Walthert & Meier 2017), conifers often dominate at high elevations where low temperatures and short growing seasons severely limit growth and survival (Bannister & Neuner 2001; Körner 2012). For example, it is very common to find conifers at the upper tree line with growing season temperatures as low as 5.5-7.5 °C (Körner & Paulsen 2004). Under such temperature-limiting conditions, growth is known to be highly sensitive to ongoing climate change (Beniston 2003; Soja *et al.* 2007; IPCC 2013). Recent studies indicated that warmer and drier conditions in temperature-limited ecosystems (at high elevations and latitudes) are altering the forest composition and the timing and duration of both primary and secondary growth (e.g., Esper & Schweingruber 2004; Steltzer & Post 2009; Allen *et al.* 2010; Meier *et al.* 2012; Rigling *et al.* 2013; Peters *et al.* 2017). Subsequently, these changes have consequences for the terrestrial biogeochemical cycles and the global climate system (Myneni *et al.* 2001; Bonan *et al.* 2008).

When growing under a wide range of climatic conditions, trees need to optimize carbon assimilation and its use, i.e., the formation and maintenance of (woody and non-woody) tissues (see Maseyk *et al.* 2008; Rossi *et al.* 2008; Körner 2012; Fatichi *et al.* 2014). Both the processes of producing carbohydrates (via photosynthesis; Nobel 2009) and the generation of turgidity within the cambium required for growth (Lockhart 1965), depend on the way a tree regulates the flow of water through the soil-plant-atmosphere continuum (Mencuccini 2003; Tuzet *et al.* 2003; Damour *et al.* 2010; De Schepper & Steppe 2010). Conifers thus underwent strong selective pressure to develop specialized ways to regulate their internal hydraulics (Brodribb *et al.* 2014; Klein 2014; Anderegg *et al.* 2016). Main mechanisms for controlling tree water use usually include anatomical adjustments of the water conducting xylem (e.g., Mayr *et al.* 2006;

Bouche *et al.* 2014) and the optimization of the stomatal conductance (g_s) to quickly respond to varying environmental conditions (Hetherington & Woodward 2003; Lin *et al.* 2015). The regulation of g_s sensitivity is crucial under temperature-limiting conditions, as transpiration has to be optimised for minimal water loss during cold spells and under frozen soil conditions (Mayr 2007) and maximum photosynthetic yield during the short vegetative season (i.e., to produce ample sugars for frost damage protection; see Körner *et al.* 2016; Lintunen *et al.* 2016). This optimization is supported by observations of increasing maximum g_s with increasing elevation (Körner 2012) and deciduous conifers like *Larix decidua* Mill. (with a shorter growing season) showing an overall higher conductance than evergreen *Picea abies* (L.) Karst. and *Pinus cembra* L. (Anfodillo *et al.* 1998). However, although the species-specific difference in the sensitivity of g_s to temperature could be relevant for optimizing tree water use under temperature-limited conditions, most studies have focussed on stomatal responses to atmospheric and soil droughts (e.g., Lindroth 1985; Arneth *et al.* 1996; Day 2000; Leo *et al.* 2014; Wieser *et al.* 2014).

Under rapidly changing climatic conditions, the future performance and occurrence of a species depends on its plasticity (Valladares *et al.* 2014), i.e., the ability to adjust physiological functioning under a wide range of growing conditions. This also holds for tree water use, since species survival in persistent warmer and drier conditions largely depends upon the plastic adjustment of its hydraulic functioning (e.g., Körner *et al.* 1986; Cordell *et al.* 1998; Martínez-Vilalta *et al.* 2009; López *et al.* 2013). Thus, there has been interest in comparing inter- and intra-specific shifts in g_s response to vapour pressure deficit (D) at sites with contrasting climatic conditions (e.g., Poyatos *et al.* 2007). For example, a study by Grossiord *et al.* (2017) on conifers growing in a semi-arid climate found a reduced stomatal sensitivity to D when exposed to persistent warming. Although conifers growing at different thermal conditions (e.g., along elevational gradients) show a uniform g_s response to D (Mayr 2007), their ability to adjust their g_s response to air temperature (T_a) and solar radiance (R_g) might be crucial for optimizing tree water use (Livingston & Black 1987; Buckley & Mott 2013). For example - due to the shorter growing season, low temperatures and reduced partial pressure of CO_2 at higher elevations (Körner 2012) - a strategy to optimize carbon assimilation might allow higher g_s at low temperatures, despite thermal conditions being less favourable for photosynthetic activity (Wieser 2007; Damour *et al.* 2010). In addition, due to low drought stress conditions (Körner 2012), high-elevation conifers could reduce g_s sensitivity to R_g , where incomplete stomatal closure during the night allows for a faster supply of water to the leaves at sunrise (e.g., Daley

122 & Phillips 2006). Yet, the ability of high-elevation conifers to adjust their g_s response to these
123 environmental drivers in the context of a warming atmosphere remains largely unexplored.

124 In this study, we investigated the stomatal regulation of *P. abies* and *L. decidua* and its
125 plasticity along an elevational gradient in the central Swiss Alps that stretches up to the species'
126 upper distribution limits (Ellenberg & Leuschner 2010) and shows a genetically well-mixed
127 population (King *et al.* 2013a). In addition to a thermal gradient, with a persistent difference in
128 mean growing season temperature of up to 3.2 °C, trees at contrasting soil moisture conditions
129 were also monitored. At five different sites, we installed thermal dissipation probes to obtain
130 four years of sap flow measurements, including a strong drought event in the summer of 2015.
131 The sap flow measurements were used to calculate g_s and analyse its sensitivity to
132 environmental conditions at each site. We hypothesize that drought sensitive *P. abies*
133 (Anfodillo *et al.* 1998; Ježík *et al.* 2015) will show a relatively stronger downregulation of its
134 stomatal conductance to increasing D and increasing drought (by measuring soil water
135 potential, ψ_{soil}) compared to *L. decidua*. Additionally, for each species we quantified the
136 sensitivity and plasticity of g_s response functions to multiple environmental drivers (including
137 D , ψ_{soil} , T_a and R_g) across the elevational gradient, where we specifically differentiate between
138 soil and atmospheric drought (Klein *et al.* 2014; Tatarinov *et al.* 2016). As pioneer species are
139 expected to show higher plasticity (Sultan 2000; Barigah *et al.* 2006), we hypothesize that the
140 pioneer *L. decidua* (Gower & Richards 1990) will show a more plastic adjustment of its g_s
141 response to environmental drivers compared to the late-successional species *P. abies*. The
142 analysis of the stomatal behaviour of high-elevation conifers offers a unique perspective on the
143 plasticity of their hydraulic functioning and provides insights into their ability to optimize water
144 use under future climatic conditions.

