Diversity comes at a cost: multifaceted diversity reduces plant community stability in peatlands

Heikel Balti (https://orcid.org/0009-0006-2283-6767)[1]
Alexandre Buttler (https://orcid.org/0000-0001-5900-4573)[2, 3]
Lise Pinault (https://orcid.org/0000-0002-6971-0823)[1]
Guillaume Bertrand (https://orcid.org/0000-0001-5927-168X)[4]
Philippe Binet (https://orcid.org/0000-0003-2272-618X)[4]
Daniel Gilbert (https://orcid.org/0000-0001-9956-345X)[4]
Geneviève Magnon [5]
Pierre Agnola [5]
Arnaud Mouly (https://orcid.org/0009-0007-8127-6728)[1]*
Cyrille Violle (https://orcid.org/0000-0002-2471-9226)[6]*

*These authors contributed equally to this work (alphabetical order)

[1] Université Marie et Louis Pasteur, CNRS, Chrono-environnement (UMR 6249), F-25000 Besançon, France
[2] Ecole Polytechnique Fédérale de Lausanne (EPFL), School of Architecture, Civil and Environmental Engineering (ENAC), Laboratory of Ecological Systems (ECOS), Lausanne, Switzerland
[3] Swiss Federal Institute for Forest Snow and Landscape Research (WSL), Lausanne, Switzerland
[4] Université Marie et Louis Pasteur, CNRS, Chrono-environnement (UMR 6249), F-25200 Montbéliard, France
[5] EPAGE Haut-Doubs Haute-Loue, France
[6] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

Correspondence

Heikel Balti, Université Marie et Louis Pasteur, CNRS, Chrono-environnement (UMR 6249), F-25000 Besançon, France
Email: heikel.balti.research@gmail.com

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Author contributions

Heikel Balti: Conceptualization, Methodology, Formal analysis, Data curation, Writing - Original Draft, Writing - Review & Editing, Visualization. **Alexandre Buttler**: Methodology, Investigation, Data curation, Writing - Review & Editing. **Lise Pinault**: Visualization, Writing - Review & Editing. **Guillaume Bertrand**: Resources, Writing - Review & Editing. **Philippe Binet**: Investigation, Writing - Review & Editing. **Daniel Gilbert**: Methodology, Resources, Writing - Review & Editing. **Geneviève Magnon**: Resources, Writing - Review & Editing. **Pierre Agnola**: Resources, Writing - Review & Editing. **Arnaud Mouly**: Conceptualization, Methodology, Investigation, Data curation, Supervision, Writing - Review & Editing. **Cyrille Violle**: Conceptualization, Methodology, Validation, Supervision, Writing - Review & Editing. All authors contributed to the drafts and gave final approval for publication.

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The authors report no conflicts of interest in this work.

Data availability statement

Upon acceptance, the data and code supporting this study will be deposited in a public repository providing a DOI.

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Abstract

1. **Aim**: Understanding how ecological stability relates to diversity is of crucial importance under global change. Greater biodiversity is expected to stabilize aggregate community properties through compensatory dynamics, yet diversity-stability relationships can vary across ecosystems, particularly in wetlands where strong abiotic filters shape community assembly and temporal dynamics. We examined how multiple facets of diversity (taxonomic, functional, and phylogenetic) and functional trait identity relate to temporal stability (invariability) and species asynchrony in peatland vegetation.
2. **Location**: Forbonnet peatland, Jura Mountains, northeastern France.
3. **Methods**: We used a 17-year field experiment in a montane peatland complex spanning a bog and a transitional poor fen, combining passive open-top chamber warming with natural hydrological contrasts.
4. **Results**: Water table depth was the dominant environmental filter of plant communities, explaining 46 % of total compositional variance, whereas experimental warming had no detectable effect. Community temporal stability and species asynchrony were higher under drier conditions (deeper water table), consistent with moisture-driven constraints on peatland vegetation dynamics. Contrary to insurance hypothesis predictions, temporal stability decreased with multiple biodiversity facets, particularly phylogenetic diversity and species richness, but increased with deeper-rooted plant strategies and functional redundancy, after controlling for experimental conditions. Species asynchrony was largely unrelated to biodiversity, except for functional redundancy, which was negatively associated with asynchrony. The stability-asynchrony association weakened substantially after controlling for hydrology.

