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Temperature-driven vapor pressure deficit structures forest bryophyte communities across the landscapes

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Abstract

Atmospheric vapor pressure deficit (VPD) controls local plant physiology and global vegetation productivity. However, at ecologically crucial intermediate spatial scales, the processes controlling VPD variability and the role of this variability in forest bryophyte community assembly are little known.

To disentangle processes controlling landscape-scale VPD variability and explore VPD effects on bryophyte community composition and richness, we recorded bryophyte communities and simultaneously measured forest microclimate air temperature and relative humidity across topographically diverse landscape representing bryophyte diversity hotspot in temperate Europe. Based on VPD importance for plant physiology, we hypothesize that VPD can be an important also for bryophyte community assembly and that VPD variability will be jointly driven by saturated and actual vapor pressure across the topographically diverse landscape with contrasting forest types and steep microclimatic gradients.

Contrary to our expectation, VPD variability in the forest understory was dictated by temperature-driven differences in saturated vapor pressure, while actual vapor pressure was surprisingly constant across the landscape. Gradients in bryophyte community composition and species richness followed closely the VPD variability. While mesic forest bryophytes occurred along the whole VPD gradient, azonally occurring and rare species preferred sites with low VPD. In result, low VPD sites represent species-rich microrefugia within the landscape and host regionally abundant mesic bryophytes simultaneously with rare species near their distributional range limits.

Our results showed that VPD variability at ecologically crucial landscape scales is controlled by saturated vapor pressure and consequently by the maximum air temperature. Future climate warming will thus increase evaporative stress and reshuffle VPD-sensitive forest bryophyte communities even in topographically diverse landscapes, which are traditionally considered as microclimatic refugia. Azonally occurring rare bryophyte species concentrated in low VPD sites will be especially vulnerable to the future changes in atmospheric VPD.

1. Introduction

Atmospheric vapor pressure deficit (VPD) is a key driver of plant functioning in terrestrial ecosystems (Grossiord et al., 2020; Ruehr et al., 2014). Higher VPD means higher evaporative stress for plants, which leads to reduced photosynthesis in the short term and drought-induced mortality in the long term (McDowell et al., 2008; Fu et al., 2022). Ongoing climate changes further exacerbate this evaporative stress because higher temperatures lead to an exponential increase in VPD (Lawrence, 2005; Grossiord et al., 2020). Increasing atmospheric VPD already limits

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global vegetation productivity (Yuan et al., 2019; López et al., 2021; Lu et al., 2022) and triggers large-scale forest diebacks (Breshears et al., 2013; Eamus et al., 2013; Williams et al., 2013).

In contrast to VPD effects on local plant physiology and global vegetation functioning, the understanding of the processes that control landscape-scale VPD variability and the effects of this variability on plant community assembly is limited (Novick et al., 2024). Yet this knowledge is crucial for more realistic predictions of climate change impacts on vegetation and the identification of microclimatic refugia (Ashcroft and Gollan, 2013; Davis et al., 2019; Finocchiaro et al., 2024; Ogée et al., 2024). VPD variability across space reflects the complex interplay between spatial patterns in saturated and actual vapor pressures. While saturated vapor pressure (P_{sat}) is controlled solely by air temperature, actual vapor pressure (P_{air}) is influenced by many processes operating at different spatial scales ranging from regional atmospheric circulation and precipitation to local evaporation from soil and water surfaces and plant transpiration (Campbell and Norman, 1998). Yet how these contrasting processes integrate into the resulting VPD variability over the landscape is still unknown.

A deeper understanding of the mechanisms behind landscape-scale VPD variability is particularly important for climate change biology. Scientists predict a temperature increase of up to 4.4 °C by 2100 (IPCC, 2023), which would lead to a more than 40 % increase in VPD for the same atmospheric water vapor content (Will et al., 2013). These changes can also modify VPD variability over the landscape and therefore potentially change the distribution of individual species and alter the composition of plant communities. However, VPD effects on plant distribution and community assembly over the landscape are not sufficiently known.

Among plants, bryophytes are exceptionally sensitive to evaporative stress because they lack roots, lignified water-conducting system, water storage tissues, and active stomata and have a large surface area in proportion to biomass (Rice et al., 2001, Goffinet and Shaw, 2009). Bryophytes transport water passively, mainly through external capillary spaces between tiny parts of their body (Schofield, 1981), and their internal water content is thus a function of the water availability in the surrounding environment (Vanderpoorten and Goffinet, 2009). When this water evaporates, bryophytes can survive in a desiccated state (Proctor, 2000, 2001). Despite this unique bryophyte ability to tolerate desiccation, bryophyte assemblages are potentially highly sensitive to evaporative stress, because desiccation tolerance widely differs among bryophyte species (Hinshiri and Proctor, 1971; Wagner and Titus, 1984, Oliver et al., 2000; Proctor, Ligrone, et al., 2007; Proctor, Oliver, et al., 2007). Yet surprisingly little is known about the VPD effect on bryophyte assemblages in temperate forests (Fenton and Frego, 2005).

Here we combine detailed in-situ forest microclimate measurements with simultaneous bryophyte inventories to provide this missing knowledge. Specifically, we quantified VPD variability over the topographically diverse landscape, identified which processes drive this variability, and explored how landscape-scale VPD variability affects bryophyte community composition and species richness in temperate forests.

2. Material and methods

2.1 Study area

We recorded bryophytes and measured microclimate in the Bohemian Switzerland National Park in the Czech Republic (Fig. 1). The rugged terrain of this sandstone landscape creates a fine-scale mosaic of contrasting habitats with steep microclimatic gradients over short distances (Wild et al., 2013). The elevation within the national park ranges from 125 to 619 m and the mean elevation is 340 m. According to the data from the Tokáň weather station

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(Fig. 1), the mean annual air temperature during the 2011-2019 period was 8.3 °C, and the mean annual precipitation was 765 mm.