Materials and methods

Site description

The studied trees are located on several sites situated within the Lötschental valley in the Swiss Alps (46°23'40"N, 7°45'35"E; Figure 1a). The valley is characterised by steep slopes (>60%) and covered with a mixed forest of naturally occurring evergreen *P. abies* and deciduous *L. decidua*. Average forest stand density at the sites is 401±144 trees ha⁻¹, with an average tree age of 173±45 years, diameter at breast height (DBH) of 45±4 cm and canopy height of 22±4 m (Peters *et al.* 2017). Soils are formed from calcareous-free substrate, including moraines and crystalline bedrock (gneiss and granite) from the Aar massif. Several different soil types were classified on the valley slope, including Leptosol, Cambisol to Podzol. Soil texture consists of 10±4% clay, 56±10% sand and 35±8% silt content and with fine soil bulk density of 0.77±0.42 g cm⁻³. At the valley bottom with wetter soil conditions, organic soils (Histosol) with low bulk density (0.19±0.07 g cm⁻³) occur. Long-term mean annual total precipitation and mean annual air temperature in the valley exceeds 800 mm and approximates 5.7 °C, respectively (King *et al.* 2013b).

Sap flow and environmental conditions were continuously monitored from April 2012 to October 2015 at five sites distributed across a thermal and moisture gradient. Four of these sites are situated along an elevational gradient on a south-facing slope with a 300 m interval from the valley bottom at 1300 m above sea level to the treeline at ~2200 m a.s.l.. The site at the treeline, close to the distribution limit of *L. decidua* (hereafter referred as S22, where S indicates the south-facing slopes), showed a mean growing season (May-October) air temperature of 8.3 °C (covering 2012-2015). The site at 1900 m a.s.l. (S19), corresponding to the distribution limit of *P. abies*, showed slightly warmer conditions with a mean growing season air temperature of 9.2 °C. The two sites at 1600 (S16) and 1300 m a.s.l. (N13, where N indicates the north-facing slopes) experienced sequentially drier and warmer conditions, with a mean growing season air temperature of 10.4 and 11.5 °C, respectively. A fifth contrasting wet site was established at the valley bottom close to the Lonza river, providing constant water saturation at 70 cm soil depth (N13W), with a slightly cooler mean growing season air temperature of 10.4 °C.

174 *Environmental measurements*

175 Radiation-shield covered sensors were installed at each site on a central tower (~2.5 m
176 above the ground) within the canopy to measure air temperature (T_a [°C]) and relative humidity
177 (RH [%]; Onset, USA, U23-002 Pro) with a 15-minute temporal resolution. Vapour pressure
178 deficit (D [kPa]) was calculated from T_a and RH (WMO 2008). Soil temperature (T_s [°C]) was
179 recorded at each site with an hourly resolution at a depth of 10 cm (Onset, USA, TdbiT). At
180 N13 solar irradiance (R_g [W m⁻²]) was measured with 15-minute resolution using a micro-
181 station (Onset, USA, H21-002 Micro Station) and pyranometer (Onset, USA, S-LIB-M003)
182 positioned in an open field. For the other sites, R_g measurements were adjusted for aspect and
183 topographic shading after Schulla (2015). Calculations for topographic shading were based on
184 the digital height model DHM25 (Swiss Federal Office of Topography Swisstopo).

185 Soil volumetric water content was measured hourly with five sensors at 10 and 70 cm
186 depth at each site (θ [%]; Decagon, USA, EC-5). At the same depth, soil water potential was
187 also measured (ψ_{soil} [MPa]; Decagon, USA, MPS-2) for 2015. These measurements were used
188 for establishing soil water retention curves using the van Genuchten model (van Genuchten
189 1980), where the saturated water content was established according to Teepe *et al.* (2003; see
190 Table S1). This allowed retrospective determination of ψ_{soil} for the entire monitoring period.
191 The water content at permanent wilting point and field capacity was visually determined to
192 normalize θ to relative extractable water (in %; Granier *et al.* 1999). The wettest conditions
193 from both depths for θ and ψ_{soil} were used to represent the site conditions.

194 Daily precipitation was obtained from the nine nearest weather stations (6 to 43 km
195 distance to the transect, including Adelboden, Blatten, Grächen, Montana, Jungfraujoche, Sion,
196 Ulrichen, Visp and Zermatt; Federal Office of Meteorology and Climatology MeteoSwiss). The
197 environmental measurements at each site were quality controlled and the few sporadic data-
198 gaps were filled by linear interpolation or by using a regression approach with a stiff cubic
199 spline on data from other sites and hourly averaged (using the *mgcv* package in R software
200 version 3.2.00, R development core team 2013).

201 *Physiological measurements and conductance calculations*

202 At every site three mature trees per species (a total of 15 *L. decidua* and 12 *P. abies*
203 trees; Table 1) were instrumented with commercially available thermal dissipation probes
204 (Granier 1985; Tesaf, University of Padova, Italy) to estimate sap flux density (F_d [g H₂O cm⁻²
205 sapwood area h⁻¹]). Two 2 cm long probes were radially inserted into the xylem (below the

cambium), with a vertical distance of 10 cm on the slope-facing side of the stem at ~1.6 m height. The temperature difference between the probes (ΔT [°C]) was recorded with 15-minute resolution on a data logger (Campbell Scientific, USA, CR1000). The normalized difference (denoted as unitless K [-]) between measured ΔT and zero sap flow conditions ($\Delta T_{\max}$; Lu *et al.* 2004) was calculated. F_d was calculated with K by using the data-processing method described in Peters *et al.* (2018), correcting for the probe in non-conductive xylem, applying a species-specific calibration, dampening correction and environmental dependent determination of zero-flow conditions. The internal tree water status was monitored at the dry site (N13) by measuring leaf water potential (ψ_{leaf} [MPa]) on three mature trees per species for which the crown was reachable by pole-pruner. During three sampling campaigns we measured predawn ψ_{leaf} (<6:00 CET on 19-04-2014, 21-07-2015 and 24-09-2015), while we measured weekly midday ψ_{leaf} (11:00-15:00 CET) during the 2015 growing season (June-September). Measurements were performed by using a Scholander pressure chamber (Boyer 1967) on four twigs (~5 cm) per tree.

Sapwood thickness was measured from two increment wood cores (using an increment borer; Haglöf, Sweden) taken perpendicular to the slope at breast height (~1.3 m) from the monitored trees (based on discolouration for *L. decidua* and translucence for *P. abies*). F_d was multiplied by the sapwood area (A_s [cm²]) to obtain whole-tree water flux (W_u [kg H₂O h⁻¹]; see Table 1), where *P. abies* has a mean A_s of 710 cm² (with exceptionally high values for N13W), and *L. decidua* has a mean A_s of 307 cm². Whole-tree water flux was then used to estimate transpiration per unit of leaf area (i.e., E [g H₂O m⁻² leaf area h⁻¹]) by using allometric relationships between A_s [cm²] and total projected needle area (A_L [m²]; Figure 1b, c). To generate a robust relationship between DBH and A_s , over 450 trees were measured across the alpine range (Figure 1b; see Table S2). Species-specific allometric relationships of DBH- A_s were then used together with a leaf area database (constructed with the measurements from Burger 1953), recording A_L and DBH, to establish $A_L:A_s$ values (Figure 1c; Tyree & Zimmermann 2002). To account for the delay between E and F_d , the mean difference between the time of sunrise and the onset of F_d (15-minute resolution) was calculated to shift back F_d to represent E . The timing of sunrise was defined every day as the time when R_g exceeds 10 W m⁻². The onset of F_d was determined when a persistent increase in F_d occurred after 3:00 am. Finally, we made use of weekly observations of phenological stages performed from 2008 till 2011, to remove periods where *L. decidua* did not have full foliage (Moser *et al.* 2010; see Figure S1).