5. **Conclusions**: Our results suggest that in peatlands, hydrology simultaneously structures biodiversity patterns, temporal stability and species asynchrony, yielding negative diversity-stability relationships that contradict classical insurance hypothesis predictions. Stability arises primarily from hydrological constraints, with limited contribution from compensatory dynamics among plant species. In strongly constrained, species-poor ecosystems, conservation may therefore prioritize maintaining or restoring the key abiotic conditions that favor functionally adapted communities over increasing diversity to sustain stable ecosystem functioning under global change.

Keywords: community temporal stability, diversity-stability relationships, experimental warming, global change ecology, mires, peatland vegetation, plant functional traits, plant population and community dynamics, species asynchrony, wetland ecology

1. INTRODUCTION

The diversity-stability relationships remain one of the most debated topics in ecology (McCann 2000; Polazzo et al. 2025). Empirical studies have revealed a range of associations between different facets of diversity and ecological stability, including positive, neutral and negative associations (Pennekamp et al. 2018). The diversity-stability relationships debate is even more important in the context of global change, especially in sensitive ecosystems such as peatlands, where community trajectories are tightly contingent on environmental conditions (Buttler et al. 2023; Hautier et al. 2015). Long-term *in-situ* experimental approaches provide an ideal framework for disentangling these dynamics and understanding how different facets of diversity are associated with temporal stability (Zhang et al. 2026).

How ecological stability relates to diversity has been an ongoing debate in the field of ecology since the 1950s (Elton 1958; Ives and Carpenter 2007; Michel Loreau and de Mazancourt 2013; May 1973; McCann 2000; Pimm 1984; Polazzo et al. 2025). Positive relationships were first considered the rule, in which diverse ecosystems should be more stable than simpler ones (Elton 1958). However, conflicting stability-diversity associations have been reported (Huang et al. 2026; Pennekamp et al. 2018; Polazzo et al. 2025), with evidence of positive (Frank and McNaughton 1991; Liang et al. 2022; Rodrigues et al. 2025), neutral (Ives and Carpenter 2007; Z. Xu et al. 2015), or negative relationships (Pan et al. 2026; Pfisterer and Schmid 2002). Several mechanisms may explain stability and its relationships to diversity. Under the insurance hypothesis, it is classically expected that greater diversity promotes stability by increasing asynchrony among species (i.e., compensatory dynamics), which in turn produces portfolio effects that mitigate fluctuations and reduce the total variance in the community (Hector et al. 2010; Lisner et al. 2024; M. Loreau et al. 2021; Q. Xu et al. 2021, 202; Yachi and Loreau 1999). In this framework, species asynchrony is considered to be the key mechanism through which diversity increases community stability (Craven et al. 2018; Gross et al. 2014; Michel Loreau and de Mazancourt 2013; Valencia et al. 2020). Despite decades of research, the relationships between community stability and the various facets of diversity remain unpredictable, even though understanding the relationships is critically important in vulnerable ecosystems subject to multiple pressures (Hautier et al. 2015).

The variability in the relationships between diversity and stability partly stems from taking a one-dimensional approach to diversity, in which researchers often consider diversity solely through the lens of species richness. However, species richness is a limited proxy for diversity (Fletcher et al. 2025; Hillebrand et al. 2018). Diversity is inherently multifaceted, and ecological stability itself encompasses multiple dimensions (I. Donohue et al. 2016; Kéfi et al. 2019); here, we focus on temporal stability (invariability or constancy) of aggregate community properties such as cover or biomass (Y. Meng et al. 2023; Valencia et al. 2020; Zhao et al. 2022). Several indicators of composition, structure and functions might have different relationships with stability (Ives and Carpenter 2007), and can stabilize communities through different mechanisms and respond differentially to environmental stress and constraints (Naeem et al. 2016). Among these mechanisms, species richness acts through statistical averaging (i.e., portfolio effect), functional diversity reflects differential trait responses to environmental variation and phylogenetic diversity captures evolutionary constraints on responses to environmental variations (Cadotte et al. 2012; Craven et al. 2018; De Bello et al. 2021; Flynn et al. 2011; Liu et al. 2025). From a trait-based perspective (Violle et al. 2007), a community can be characterized by its mean trait values (i.e., functional identity), which reflect the dominant strategy, as well as its dispersion of trait values around this mean (i.e., functional diversity), which reflects the range of strategies (Enquist et al. 2015). These two components of the functional structure of a community can show distinct relationships with stability (Craven et al. 2018; Liu et al. 2025). Hence, examining both multifaceted diversity and the functional composition of communities (Garnier et al. 2016) is essential for disentangling the drivers of the diversity-stability relationships. However, empirical tests integrating multiple facets of diversity remain scarce and studies have mainly focused on taxonomic diversity effects on stability (Liang et al. 2022; Rodrigues et al. 2025; Wisnoski et al. 2023). Despite growing interest in diversity-stability relationships across ecosystems (Craven et al. 2018; Liu et al. 2025; B. Meng et al. 2025; Pennekamp et al. 2018; Polazzo et al. 2025), these relationships remain understudied in peatlands, where strong environmental gradients differentially filter multifaceted diversity (Robroek et al. 2017) and with potential consequences for community temporal stability.