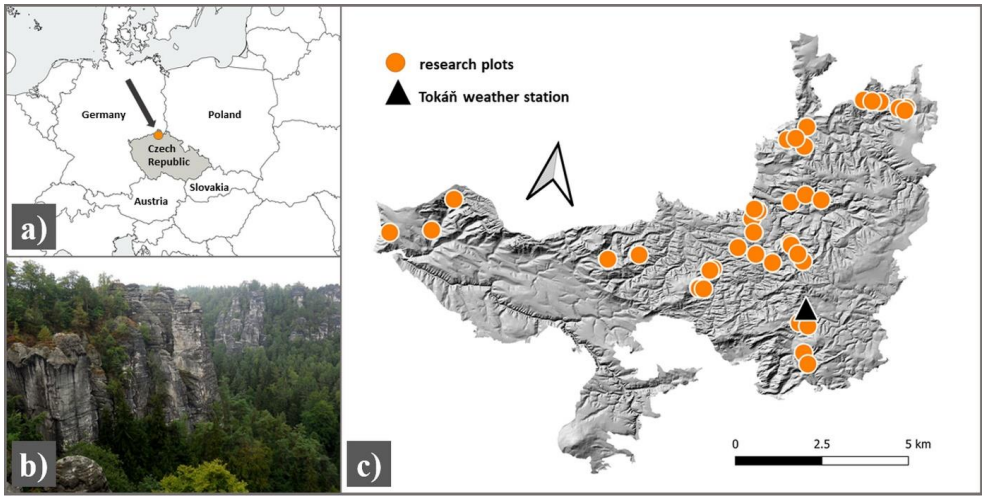

Figure 1: We measured microclimate and simultaneously recorded bryophyte species composition at 38 permanent research plots within the Bohemian Switzerland National Park in Central Europe (a). This forested area has rugged terrain creating steep environmental gradients over short distances (b). The location of the 38 research plots and the Tokáň weather station within the area of the national park (c).

Most of the Bohemian Switzerland is covered with coniferous forests. Historically planted Norway spruce (*Picea abies*) predominates in the valleys and on the plateaus, while patches of semi-natural forests are dominated either by Scots pine (*Pinus sylvestris*) on the upper slopes and rocky ridges or by European beech *(Fagus sylvatica*) on more mesic sites.

The nutrient-poor and strongly acidic soils result in a relatively low diversity of vascular plants, which contrasts with the rich bryophyte flora (Härtel et al., 2007). With more than 300 bryophyte species, the Bohemian Switzerland is a hotspot of bryophyte diversity in Central Europe (Marková, 2008).

The bryophyte flora of the Bohemian Switzerland is dominated by species like *Tetraphis pellucida*, *Bazzania trilobata*, and *Dicranum scoparium*. These dominant floristic elements are enriched by azonal occurrences of (sub)alpine or (sub)montane (e.g., *Hygrobiella laxifolia*, *Geocalyx graveolens*, *Anastrophyllum michauxii*), boreal (e.g., *Dicranum majus*, *Rhytidiadelphus subpinnatus*) and (sub)oceanic (e.g., *Tetrodontium brownianum*, *Plagiothecium undulatum*) species (Härtel et al., 2007; Marková, 2008).

2.2 Field data collection

We recorded bryophyte species composition and measured microclimate on 38 permanent plots within the Bohemian Switzerland National Park (Fig. 1). These plots were selected through stratified-random sampling to capture the main microclimatic gradients within the core zone of the national park. Within each permanent plot, we installed HOBO U23 ProV2 (Onset, USA) microclimatic datalogger protected by a white radiation shield with good ventilation and placed at 1.5 m height on the north side of a tree nearest to the plot center. Each HOBO datalogger measured air temperature (resolution 0.02 °C, accuracy ± 0.21 °C) and relative humidity (resolution 0.05 %, accuracy ± 2.5 %) every 30 minutes from 1 June to 31 August 2022.

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Simultaneously with microclimate measurements, we recorded the presence of all bryophyte species in each research plot following the nomenclature of the Czech national checklist (Kučera et al., 2012). We deliberately sampled bryophytes in a relatively small area (3.14 m^2) to reduce the possible effects of within-plot environmental heterogeneity (Rambo and Muir, 1998; Vanderpoorten and Engels, 2002; Schmalholz and Hylander, 2011).

2.3 Microclimate data processing

First, we checked the microclimatic time series using visual inspection and standard automated procedures implemented in the *myClim* R package (Man et al., 2023). Using checked air temperature and relative humidity data, we calculated the saturated vapor pressure (P_{sat}) following the updated Buck formula (Buck, 1981, 1996):

$$P_{sat} = (1.003 + 4.18 \times 10^{-6} \times 101\ kPa) \times 0.61115 \times e^{((23.036 - t/333.7) * (t/(279.82 + t)))},$$

where t is air temperature [°C].

Then, we calculated the actual vapor pressure (P_{air}) using the Tetens´s formula (Tetens, 1930):

$$P_{air} = P_{sat} \times \left(\frac{rh}{100}\right),$$

where rh is relative humidity [%].

Finally, we calculated atmospheric VPD as the difference between P_{sat} and P_{air} (Jones, 2014).

From the resulting time series, we extracted plot-specific daily maximum VPD and P_{sat} and P_{air} values at the time of daily maximum VPD (Tab. 1).

Table 1: Summary statistics of microclimatic variables measured in 38 forest research plots during summer (June-August 2022). Vapor pressure deficit is the average daily maximum, while saturated and actual vapor pressure are averages of these variables at the time of maximum daily VPD.

	Abbreviation	Mean across all plots	Range of plot means
Saturated vapor pressure	P_{sat}	4.00 kPa	2.61–5.02 kPa
Actual vapor pressure	P_{air}	1.90 kPa	1.75–2.08 kPa
Vapor pressure deficit	VPD	2.09 kPa	0.62–3.17 kPa

2.4 Data analysis

2.4.1 Spatial VPD variability

To quantify spatial variability in daily VPD, P_{sat} and P_{air}, we calculated the standard deviation (SD) of the daily maximum VPD and corresponding P_{sat} and P_{air} values and averaged these daily SD values over the study period as an overall measure of spatial variability for each microclimatic variable.