Crown and stomatal conductance and their response to environmental drivers

Both crown conductance (g_{sap} [$\text{g H}_2\text{O m}^{-2} \text{ sapwood area s}^{-1} \text{ kPa}^{-1}$]) and stomatal conductance (g_s [mm s^{-1}]) were calculated for all individuals. We complemented the g_s calculation with g_{sap} , as the latter is less dependent upon model assumptions when comparing species-specific differences. We determined g_{sap} by using D and F_d (adopted from Meinzer *et al.* 2013 and Pappas *et al.* 2018):

$$g_{sap} = \frac{(F_d * 10000/3600)}{D} \quad (1)$$

In order to minimize the effect of stem hydraulic capacitance (see Braun *et al.* 2010), only peak-of-the-day hourly values of g_{sap} were considered. Peak-of-the-day was defined as the hours when $R_g > 500 \text{ W m}^{-2}$. Next, the hourly g_{sap} values were standardized to the individual specific 99th quantile of the time-series ($g_{sap,max}$), to correct for absolute difference in conductance. The relative hourly crown conductance values ($g_{sap}/g_{sap,max}$) were average per site and species and aggregated to daily mean values. Species-specific g_{sap} responses to atmospheric drought (approximated with D) and soil drought (approximated with ψ_{soil}) were analysed for periods where other factors were less limiting. For the response of g_{sap} to D , days were selected with $T_a > 12^\circ\text{C}$, $\theta > 60\%$ and precipitation $< 10 \text{ mm d}^{-1}$, while for ψ_{soil} we selected days with $D < 0.8 \text{ kPa}$ instead of θ . To explain responses in g_{sap} to D and ψ_{soil} we fitted linear functions as $g_{sap,ref} - \delta * \ln D$ ($g_{sap,ref}$ is the reference conductance when $D = 1 \text{ kPa}$; see Oren *et al.* 1999) and $g_{sap,int} + A * \psi_{soil}$, respectively. Linear-mixed effect modelling was applied, where the individual is considered as the random effect while accounting for first-order auto-correlation. Due to high variability in $g_{sap}/g_{sap,max}$ at low ψ_{soil} values, the linear function for ψ_{soil} only considers data $< -0.2 \text{ MPa}$.

An inversed simplified Penman-Monteith equation was used to calculate g_s (Monteith 1965; Granier & Loustau 1994), assuming that conifer forests are aerodynamically well coupled to the atmosphere (Monteith & Unsworth 2013). Together with the hourly averaged T_a , D and E estimates, g_s was calculated according to the following equation (see Note S1):

$$g_s = \frac{\lambda E \gamma}{\rho C_p D} \quad (2)$$

where λ is the latent heat of vaporization ($[\text{J g}^{-1}]$; as a function of T_a), γ is referred to as the psychrometric constant [hPa K^{-1}] (as a function of air pressure, which is calculated from elevation and T_a), ρ is the air density [kg m^{-3}] (as a function of T_a and atmospheric pressure) and C_p is the heat capacity of air [$\text{J kg}^{-1} \text{ K}^{-1}$] (taken as $1.01 \text{ J kg}^{-1} \text{ K}^{-1}$). The g_s was standardized

to the 99th quantile of the individual specific stomatal conductance ($g_{s,max}$), after which hourly $g_s/g_{s,max}$ values were averaged per site and species. A Jarvis-type approach (Jarvis 1976) was used to analyse the $g_s/g_{s,max}$ response to D , T_a , θ , ψ_{soil} , and R_g . We excluded conductance values from rainy days (precipitation >1 mm d⁻¹) and with $D < 0.1$ kPa as these conditions generate unrealistic values (e.g., Philips & Oren, 1998). For $g_s/g_{s,max}$ values, a bootstrap resampled boundary-line analysis was performed to disentangle when the independent variable is limiting (Chambers *et al.* 1985; Shatar & McBratney 2004). Within this analysis a predefined upper quantile was selected when binning the independent variable (e.g. dividing the x-axis into classes of a specified size as described in Chambers *et al.* 1985; Table 2). A bin width of 2% of the total range was used and overlapped by 1% with the previous bin to reduce the effect of uneven distribution of data. For the boundary-line analysis we excluded conditions where the selected independent variable could show collinearity with other meteorological variables (Table 2). Models were fitted through the upper quantiles to describe the relationship, referred hereafter as response functions (Table 3).

To elucidate the effect of differences in response function parameters, the species- and site-specific g_s curves were used to model transpiration patterns. We multiplied the site- and species-specific average $g_{s,max}$ with the response functions of D , T_a , ψ_{soil} , and R_g to obtain g_s , which was used together with T_a , D in equation 2. To highlight the effect of different response function parameters on daily E dynamics, curves for T_a , D and R_g between high and low elevation sites were alternated. The effects of spring and autumn phenological development of *L. decidua* on the resulting g_s were simulated with the models of Murray *et al.* (1989) and Delpierre *et al.* (2009) using daily mean T_a and day length data, respectively. All analyses were performed with the R software (version 3.2.00, R development core team 2013).

Results

Allometry and temporal dynamics of sap flow and transpiration

Species-specific allometric relationships between A_s and DBH were established for *L. decidua* and *P. abies* (Figure 1b). The quadratic function showed a significantly steeper increase in A_s with increasing DBH for *P. abies* ($p < 0.001$; $A_s = 10.76 \text{ DBH} + 0.18 \text{ DBH}^2$) than *L. decidua* ($A_s = 4.78 \text{ DBH} + 0.02 \text{ DBH}^2$). When applying these functions on the leaf area data (covering 59 sites across Switzerland), similar $A_L:A_s$ values of 0.457 and 0.532 were found for *P. abies* and *L. decidua*, respectively ($p = 0.265$ using a linear mixed-effect model; Figure 1c; see Table S2).

A substantial time-lag between sunrise and start of F_d was revealed for both *P. abies* and *L. decidua*. No significant difference in delay was found between sites ($p > 0.1$; using a linear mixed-effect model, see Table S3), despite intra-specific differences in height and DBH across the sites (Table 1). *P. abies* showed a significantly longer delay of 2 h and 45 min, while *L. decidua* showed an average delay of 1 h and 45 min ($p < 0.001$; Table S3). Also, the absolute spread of the delay was higher for *P. abies* (Standard error is ~17, against ~12 min delay for *L. decidua*; see Table S3).

Over the four years of monitoring sap flow, E was consistently higher for *L. decidua* (Figure 2a) than *P. abies* (Figure 2b). Additionally, the seasonal pattern of E was more pronounced for *L. decidua* (showing a stronger parabolic shape) and showed stronger differences between sites than *P. abies* with the highest E at N13 (Figure 2a, b). In July 2015, a strong drought was recorded, resulting in a gradual decrease in E for *L. decidua* at N13 (Figure 2c), while *P. abies* showed an even stronger response and paused transpiration at N13 and S16 (Figure 2d). This drought caused an inverse pattern between N13 and N13W, where N13 showed lower E within July 2015 compared to N13W for both species.

Species-specific conductance response to environmental conditions

The analysis of *L. decidua* and *P. abies* crown conductance revealed that there is a species-specific difference in their maximum values ($g_{\text{sap.max}}$), while no significant effect of mean growing season temperature was found (Figure 3; $p > 0.5$, also for g_s). *L. decidua* showed a significantly higher mean $g_{\text{sap.max}}$ of $261.31 \text{ g m}^{-2} \text{ s}^{-1} \text{ kPa}^{-1}$ compared to *P. abies* ($81.34 \text{ g m}^{-2} \text{ s}^{-1} \text{ kPa}^{-1}$; $p < 0.001$; using a linear mixed-effect model). This difference was also found for maximum stomatal conductance ($g_{s.\text{max}}$), which was significantly higher for *L. decidua* (7.8 mm

s⁻¹) compared to *P. abies* (with a value of 3.5 mm s⁻¹; $p = 0.008$). The calculated $g_{s,max}$ fell within the expected range for gymnosperms (Kelliher *et al.* 1993; Arneth *et al.* 1996).

Only the N13 site experienced a large enough variability in ψ_{soil} for addressing species-specific crown conductance response to soil drought (Figure 4). Daily $g_{sap}/g_{sap,max}$ showed a slightly more negative response to D for *L. decidua* (Figure 4a). Significant changes in $-\delta$ and $g_{sap,ref}$ were obtained when using a linear mixed effect model ($-\delta$ changed by 0.102, $p < 0.001$; $g_{sap,ref}$ change by -0.141, $p < 0.037$). For the response to ψ_{soil} , *L. decidua* showed consistently higher $g_{sap}/g_{sap,max}$ values ($g_{sap,ref}$ *L. decidua* > *P. abies*; Figure 4b; $p = 0.051$). The slopes of the linear relationship between $g_{sap}/g_{sap,max}$ and ψ_{soil} did not significantly differ between the two species (A in Figure 4b). Although less affected by assumptions on delay time and projected leaf area, daily g_{sap} could not be used at the intra-daily time scale to uncover potential inter-specific variability in water conductance.

Intra-specific differences in $g_s/g_{s,max}$ response to environmental conditions

The response of standardized stomatal conductance ($g_s/g_{s,max}$) to D , T_a , R_g and ψ_{soil} revealed different sensitivities between sites and species (Figure 5). The response of $g_s/g_{s,max}$ to D showed a typical negative exponential behaviour in agreement with theoretical expectations (Roman *et al.* 2015; Figure 5a, b), with a stronger initial decrease in $g_s/g_{s,max}$ for *L. decidua* than for *P. abies* (Table 4; with $a = -0.364 \pm 0.051$ and $b = -0.676 \pm 0.084$ compared to -0.402 ± 0.071 and -0.753 ± 0.080 , respectively). Yet, little intra-specific difference in *L. decidua* and *P. abies* response to D was found between the sites, except for the more gradual slope of the function for *L. decidua* trees at S22 (Figure 5a).

The sensitivity of stomatal conductance to T_a showed distinct differences between the species (Figure 5c, d). The fitted Gompertz functions (Table 3), to describe the response of $g_s/g_{s,max}$ to T_a , revealed little difference in the inflection point (T_a where the slope of the function is steepest; b parameter in Table 4) between sites for *P. abies* (average of 3.3 °C; Figure 5d). On the other hand, *L. decidua* showed changing inflection point temperatures for higher elevation sites, decreasing from 6.5 to 3.2 °C (Figure 5c). The slope of the inflection point did not differ from the 95% confidence interval between the sites (parameter a in Table 4). Although the shift of the inflection points to lower T_a at sites with lower growing season temperature for *L. decidua* did not surpass the inflection point found for *P. abies*, an absolute offset between the species became apparent when considering the higher $g_{s,max}$ values for *L. decidua* (see Figure S2a). Similar differentiation between sites was found when considering T_s ,

although the 95% confidence interval was substantially larger (especially for *P. abies*; see Figure S2b).

The $g_s/g_{s,max}$ response to R_g (Table 3) showed for both species that higher elevation sites appeared to respond more slowly to increasing R_g when considering the slope of the fitted function (parameter a in Table 4), where S19 showed the flattest slope with 0.003-0.004 $W^{-1} m^{-2}$ (Figure 5e, f). Additionally, the response functions indicated that higher elevation sites allowed for higher stomatal conductance when R_g approached 0 $W m^{-2}$ (parameter b in Table 4). Only the N13 site showed sufficient spread in ψ_{soil} for response curve fitting, where *P. abies* showed a stronger decrease in conductance with increasing ψ_{soil} , as was found for g_{sap} (Figure 5g, h).

Impact of plastic g_s response functions

The impact of differences in the g_s response functions to D , T_a and R_g became apparent when modelling daily mean E for high- (S22 and S19) and low-elevation (N13) *L. decidua* (Figure 6a, d) and *P. abies* (Table 5). After considering the phenological development (Figure 6 c, f), S22 *L. decidua* would transpire up to 5.1 ± 0.7 $kg m^{-2} yr^{-1}$ less (4.6 ± 0.7 for S19) if it had a similar T_a response as N13 *L. decidua* (Table 5). The difference in E due to the altered T_a response is mainly caused by the additional transpiration at the end of the growing season (Figure 6b). For N13 an increase of 3.7 ± 1.0 (added to 124.8 ± 12.1 $kg m^{-2} yr^{-1}$) would be expected if *L. decidua* responded like the trees at S22 (Table 5). Here, the main difference is detected at the beginning of the growing season during colder conditions (Figure 6e). Both the alteration in R_g and D response affect E less consistently, although N13 *L. decidua* would transpire up to 22.2 ± 1.8 $kg m^{-2} yr^{-1}$ more if it had the more gradual D response function of S22 *L. decidua* (Table 5).

Discussion

Conifers growing at temperature-limited conditions and exposed to shorter growing seasons optimize water transport to facilitate carbon assimilation and use (Wieser 2007; Körner 2012). Here, we showed that two conifers commonly occurring at high elevations in Europe apply contrasting strategies in regulating their stomatal conductance (g_s), a key mechanism for controlling tree water use dynamics. The analysis of four years of sap flow measurements revealed that the pioneer *L. decidua* facilitated higher water conductance (Figure 3), while regulating water loss during atmospheric droughts more tightly than a late-successional species as *P. abies* (Figure 4a). Additionally, the within species ability to adjust their g_s sensitivity to environmental conditions differed between species, where *L. decidua* appeared more plastic (Figure 5c, d).