To disentangle the contribution of P_{sat} and P_{air} to the VPD variability, we performed variation partitioning (Legendre, 2008) based on a multiple linear regression model with the average daily maximum VPD as the response variable and the average daily values of P_{sat} and P_{air} at the time of daily maximum VPD as the predictors.

2.4.2 Bryophyte communities

We explored the relationship between atmospheric VPD and bryophyte communities through three steps. First, we quantified the VPD link to species richness, then, we explored the VPD, $P_{sat,}$ and P_{air} relationship to main gradients in community composition and finally, we directly tested VPD effects on species composition.

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To quantify the relationship between the VPD and species richness expressed as a number of bryophyte species recorded in the plot, we used a generalized additive model (GAM) fitted with the R package *mgcv* 1.9.1 (Wood, 2011). We used GAM with Poisson distribution, log link function, and smooth terms fitted by thin plate regression splines without null space penalization and smoothing parameter estimation using restricted maximum likelihood. To explore the main gradients in the bryophyte community composition, we used non-metric multidimensional scaling (NMDS) based on the Sørensen dissimilarity. We calculated two-dimensional NMDS with the weak treatment of ties, a maximum of 500 random starts, and 999 iterations in each NMDS run using *metaMDS* function from the *vegan* R package version 2.6-4 (Oksanen et al., 2022). To maximize variance along the first ordination axis, we centered and rotated the resulting two-dimensional configuration with principal component analysis.

To explore whether main compositional gradients correlate with microclimate variables, we passively projected gradients in VPD, P_{sat} and P_{air} into the NMDS ordination space and tested the significance of the fit with 999 random permutations using the *envfit* function from *vegan* R package (Oksanen et al., 2022). Finally, we projected bryophyte species richness gradients into the NMDS ordination space using a generalized additive model fitted through *ordisurf* function from *vegan* R package (Oksanen et al., 2022).

To directly test the effect of the average daily maximum VPD on bryophyte species composition, we used distance-based redundancy analysis (db-RDA) (McArdle and Anderson, 2001). As a response variable, we used two community dissimilarity matrices, each reflecting different aspects of community composition. First, we used a community dissimilarity matrix based on the Sørensen index, which expresses differences in species composition including differences in species richness. Second, we used the Simpson index, which expresses species turnover independent of the species richness differences (Lennon et al., 2001). To assess the statistical significance of the VPD effect, we used a permutation test with 999 random permutations (Legendre et al., 2011).

We used R version 4.4.0 (R Core Team 2024) for complete data analysis and figure preparation. For the colour scheme of Fig. 2 and Fig. 4, we used the R package *scico* 1.5.0 (Pedersen and Crameri, 2023).

3. Results

3.1 VPD variability

VPD in the forest understory was highly variable across the landscape, Fig. 2. The VPD values measured every 30 minutes during summer months ranged from 0 kPa to 8.83 kPa with an overall mean of 0.85 kPa. The overall average daily maximum VPD was 2.09 kPa and ranged from 0.62 to 3.17 kPa among the plots (Tab. 1 and Appendix A, Fig. A1 a Fig. A2).

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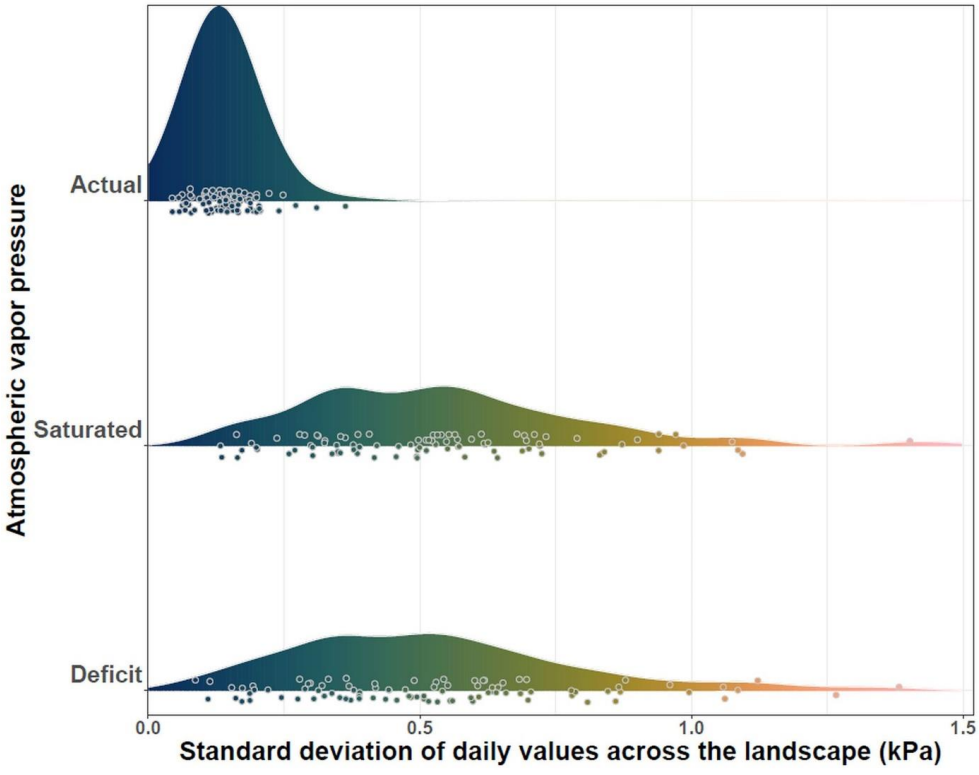

Figure 2: Spatial variability of VPD and its components – saturated and actual atmospheric vapor pressures. Each data point shows the standard deviation of the daily values simultaneously measured at 38 forest plots, and density plots summarize this spatial variability over the summer season. The individual data points were slightly jittered for better visibility.

The spatial variability of P_{sat} (average daily SD = 0.55 kPa) was almost four times higher than the spatial variability of P_{air} (SD = 0.14 kPa). Saturated vapor pressure was also the dominant driver of the VPD variability across the landscape (Fig. 3) because P_{sat} explained 97 % of VPD variability, while P_{air} explained only 3 %.