Higher maximum crown and stomatal conductance for L. decidua in comparison to P. abies

Our study revealed that the two conifers differed in their efficiency to transport water, where *L. decidua* showed a >2 times higher maximum water conductance per unit leaf area (maximum stomatal conductance, $g_{s,max}$) and per unit sapwood area (maximum crown conductance, $g_{sap,max}$) than *P. abies* (Figure 3). The species-specific difference in conductance is highlighted by the higher average transpiration (E) for *L. decidua* than *P. abies* over the four years of observations (Figure 2), although *P. abies* is able to reach higher transpiration rates at sites with warmer growing season temperatures (e.g., Wullschleger *et al.* 1998). This species-specific difference in conductance at high elevations was also found by Anfodillo *et al.* (1998). Yet, the steeper increase in A_s with the increasing size (DBH) for *P. abies* (Figure 1) translates to an overall larger leaf area, which compensates for the lower conductance and for larger individuals and even facilitates a higher overall water flux compared to *L. decidua* (see max. W_u in Table 1). Interestingly, no significant increase in maximum conductance with higher elevations was found (Figure 3), although this is commonly reported and attributed to wider tree spacing and more intense radiation (see Körner 2012). This absence of $g_{s,max}$ plasticity could be attributed to the uncertainty in A_s or $A_L:A_s$ values. Yet, *P. abies* had consistently higher A_s values and variability compared to *L. decidua*, which is in line with other studies (e.g., Tyree & Zimmermann 2002; Longuetaud *et al.* 2006; Nawrot *et al.* 2008).

Adjusting xylem anatomical properties is an important mechanism for regulating $g_{s,max}$ and could explain species-specific differences in maximum conductance (Locosselli & Ceccantini 2012; Klein 2014). The higher $g_{s,max}$ for *L. decidua* could be facilitated by generally

wider tracheids compared to *P. abies*, reducing the resistance for water transport up to the crown (Tyree & Zimmermann 2002) while allowing for lower midday leaf water potentials (ψ_{leaf} ; Figure S3). According to Hagen-Poiseuille's law (Tyree & Zimmermann 2002), when assuming a tracheid lumen diameter difference of 30 and 41 μm for *P. abies* and *L. decidua*, respectively (see Carrer *et al.* 2017), we find agreement with a three times higher hydraulic conductance for *L. decidua* compared to *P. abies*. Although these findings have to be confirmed with *in situ* anatomical measurements, they indicate that the xylem structure largely affects the maximum hydraulic conductance. Additionally, xylem density increases with elevation, where narrower tracheids and thicker cells walls help to avoid winter embolisms (Mayr 2007). This results in a decrease in lumen area and may prevent high-elevation conifers from increasing $g_{s,\text{max}}$. Otherwise, leaf related explanations include osmotic adjustments within the stomata might enable *L. decidua* to maintain higher conductance during summer (Badalotti *et al.* 2000) or species-specific differences in leaf traits like stomatal size and density (Körner *et al.* 1986; Luomala *et al.* 2005; Locosselli & Ceccantini 2012).

Species-specific variations in water use strategies

The exceptional 2015 summer drought, with low soil water potential (ψ_{soil}) and high air temperature (T_a), caused a cease in transpiration in low elevation *P. abies* (N13; Figure 2d), while *L. decidua* showed a strong reduction (Figure 2b). Surprisingly, we found no evidence to support that more drought sensitive *P. abies* would apply a stronger water-saving strategy, by down regulating conductance to increasing vapour pressure deficit (D) stronger than *L. decidua* (Figure 4). The fact that the *P. abies* response function to D is not adjusted to drier growing conditions (e.g., no steeper decrease in g_s with increasing D at the drier site compared to the wet site; Figure 5b) could be explained by the low occurrence of severe droughts within this ecosystem. This is supported by Grossiord *et al.* (2017) who did not find adjustment of the g_s response to D after five years of precipitation reduction in a semi-arid region. On the contrary, *L. decidua* appeared to show a slightly stronger downregulation with increasing D compared to *P. abies* (Figure 4a), which matches with observations by Oren *et al.* (1999) and Leo *et al.* (2014) for *Larix sp.* and *P. abies*. When considering soil drought responses, *P. abies* exhibited consistently lower relative conductance with decreasing ψ_{soil} (or increasing drought; Figure 4b). Yet, the slopes of the response of $g_{\text{sap}}/g_{\text{sap,max}}$ to ψ_{soil} are similar, hinting to the fact that the shallower rooting strategy of *P. abies* versus *L. decidua* is potentially causing less water uptake and storage refilling (Oberhuber *et al.* 2015), instead of a stomatal specific response. This hypothesis is supported by the midday ψ_{leaf} response to decreasing ψ_{soil} (see Figure S3), where

the slope of *P. abies* appears to be slightly steeper, although these results are by no means conclusive due to the low number of ψ_{leaf} measurements below a ψ_{soil} of -0.6 MPa ($n=6$, $\Delta_{\text{slope}}=0.205 \text{ MPa}^{-1}$, $p=0.502$).

The stronger downregulation of g_s to D for *L. decidua* could be explained by its larger tracheids being disputably more prone to cavitation during drought episodes (Bouche *et al.* 2014). Another explanation could be that the thinner cuticula of the deciduous *L. decidua* dehydrates faster and thus initiates stomatal closure faster with higher D (Mayr 2007). Although our results might be interpreted as *L. decidua* being slightly isohydric (i.e., more actively regulating stomatal conductance to maintain constant leaf water potential; Klein 2014) than *P. abies* in mountainous ecosystems, we did find the midday ψ_{leaf} measurements of *L. decidua* to be significantly lower under well-watered conditions ($\Delta_{\text{intercept}}=0.235 \text{ MPa}$, $p=0.015$; see Figure S3) showing that *L. decidua* might not maintain more constant ψ_{stem} . Nevertheless, the more active downregulation of g_s with increasing D does support that *L. decidua* might be better in maintaining hydraulic functioning under drier growing conditions compared to *P. abies*.

Next to the environmental regulation of g_s , a species-specific difference was found in the delay between sap flow diurnal fluctuations and the driving meteorological conditions (due to water storage in the stem; Braun *et al.* 2010). When comparing start of sap flow and sunrise, we found that *P. abies* sap flow response to sunrise took one hour longer compared to *L. decidua*. Interestingly, asynchronous and contrasting tree water use dynamics between co-occurring boreal conifers was also found in the southern limit of the boreal ecozone in central Canada (*Larix laricina* and *Picea mariana*; Pappas *et al.* 2018) and have been attributed to whole-plant traits trade-offs along the ‘fast-slow’ plant economics spectrum (Reich 2014). More specifically, the deciduous *Larix* is characterised by a “fast” traits strategy with higher rates of resource acquisition and use, resulting also in higher water conductance while the evergreen *Picea* is characterised by a “slow” traits strategy, with lower water conductance (Pappas *et al.* 2018).

Plasticity of stomatal conductance to environmental changes

We did not find evidence to support a plastic adjustment of the g_s response to D for *L. decidua* and *P. abies* when growing under persistently different growing season temperatures, as found by Grossiord *et al.* (2017). When comparing sites across the elevational gradient, only *L. decidua* growing at the tree-line site (S22) showed a different g_s response, with higher conductance below 1.5 kPa (Figure 5a, b). Although the shift in the response function at S22

potentially increases transpiration in the long term by $\sim 10 \text{ kg m}^{-2} \text{ yr}^{-1}$ (Table 5), this shift does not appear to relate to increasing elevation or decreasing growing season temperatures (as S19 and S16 show a similar response-function as N13; Figure 5a, b). This lack of apparent plasticity in stomatal response to D for high elevation conifers is consistent with Poyatos *et al.* (2007) who found little evidence for *Pinus sylvestris* L. adjusting the g_s sensitivity to D when comparing sites with mean annual temperature ranging from -3.7 to 9.8 °C.

We observed that high elevation conifers adjust their g_s response to T_a (Figure 5c) and R_g (Figure 5e, f) depending on elevation. Surprisingly, only *L. decidua* at higher elevations showed a change in g_s sensitivity to T_a (Figure 5c, d), with a significant inflection point shift of $+0.87$ °C per 1 °C increase in mean growing season temperature (May-October). Yet, due to the lack of periods where g_s is not limited by D at higher temperatures, we were only able to analyse the g_s response below 13 °C. Crop species have shown a similar plasticity in their g_s response to temperature (e.g., Yamori *et al.* 2010), but to our knowledge, few studies focus on g_s sensitivity to temperature for trees (e.g., Urban *et al.* 2017; Drake *et al.* 2018) and none have shown its plasticity. In this study, we showed that the observed plasticity of the g_s - T_a response enables high-elevation *L. decidua* to transpire up to $\sim 5 \text{ kg m}^{-2} \text{ yr}^{-1}$ more (Table 5). In particular, high-elevation *L. decidua* would benefit from this lower operational temperature at the end of the growing season (Figure 6b). At lower elevations, the adjusted g_s - T_a response was marginally beneficial in preventing water loss during cold periods in the beginning of the growing season (Figure 6e). Potential reasons for high-elevation *L. decidua* to maintain higher transpiration rates at the end of the growing season include the increase of water transport to facilitate higher carbon assimilation (Wieser 2007), or the increased facilitation of nutrient transport (Mayr 2007). More specifically, our results suggest that *L. decidua* employs a more “risky strategy” by sustaining high water conductance under colder conditions, at the cost of losing water at thermal conditions less optimal for photosynthesis (Wieser 2007) and risking freezing damage (Mayr 2007). This type of plasticity could be facilitated by changing enzymatic activity which maintains photosynthetic activity and transpiration under less favourable conditions (see Hikosaka *et al.* 2006). It could also involve a change in osmotic potential to keep stomata open (Badalotti *et al.* 2000). We hypothesize that the differences in plasticity of the two species can be explained by the deciduous life strategy of *L. decidua*, with a shorter vegetative season compared to evergreen species, although sap flow measurements for *P. abies* outside the growing season are needed to fully elucidate absolute differences in annual transpiration.

Alternatively, pioneers, like *L. decidua*, need to deal with a larger range of environmental conditions, demanding higher maintenance respiration and protection against freezing damage.

Both species showed a weaker downregulation of g_s to decreasing R_g at higher elevations (Figure 5e, f). This plasticity of the g_s - R_g response is likely regulated by an osmotic pressure change within the guard cells, facilitated by specific photoreceptors (Buckley & Mott 2013). The slower g_s increase with increasing R_g at higher elevations for both species, as well as incomplete stomatal closure at night, could facilitate a faster response to sunrise, thus extending the daily transpiration activity and counteracting the shorter growing season at these mesic sites (Daley & Phillips 2006). Another possible explanation could be the interplay between R_g and atmospheric CO₂ concentration, where the mechanisms to open the guard cells with increasing light change depending upon the CO₂ concentration (Buckley & Mott 2013; Torgern *et al.* 2014). However, additional measurements are needed to confirm that these patterns are not caused by refilling of xylem and phloem water storage (Zweifel *et al.* 2001; Meinzer *et al.* 2009; Matheny *et al.* 2015).

King *et al.* (2013a) revealed a genetically well-mixed population within the Lötschental, supporting our plasticity hypothesis over adaptation. Yet, transplantation experiments could aid in further testing this hypothesis, as changes in g_s response to environmental drivers might take a considerable amount of time to become apparent (Livingston & Black 1987). Notwithstanding, our results show that models estimating evapotranspiration patterns with generalized g_s response functions might underestimate the transpiration amount at high elevations, and potentially high latitudes. A recent modelling study also pinpointed the importance of plant trait plasticity in explaining the recent increase in forest water use efficiency (Mastrotheodoros *et al.* 2017). Moreover, the vegetation modelling community acknowledges the fundamental role of inter- and intra-specific plant trait variability in the resulting terrestrial carbon, water and energy dynamics and the need for trait-based representation of vegetation functioning (Pavlick *et al.* 2013; Scheiter *et al.* 2013; Fyllas *et al.* 2014; Sakschewski *et al.* 2015; Pappas *et al.* 2016). Finally, if we want to fully grasp the effect of climate change on the hydraulic functioning of different tree species, we should move away from focussing on only one hydraulic mechanism (like g_s) and apply a more holistic approach, including photosynthetic activity, the tree's water storage capacity and wood anatomical structure (e.g., Egea *et al.* 2011; Köcher *et al.* 2013). Such information would improve the parameterization of terrestrial ecosystem models and would result in more constrained predictions of the water, carbon and energy dynamics under changing environmental conditions.

Conflict of Interest Statement

The authors declare that they have no conflict of interest.

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848

Supporting information

Figure S1. Phenological observations of the dates when *Larix decidua* showed 50% coverage of its crown with leaves, during leaf development and senescence.

Figure S2. Non-linear stomatal conductance (g_s) curves fitted against (a) air (T_a) and (b) soil temperature (T_s) scaled to the maximum average site conductance ($g_{s,max}$).

Figure S3. Predawn and midday leaf water potential (ψ_{leaf}) response to soil water potential (ψ_{soil}) for *L. decidua* and *P. abies* trees at N13.

Table S1. Parameters for the pedotransfer functions established for converting θ into ψ_{soil} at two depths per monitoring site.

Table S2. Results for linear mixed-effect models analysing allometric relationships between diameter at breast height (DBH), sapwood area (A_s) and leaf area (A_L) as presented in Figure 1.

Table S3. Results for linear mixed-effect models analysing the delay between sunrise and start of sap flow, as presented in Figure 2. Relative delay time frequency, as the dependent variable, was tested against species and site as independent variables.

Note S1. Calculations of stomatal conductance (g_s) with R code.

Symbol	Description	Unit
D	Vapour pressure deficit	kPa
T_a	Air temperature	°C
T_s	Soil temperature	°C
θ	Volumetric soil water content	%
ψ_{soil}	Soil water potential	MPa
R_g	Solar irradiance	W m ⁻²
RH	Relative humidity	%
g_s	Stomatal conductance (standardized to A_L)	mm s ⁻¹
g_{sap}	Crown conductance (standardized to A_s)	g m ⁻² s ⁻¹ kPa ⁻¹
$g_s/g_{s,\text{max}}$	Stomatal conductance relative to the maximum (99 th quantile)	-
$g_{\text{sap}}/g_{\text{sap},\text{max}}$	Crown conductance relative to the maximum (99 th quantile)	-
F_d	Sap flux density	g cm ⁻² h ⁻¹
W_u	Whole-tree water flux	kg h ⁻¹
ΔT	Temperature difference between heated and unheated sap flow probe	°K
ΔT_{max}	Temperature difference during zero-flow conditions	°K
K	ΔT standardized for ΔT_{max}	-
E	Transpiration	g m ⁻² h ⁻¹
$g_{\text{sap},\text{ref}}$	Reference conductance when $D = 1$ kPa	-
$-\delta$	Slope coefficient of the power function between T_a and g_{sap}	kPa ⁻¹
$g_{\text{sap},\text{int}}$	Intercept of the linear relationship between ψ_{soil} and $g_{\text{sap}}/g_{\text{sap},\text{max}}$	-
A	Slope coefficient of the linear relationship between ψ_{soil} and $g_{\text{sap}}/g_{\text{sap},\text{max}}$	MPa ⁻¹
λ	Latent heat of vaporization	J g ⁻¹
γ	Psychrometric constant	hPa K ⁻¹
ρ	Air density	kg m ⁻³
C_p	Heat capacity of air	J kg ⁻¹ K ⁻¹
A_s	Sapwood area	cm ²
A_L	Leaf area	m ²
DBH	Stem diameter at breast height (1.3 m)	cm

Table 1. Characteristics of trees instrumented with thermal dissipation probes. Age and sapwood area (A_s) were determined using increment core measurements. Additionally, the maximum water flux (W_u) measured during the monitoring period is provided.