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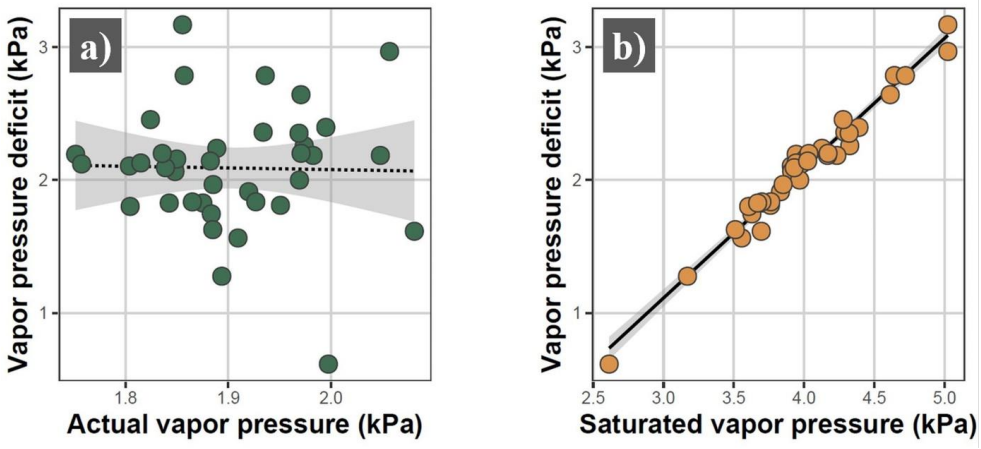

Figure 3: Atmospheric vapor pressure deficit (VPD) at 38 forest plots sampled over topographically diverse landscape was dictated by temperature-dependent saturated vapor pressure (b), while actual vapor pressure was not related to local VPD (a). Each dot represents the average daily maximum VPD and the corresponding average saturated and actual vapor pressure during the summer season.

3.2 Bryophyte communities

In total, we recorded 39 bryophyte species: 14 liverworts and 25 mosses (Appendix C, Tab. C1). The average number of species per plot was 8, minimum 1 and maximum 21. The most frequent species were *Dicranum scoparium*, *Leucobryum juniperoideum* and *Hypnum cupressiforme*.

Main patterns in community composition and species richness reflected VPD variability (Fig. 4). While the gradients in VPD and P_{sat} were significantly related to the main patterns in community composition (VPD: R^2 = 0.37, p = 0.001; P_{sat}: R^2 = 0.34, p = 0.001), the gradient in P_{air} was not (R^2 = 0.09, p = 0.17). The number of bryophyte species was higher in plots with low VPD and declined with increasing VPD (GAM: explained deviance D^2 = 31.2 %, χ^2 = 23.37, p = 0.0008).

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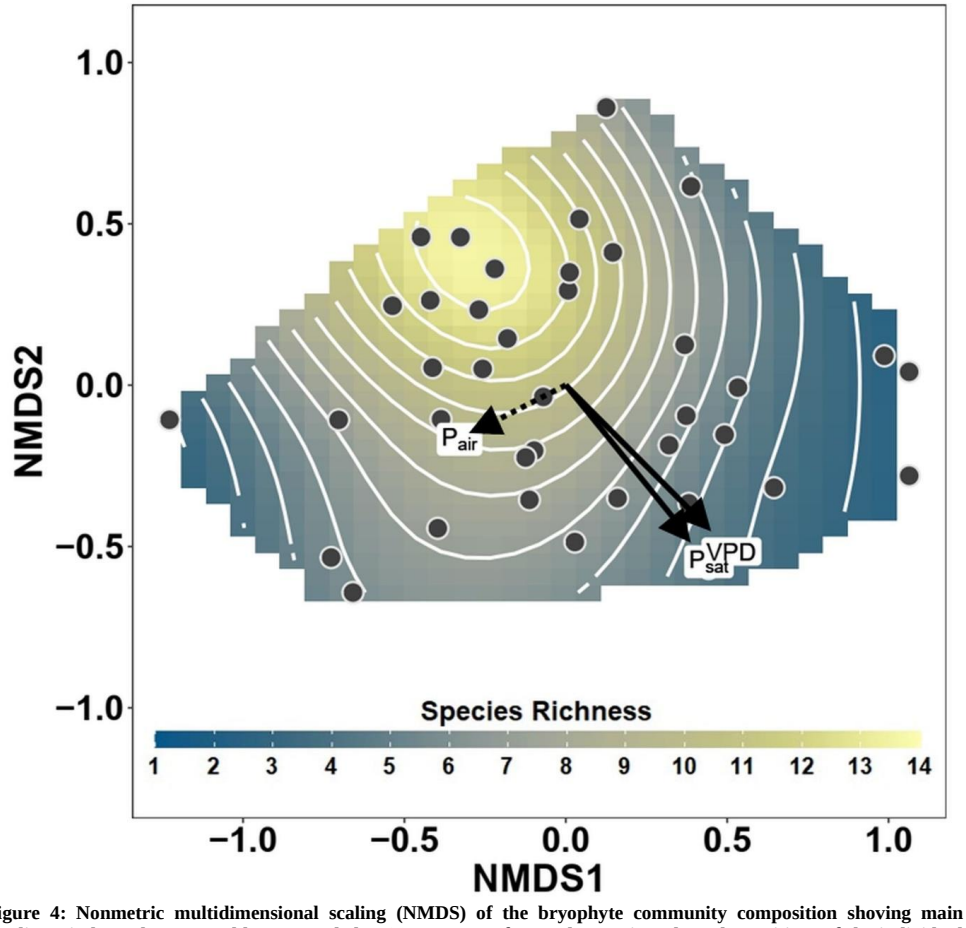

Figure 4: Nonmetric multidimensional scaling (NMDS) of the bryophyte community composition shoving main gradients in bryophyte assemblages sampled at 38 temperate forest plots. Points show the positions of the individual plots within the NMDS ordination space, and the vectors show the gradients in the average daily maximum VPD and corresponding saturated and actual vapor pressures. The smooth surface and associated contours show the pattern in species richness (number of species per plot) fitted into the NMDS ordination space with a generalized additive model.