Species	Site	Elevation [m a.s.l.]	Tree ID	Age [yr]	DBH [cm]	Height [m]	A_s [cm ²]	Max. W_u [kg h ⁻¹]
<i>Larix decidua</i>	N13	1300	N13Bd_L1	131	29.5	20.1	105	10.8
			N13Bd_L2	128	32.0	18.5	142	2.7
			N13Ad_L4	131	30.8	18.7	125	8.0
	N13W	1300	N13WAd_L1	148	78.0	27.7	464	16.4
			N13WBd_L2	164	89.3	33.3	541	19.4
			N13WBd_L3	134	52.0	25.7	304	9.4
	S16	1600	S16Bd_L1	371	75.2	31.5	629	5.7
			S16Ad_L1	69	38.5	24.5	251	17.3
			S16Ad_L4	69	41.5	23.8	369	8.7
	S19	1900	S19Ad_L1	200	48.0	23.7	300	8.7
			S19Ad_L3	170	35.5	26.3	224	6.5
			S19Bd_L1	326	48.7	22.4	208	6.6
	S22	2200	S22Ad_L1	269	47.0	17.8	292	5.2
			S22Ad_L2	280	55.7	17.2	434	15.7
			S22Ad_L3	295	45.5	16.6	218	7.1
<i>Picea abies</i>	N13	1300	N13Ad_S1	90	30.7	14.5	210	3.0
			N13Ad_S2	93	48.1	19.8	680	17.6
			N13Bd_S3	87	37.0	19.2	473	12.3
	N13W	1300	N13WAd_S1	85	81.0	29.5	1905	49.1
			N13WAd_S2	81	62.8	33.5	1155	23.6
			N13WBd_S3	109	80.7	33.6	1918	31.0
	S16	1600	S16Bd_S4	-	45.3	21.5	257	10.1
			S16Ad_S2	62	38.2	25.3	411	4.8
			S16Bd_S2	461	56.2	23.5	315	5.1
	S19	1900	S19Bd_S3	245	37.2	21.2	353	2.2
			S19Ad_S2	137	34.1	25.0	161	23.5
			S19Bd_S2	229	47.5	24.5	680	4.6

Table 2. Model criteria for the boundary line analysis. Variable conditions are provided for every climatic factor to reduce collinearity. The boundary line is described with non-linear functions by dividing the dataset into bins (segments with a 2% size of the total independent variable range) and a specified quantile was selected per bin (see bin properties). Points where excluded where the bin included less than a specific minimum sample size (see min. n). The quantiles and minimum sample size was increased for θ and ψ_{soil} , due to the larger and unequal spread of the data.

Independent variable	Variable conditions						Bin properties	
	D [kPa]	T_a [°C]	R_g [W m ⁻²]	θ [-]	T_s [°C]	ψ_{soil} [MPa]	Quantile	Min. n
Vapour pressure deficit (D)	-	>10	>300	>0.5	-	-	0.95	5
Air temperature (T_a)	<1.5	<13	>300	>0.5	-	-	0.95	5
Solar irradiance (R_g)	<0.5	>10	<800	>0.5	-	-	0.95	5
Relative extractable water (θ)	<1.5	>10	>300	>0.8	-	-	0.98	15
Soil temperature (T_s)	<1.5	-	>300	>0.5	<11	-	0.95	5
Soil water potential (ψ_{soil})	<1.5	>10	>300	-	-	<-0.01	0.98	15

Table 3. Selected models used within the boundary-line analysis. Models were selected from literature or constructed to provide parameters which can be interpreted (see a and b). A general description of the model is provided in addition to the effect of the individual parameters. When relevant a source is provided.

Formula	Description	a	b
$g_s/g_{s,max-D} = a - bD^{0.5}$	An exponential functions according to Katul <i>et al.</i> (2009).	Asymptote of $g_s/g_{s,max}$ at high D values	Slope
$g_s/g_{s,max-Ta} = 1/(1 + e^{-a(Ta-b)})$	Instead of applying parabolic shaped functions as proposed by Jarvis (1976), due to the collinearity with D and g_s values approaching zero at low temperatures, a Gompertz function that saturates to 1 $g_s/g_{s,max}$ was used.	Slope of the inflection point (IP)	T_a of the inflection point (IP)
$g_s/g_{s,max-Rg} = 1 - e^{-a(Rg-b)}$	An adaptation of the model proposed by Price & Black (1989) which allows for night-time activity.	Slope at the x-intercept ($g_s/g_{s,max} = 0$)	Shift in R_g for the x-intercept ($g_s/g_{s,max} = 0$)
$g_s/g_{s,max-\psi_{soil}} = 1/(1 + a e^{(-\psi_{soil} b)})$	As most response functions are based on θ , a new functions was used to describe ψ_{soil} response which saturated at 1 $g_s/g_{s,max}$.	The point of the y-intercept ($\psi_{soil} = 0$), depending upon the slope	Slope of the inflection point (IP)

Table 4. Non-linear models used within the boundary-line analysis. For each site and species (LD= *Larix decidua* and PA= *Picea abies*) median and standard deviation of a and b parameters are provided, as obtained from the bootstrap resampling ($n = 1000$).