Atmospheric VPD was a significant predictor of the community composition of forest bryophytes. The average daily maximum VPD explained 10.95 % of the variation in species composition expressed with the Sørensen index (pseudo-F = 4.43, p = 0.001) and 13.52 % of the variation in species composition expressed with the Simpson index (pseudo-F = 5.63, p = 0.004).

Small liverworts (e.g. *Riccardia multifida*, *Lophozia ventricosa*) and hygrophilous bryophytes (e.g. *Polytrichum commune*, *Bazzania trilobata*), as well as boreal (e.g. *Dicranum majus*) and (sub)oceanic (e.g. *Mylia taylorii*, *Plagiothecium undulatum*) species preferred plots with low atmospheric VPD (Fig. 5). In contrast, mesic species like *Hypnum cupressiforme*, *Polytrichum formosum* or *Dicranum scoparium* occurred also in plots with higher atmospheric VPD.

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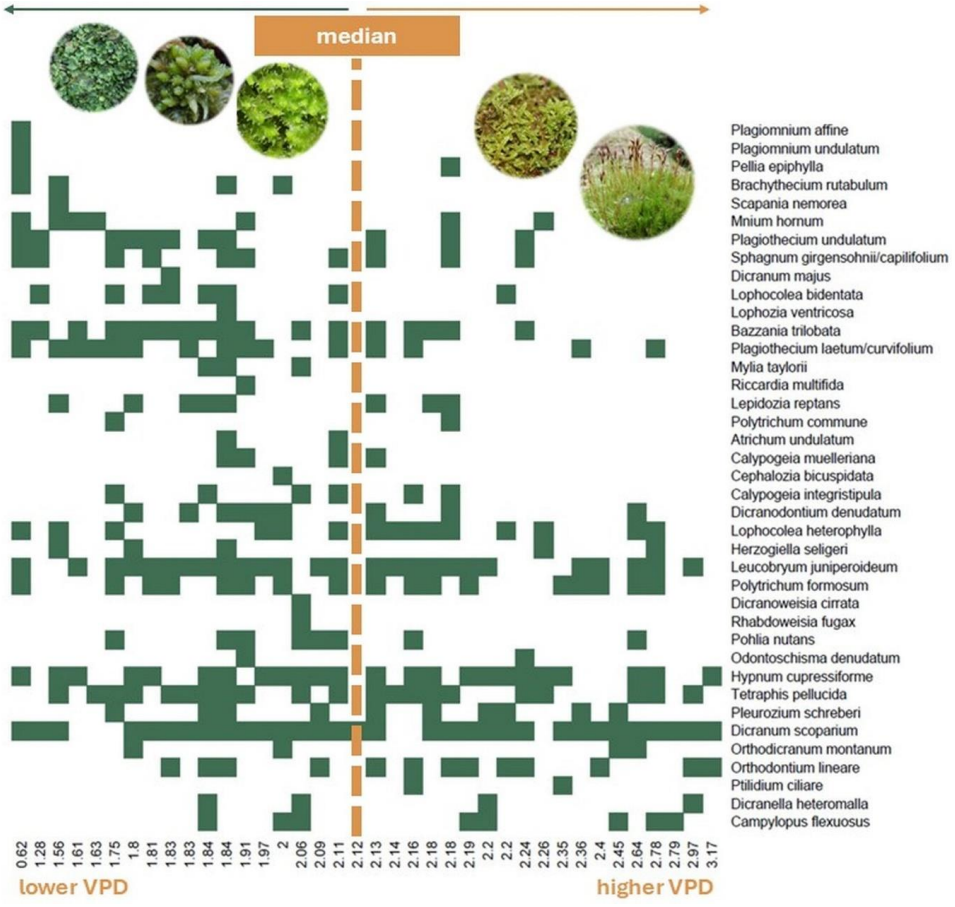

Figure 5: Occurrences of all recorded bryophyte species along the gradient of the average daily maximum VPD measured at 38 forest plots. Plots are sorted from the lowest to highest VPD and each filled square shows the presence of the focal species within the plot. While rare and azonally occurring species prefer sites with low VPD, mesic species occur along the whole VPD gradient.

4. Discussion

Our findings have important implications both for theoretical and applied ecology. First, the variation in VPD over the landscape was controlled by maximum air temperature. Therefore, these two microclimatic variables are tightly coupled at biologically relevant scales, and their effects are hard to disentangle with observational data. Maximum temperatures were identified as a key driver of bryophyte and vascular plant species distribution in temperate forests (Macek et al., 2019; Man et al., 2022). Unfortunately, these studies did not measure VPD. Considering our results, the importance of maximum temperature does not necessarily stem from its direct effects on plant ecophysiology, but more likely from strong temperature control of VPD variability over the landscape. Nevertheless, this new hypothesis needs further testing.

Second, our results imply that it is possible to estimate VPD from local microclimate air temperature measurements combined with non-local measurements of air relative humidity, for example from a nearby weather station. While the general applicability of this approach should be further tested in various environmental settings and across

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different vegetation types, our findings suggest that local VPD can be reasonably estimated (Appendix B, Fig. B1). This finding thus opens exciting possibilities for further research as local temperature measurements are increasingly available all over the world (Lembrechts et al., 2020).

4.1 VPD variability across the landscape

Large spatial variability in atmospheric VPD structured forest bryophyte communities across the landscape. Interestingly, VPD variation was driven by temperature-controlled P_{sat}, while P_{act} was relatively constant across the landscape. This finding is important, as the actual vapor pressure should also be variable across the landscape (Johnston et al., 2025, Ogeé et al. 2024). However, our findings suggest that the local and spatially highly heterogeneous processes like evaporation from soil and water surfaces and plant transpiration do not contribute much to the landscape-scale variation in VPD.