Formula	Spec.	Var.	Site				
			N13	N13W	S16	S19	S22
$g_s/g_{s,max-D} = a - bD^{0.5}$	LD	a	-0.347±0.02	-0.294±0.01	-0.385±0.02	-0.361±0.02	-0.443±0.03
		b	-0.663±0.02	-0.571±0.01	-0.685±0.03	-0.642±0.02	-0.827±0.03
	PA	a	-0.386±0.06	-0.320±0.02	-0.450±0.05	-0.408±0.05	-
		b	-0.743±0.07	-0.657±0.03	-0.805±0.06	-0.764±0.06	-
$g_s/g_{s,max-Ta} = 1/(1 + e^{-a(Ta-b)})$	LD	a	0.916±0.29	1.012±0.38	1.195±0.32	0.733±0.10	0.729±0.09
		b	6.480±0.29	5.246±0.24	5.241±0.24	3.239±0.21	4.173±0.16
	PA	a	0.650±0.29	0.481±0.08	0.602±0.08	0.558±0.06	-
		b	3.399±0.40	3.051±0.38	3.301±0.25	3.426±0.17	-
$g_s/g_{s,max-Rg} = 1 - e^{-a(Rg-b)}$	LD	a	0.012±0.00	0.010±0.00	0.006±0.00	0.003±0.00	0.006±0.00
		b	-12.18±58.68	-7.48±97.69	-50.64±35.99	-115.71±32.25	-85.76±25.93
	PA	a	0.014±0.00	0.015±0.00	0.006±0.00	0.004±0.00	-
		b	9.134±9.09	5.350±9.20	-38.56±25.65	-51.28±23.13	-
$g_s/g_{s,max-\psi_{soil}} = 1/(1 + a e^{(-\psi_{soil} b)})$	LD	a	0.072±0.02	-	-	-	-
		b	3.654±0.39	-	-	-	-
	PA	a	0.142±0.03	-	-	-	-
		b	3.239±0.31	-	-	-	-

Table 5. Modelled transpiration (E) considering alternative response functions for air temperature (T_a), global irradiance (R_g) and vapour pressure deficit (D), compared to site-specific response functions. As an example, if *Larix decidua* g_s -response to T_a for S22 (presented in Figure 5) would be similar to that of N13, then transpiration would have been reduced by $5.1 \text{ kg m}^{-2} \text{ yr}^{-1}$. The annual mean and standard deviation of modelled transpiration are provided for the transpiration seasons of 2012-2015 for *L. decidua* and *Picea abies* growing under climatic conditions for S22, S19 and N13. The transpiration season is defined by the sap flow measurements (see Figure 2).

Species	Site	E [$\text{kg m}^{-2} \text{ yr}^{-1}$]	Effect of alternative response function [$\text{kg m}^{-2} \text{ yr}^{-1}$]		
<i>Larix decidua</i>	S22	63.7 $\pm$ 4.8	T_a (N13) -5.1 $\pm$ 0.7	R_g (N13) -7.3 $\pm$ 0.9	D (N13) -9.6 $\pm$ 1.3
	S19	59.7 $\pm$ 5.4	T_a (N13) -4.6 $\pm$ 0.7	R_g (N13) +0.6 $\pm$ 0.5	D (N13) +4.7 $\pm$ 1.0
	N13	124.8 $\pm$ 12.1	T_a (S22) +3.7 $\pm$ 1.0	R_g (S22) +10.6 $\pm$ 0.9	D (S22) +22.2 $\pm$ 1.8
			T_a (S19) +4.8 $\pm$ 1.3	R_g (S19) -7.1 $\pm$ 2.4	D (S19) -11.3 $\pm$ 0.8
	S19	46.0 $\pm$ 4.0	T_a (N13) +0.4 $\pm$ 0.1	R_g (N13) +0.3 $\pm$ 0.4	D (N13) -0.2 $\pm$ 0.1
	N13	46.6 $\pm$ 6.4	T_a (S19) -0.3 $\pm$ 0.0	R_g (S19) -2.6 $\pm$ 0.6	D (S19) 0.0 $\pm$ 0.1

899 **Figure legends**

900 **Figure 1.** Research site, sampling locations and derived allometric relationships. (a) Location
901 of the Löttschental, trees sampled in the leaf area database and trees of which the sapwood area
902 was measured. (b) Relationship between diameter at breast height (DBH) and sapwood area
903 (A_s) and (c) relationship between projected leaf area (A_L) and modelled A_s (using DBH
904 measurements and the relationship presented in b) for the respective $A_L:A_s$ values. Lines
905 indicate model fits for *Larix decidua* (dotted) and *Picea abies* (solid). Grey areas present the
906 Bayesian credible interval of the fitted function (see Gelman & Hill 2007).

907 **Figure 2.** Seasonal and diurnal variations of transpiration (E) per site (indicated with elevation
908 in m a.s.l. and specific dry or wet growing conditions) and species. The average E per site and
909 species is presented (in $\text{g H}_2\text{O m}^{-2} \text{ leaf area h}^{-1}$), accounting for the delay time of F_d
910 measurements. Weekly means of daily maximum E are shown for *Larix decidua* (a) and *Picea*
911 *abies* (b) for the four years of monitoring to highlight seasonal variation. Additionally, for a
912 drought period in 2015 a snap-shot of hourly E is provided for *L. decidua* (c) and *P. abies* (d).
913 Note that *L. decidua* at the lowest dry site (N13) showed highest E under normal conditions (a),
914 but lowest E during a drought period (c). For every panel the daily mean T_a and ψ_{soil}
915 measurements are provided.

916 **Figure 3.** Dependency of maximum crown conductance (99th quantile $g_{\text{sap,max}}$) on mean
917 growing season air temperature (T_a ; from May to October), measured during the four years of
918 monitoring, for all individuals (dots) and averaged for both species (L = *Larix decidua* and P =
919 *Picea abies*). Days with precipitation >1 mm and mean daily D <0.1 kPa were excluded.

920 **Figure 4.** Daily mean standardized crown conductance ($g_{\text{sap}}/g_{\text{sap,max}}$) for *Larix decidua* and
921 *Picea abies* against D and ψ_{soil} at N13, which was the driest site in the study. The species-
922 specific conductance response to D (a) and ψ_{soil} (b) are provided. Additionally, we show the
923 Gaussian distribution of the fitted parameters using μ (mean) and σ (standard deviation), derived
924 from the linear mixed effect model (using the individual as a random factor), and indicate
925 significant difference with lines ($p < 0.05$; using a bootstrap resampling, with $n = 1000$).

926 **Figure 5.** Response functions of the bootstrap boundary-line analysis for *Larix decidua* and
927 *Picea abies* with standardized stomatal conductance ($g_s/g_{s,\text{max}}$) fitted against (a, b) vapour
928 pressure deficit (D), (c, d) air temperature (T_a), (e, f) solar irradiance (R_g) and (g, h) soil water
929 potential (ψ_{soil}). For T_a (c,d) the inflection points (see the parameter b in Table 3) and for R_g (e,
930 f) the slopes (see parameter a in Table 3) are presented in the inset boxplots, originating from

the 1000 times bootstrap resampling. The mean (μ) curve and the 95% confidence interval (CI) are provided.

Figure 6. Modelled daily transpiration (E) patterns for *Larix decidua* under the climatic conditions of S22 (a-c) and N13 (d-f). Note the different scales of E for the S22 and N13 conditions. Response functions presented in Figure 5 are used to model the site response of E , where the T_a response was site-specific or exchanged with the response function of the site at the opposite end of the elevational transect. For example, for *L. decidua* growing at S22 the g_s -response to T_a would be replaced with the T_a response function observed at N13, resulting in a difference in modelled daily E (highlighted in blue in a and b). The difference in E induced by the replaced T_a response function is presented with ΔE (in $\text{g m}^{-2} \text{d}^{-1}$; purple lines in a and d). Additionally, mean daily T_a is provided (orange) with the dashed line indicating 0°C . To highlight the differences, a snap-shot is provided for the growing season of 2015 for S22 (b) and N13 (c). The modelled E was corrected for phenological development, where we corrected E for absence (0) to full crown development (1) using a phenological development model (c and f).

950 **Figure 2**

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