Microclimate variation over the landscape, crucial for community ecology, is largely dictated by land-surface topography (Dobrowski, 2011). Land-surface topography controls also maximum air temperatures in the forest understory (Macek et al., 2019) and therefore spatial variability in saturation vapor pressure. However, we were surprised that the highly localized processes like evapotranspiration did not contribute much to the spatial variability in absolute air humidity despite our study area with extremely rugged topography and contrasting forest vegetation types. Therefore, spatial variability in absolute air humidity seems to be determined mostly by processes operating at much larger scales like atmospheric circulation and precipitation patterns (Campbell and Norman, 1998).

Given the growing recognition of VPD importance for many ecosystem processes, plant distribution, and community assembly (Grossiord et al., 2020; Kopecký et al., 2024; Novick et al., 2024), the approach we developed here to disentangle the contribution of saturated versus actual vapor pressure can provide new insights into the drivers of VPD variability across spatial and temporal scales. So far, the knowledge of the relative importance of saturated versus actual vapor pressure is limited, therefore it is difficult to compare our results with other studies. Nevertheless, a comparison of the drivers of VPD variability across agricultural fields in Germany supports our conclusion (Wörlen et al., 1999).

4.2 VPD effects on bryophytes

Bryophytes inevitably lose water when exposed to the air with non-zero VPD (Hinshiri and Proctor, 1971; Busby and Whitfield, 1978). At full turgor, bryophyte cells have osmotic potential rarely more negative than -2 MPa (Proctor, 2000). An osmotic potential of -1.36 MPa is in equilibrium with air at 20 °C and 99% relative humidity (i.e. VPD < 0.03 kPa). If the temperature remains at 20 °C, but the relative humidity drops to 90 %, the water potential outside the bryophyte body decreases to -14 MPa (Proctor, 2000) and bryophytes start to lose water. To maintain full turgor and normal cell function, bryophytes thus need free liquid water close to the cells. However, this external water completely evaporates within 45-50 minutes if atmospheric VPD reaches 1.22 kPa (León-Vargas et al., 2006). Once the external water evaporates, bryophyte cells rapidly lose turgor, metabolic activity slows down, and carbon fixation decreases. In our study region, such favorable conditions without evaporative stress and VPD lower than 0.03 kPa occurred only 9 % of the measurement time.

In contrast to vascular plants, bryophytes tolerate desiccation and become metabolically inactive in the absence of water (Proctor, 2000). When conditions improve, bryophytes quickly reactivate physiological processes such as

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respiration, photosynthesis, cell cycle, or normal cytoskeleton function (Proctor, Ligrone, et al., 2007; Proctor, Oliver, et al., 2007). However, this reactivation requires a lot of energy, for example to produce specific repair proteins (Oliver and Bewley, 1984; Zeng et al., 2002) or to maintain the integrity and normal function of cell organelles and membranes (Platt et al., 1994). Prolonged periods without evaporative stress are therefore key for bryophyte growth and long-term survival (Proctor, Oliver, et al., 2007).

Large VPD variability over the landscape creates fine-scaled mosaic of sites with widely different evaporative stress and this environmental template structured bryophyte communities. Regionally rare species preferred sites with low VPD. These species – otherwise typical for (sub)montane, boreal, or (sub)oceanic regions – are approaching their distributional limits within our study area (Hill and Preston, 1998). For these species, sites with low VPD serve as microclimatic refugia within an otherwise unsuitable landscape matrix. In contrast, widespread mesic bryophytes occurred along the whole VPD gradient. Sites with low atmospheric VPD, hosting simultaneously rare as well as widespread bryophytes, thus represent hotspots of bryophyte diversity in the landscape.

With climate warming, areas with low VPD will likely shrink, and their bryophyte diversity will become more vulnerable (Pardow and Lakatos, 2013). Moreover, the increasingly frequent and severe canopy disturbances will likely increase understory temperatures and therefore also VPD (Wolf et al., 2021; Máliš et al., 2023). Our results suggest that such changes will reshuffle bryophyte communities, supporting widespread mesic bryophytes at the expense of regionally rare species near their distributional limits.

4.3 Disentangling atmospheric VPD and temperature

The close coupling between VPD and maximum temperature across the landscape clearly shows the need – and simultaneously the difficulty – of disentangling the influences of VPD and temperature on plant communities. While temperature affects basic life functions of bryophytes like photosynthesis, respiration (Dilks and Proctor, 1975), and growth (Furness and Grime, 1982), bryophytes thrive in a wide range of temperatures – from less than -30 °C (Dilks and Proctor, 1975) to over 40 °C in a dry state (Hearnshaw and Proctor, 1982). For most bryophytes, the optimal growth temperature ranges from 12 to 25 °C (Vanderpoorten and Goffinet, 2009). However, many bryophyte species grow even at temperatures around 5 °C (Dilks and Proctor, 1975), and some can even photosynthesize at temperatures below 0 °C (Lösch et al., 1983). Therefore, temperature is hardly a direct limiting factor of bryophyte distribution and community composition in temperate regions.

Several studies of vascular plants have attempted to distinguish the independent effect of VPD from other microclimatic factors affecting plant functioning and distribution (Eamus et al., 2013; Denham et al., 2021; Flo et al., 2022; Fu et al., 2022; Kopecký et al., 2024), highlighting the critical importance of VPD (Novick et al., 2016; Schönbeck et al., 2022). Unfortunately, no physiological studies addressed the independent effects of VPD on bryophytes, despite clear indications that VPD plays a key role (Busby et al., 1978; Sonnleitner et al., 2009). So far, studies of bryophyte physiology concentrated on desiccation tolerance (Morales-Sánchez et al., 2022). While desiccation tolerance is an adaptation to cope with the external lack of water, the ultimate driver of desiccation is atmospheric VPD. A deeper focus on atmospheric VPD can therefore bring a new insight into bryophyte ecology and distribution.

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5. Conclusions

Atmospheric VPD controls community composition and richness of bryophyte assemblages in temperate forest understory. Even across the landscape with extremely rugged terrain, spatial variability in atmospheric VPD was controlled by temperature-dependent saturated vapor pressure. Maximum air temperature and VPD are thus tightly coupled at biologically relevant scales and their effects are hard to disentangle. Nevertheless, both ecological and physiological studies suggest that bryophytes in temperate zone are not directly limited by temperature (Dilks and Proctor, 1975; Furness and Grime, 1982) but rather by evaporative stress represented by VPD (Busby et al., 1978; Dilks and Proctor, 1979). With climate warming, the tight coupling between VPD and local air temperature will cause nonlinear increases in VPD-driven evaporative stress, which will subsequently reshuffle bryophyte community composition and decrease species richness. Especially vulnerable will be azonally occurring bryophyte species concentrated in microclimatic refugia with low VPD.

Appendix A

VPD variability over the summer season

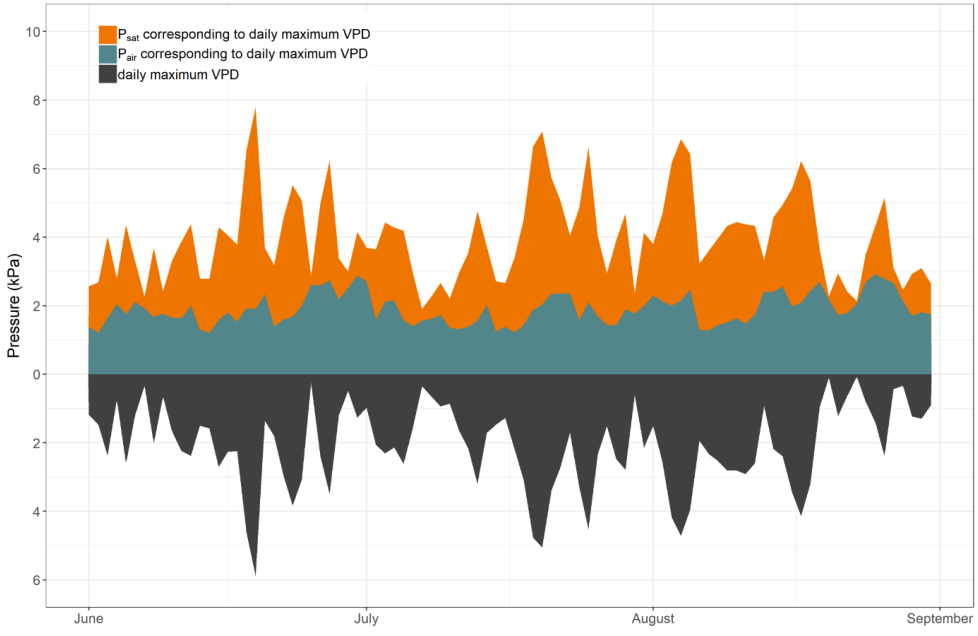

Figure A1: Daily values of maximum vapor pressure deficit (VPD) and corresponding values of saturated (P_{sat}) and actual (P_{air}) vapor pressures, averaged over 38 permanent vegetation plots during June-August 2022.

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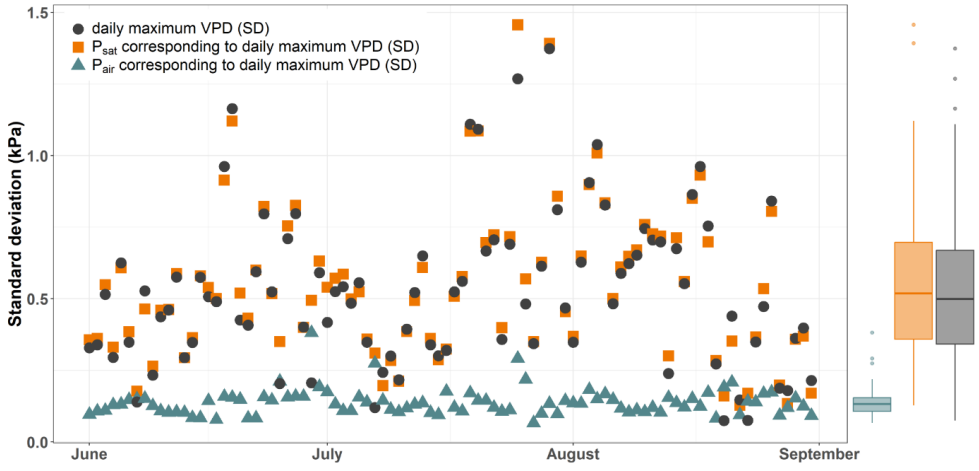

Figure A2: Spatial variability of VPD (black circles) is tightly coupled with the spatial variability in P_{sat} (orange squares) but not with P_{air} (blue triangles). Each data point shows the standard deviation of the daily value measured at 38 study sites. Marginal boxplots summarize spatial variability (daily standard deviations) during the growing season (June-August 2022).

Appendix B

VPD estimate from in-situ air temperature and regional air humidity

Based on our results, we speculated that local atmospheric VPD can be reasonably estimated using the in-situ air temperature measurements paired with relative air humidity measurements representative for the whole region (and therefore the same for all plots situated within that region).

To explore this idea, we estimated the average daily maximum atmospheric VPD using in-situ measured air temperature (HOBO U23 ProV2 dataloggers in 1.5 m height) and relative air humidity measured in the Tokáň weather station located in the study area (Fig. 1).

While the measured and estimated VPD were closely correlated (Pearson r = 0.98), estimated VPD tended to be higher than in-situ measured VPD (Fig. B1).

Therefore, we conclude that the relative position of the site on the VPD gradient can be reasonably estimated from in-situ microclimate temperature measurements paired with regional relative air humidity measurements. However, this approach does not provide a reliable estimate of local atmospheric VPD, especially on sites with locally higher air humidity.

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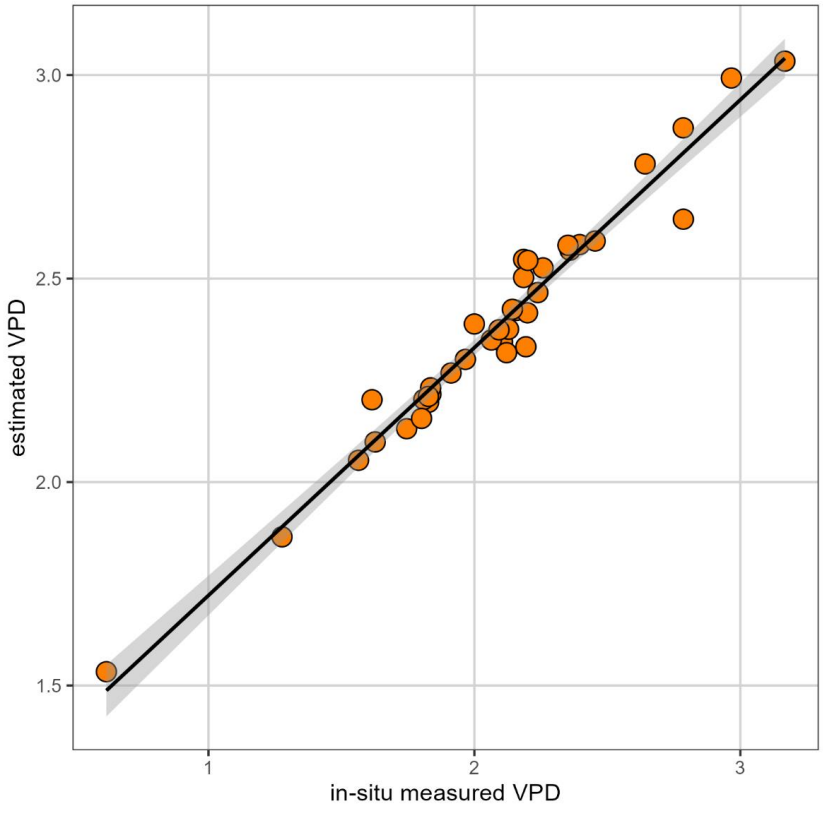

Figure B1: Relationship between in-situ measured average daily maximum VPD and average daily maximum VPD estimated from in-situ measured air temperature and relative air humidity measured in regional weather station (June-August 2022). While the measured and estimated VPD are closely correlated (Pearson r = 0.98), estimated VPD tends to be higher than in-situ measured VPD, likely because of locally higher air humidity in topographically sheltered sites near valley bottoms.

Appendix C

List of bryophyte species, their occurrence and biogeographical affinity

Table C1: Complete species list of bryophyte species recorded at 38 study plots. Biogeographical categories follow Hill and Preston (1998).

	Species name	Occurence	Taxonomic group	Major biome	Eastern limit
1	*Dicranum scoparium*	32	moss	Wide-boreal	Circumpolar
2	*Leucobryum juniperoideum*	26	moss	Temperate	European
3	*Hypnum cupressiforme*	24	moss	Wide-temperate	Circumpolar
4	*Tetraphis pellucida*	21	moss	Boreo-temperate	Circumpolar
5	*Bazzania trilobata*	18	liverwort	Temperate	Suboceanic

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6	*Polytrichum formosum*	17	moss	Boreo-temperate	Circumpolar
7	*Lophocolea heterophylla*	15	liverwort	Temperate	Circumpolar
8	*Plagiothecium laetum/curvifolium*	15	moss	Boreal-montane/Temperate	Circumpolar/European
9	*Orthodontium lineare*	13	moss	Temperate	European
10	*Plagiothecium undulatum*	11	moss	Boreo-temperate	Suboceanic
11	*Pleurozium schreberi*	10	moss	Boreo-temperate	Circumpolar
12	*Sphagnum girgensohnii/capillifolium*	10	moss	Boreo-arctic Montane/Boreo-temperate	Circumpolar
13	*Dicranodontium denudatum*	9	moss	Boreal-montane	European
14	*Campylopus flexuosus*	8	moss	Temperate	Suboceanic
15	*Lepidozia reptans*	8	liverwort	Boreo-temperate	Circumpolar
16	*Lophocolea bidentata*	8	liverwort	Temperate	European
17	*Pohlia nutans*	8	moss	Wide-boreal	Circumpolar
18	*Mnium hornum*	7	moss	Temperate	European
19	*Calypogeia integristipula*	6	liverwort	Boreo-temperate	Circumpolar
20	*Herzogiella seligeri*	5	moss	Boreo-temperate	European
21	*Brachythecium rutabulum*	4	moss	Temperate	European
22	*Calypogeia mulleriana*	4	liverwort	Boreo-temperate	Circumpolar
23	*Dicranella heteromalla*	4	moss	Boreo-temperate	Circumpolar
24	*Orthodicranum montanum*	4	moss	Boreo-temperate	Circumpolar
25	*Mylia taylorii*	3	liverwort	Boreal-montane	Suboceanic
26	*Atrichum undulatum*	2	moss	Boreo-temperate	Circumpolar
27	*Dicranum majus*	2	moss	Boreo-temperate	Circumpolar
28	*Odontoschisma denudatum*	2	liverwort	Boreo-temperate	European
29	*Pellia epiphylla*	2	liverwort	Boreo-temperate	Circumpolar
30	*Polytrichum commune*	2	moss	Wide-boreal	Circumpolar
31	*Ptilidium ciliare*	2	liverwort	Boreo-arctic Montane	Circumpolar
32	*Cephalozia bicuspidata*	1	liverwort	Boreo-temperate	Circumpolar
33	*Dicranoweisia cirrata*	1	moss	Temperate	European
34	*Lophozia ventricosa*	1	liverwort	Boreo-temperate	European
35	*Plagiomnium affine*	1	moss	Temperate	European
36	*Plagiomnium undulatum*	1	moss	Temperate	European
37	*Rhabdoweisia fugax*	1	moss	Boreal-montane	European
38	*Riccardia multifida*	1	liverwort	Boreo-temperate	Circumpolar
39	*Scapania nemorea*	1	liverwort	Boreo-temperate	European

*Data availability***.** The data supporting the findings of this study are currently provided for peer review on GitHub public repository (https://doi.org/10.5281/zenodo.14989898).

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Competing interest. The authors declare that they have no conflict of interest.

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