At the global scale, peatlands play a disproportionate role, notably as long-term carbon stores, that hold around one third of the world’s soil carbon (Austin et al. 2025; UNEP 2022). This results from peat accumulation under saturated water conditions, which limit organic matter mineralization (Charman 2002; Stivrins et al. 2017). Yet nearly half of European peatlands (48 %, excluding European Russia) have been degraded, usually throughout drainage (Tanneberger et al. 2021), leading to substantial greenhouse gas emissions of 59–113 Mt CO_2eq annually in the EU (van Giersbergen et al. 2025). Peatland functioning relies on low diversity and highly specialized plant communities (Laine et al., 2021; Pinceloup et al., 2020; Rydin et al., 2013) which makes these ecosystems particularly vulnerable to cumulative and interacting pressures from local anthropogenic disturbance and climate change (Dieleman et al. 2015; Dise 2009; Loisel et al. 2021; Page and Baird 2016). Environmental stressors act as differential filters on multifaceted diversity, with cascading effects on stability (Davidson et al. 2025), and may also play a decisive role in how stability is altered (Hautier et al. 2015). Under strong environmental filters, low-diversity communities composed of specialist plants may display higher temporal stability of community properties. Conversely, more diverse assemblages may amplify temporal fluctuations leading to reduced stability, rather than the stabilizing effects predicted by the insurance hypothesis (Pfisterer and Schmid 2002). Studies have shown that the most significant environmental stresses affecting the stability of peatlands are temperature, water table depth and CO_2 atmospheric concentrations (Dieleman et al. 2015; Turetsky et al. 2012). In these saturated ecosystems, hydrology is the primary environmental factor determining peatland vegetation dynamics and overrides the effects of experimental warming (Buttler et al. 2015, 2023). However, how multifaceted diversity modulates peatland community stability and species asynchrony under environmental filters remains poorly understood.

In this study, we used a long-term *in-situ* experiment combining artificial passive warming and contrasting hydrological conditions to test how these environmental filters shape both multifaceted diversity and community temporal stability. This approach addresses a critical knowledge gap: although long-term experimental studies in peatlands have examined multiple taxonomic groups and ecosystem processes (Binet et al. 2017; Górecki et al. 2021; V. E. Jassey et al. 2013; Obi and Lindo 2026), their application to community stability remains scarce. First, we examined how hydrological gradient and experimental warming shape community assembly and multifaceted diversity. We hypothesized that hydrology would act as the dominant environmental filter, overriding warming effects in structuring multifaceted diversity trajectories. Second, we assessed how diversity trajectories are linked to community stability and species asynchrony, by testing which facets modulate the response of peatland plant communities under combined environmental stressors.

2. MATERIALS AND METHODS

2.1 Study site

The study was conducted at the Forbonnet peatland near Frasne in the Jura Mountains, located in northeastern France (46°49'34.8"N, 6°10'20.6"E; 840 m above sea level; Appendix S1). The 7-ha experimental site is an active peatland where turfigenesis still occurs, belonging to a larger peatland complex of more than 300 ha (Lhosmot et al. 2025), which falls within the “typical raised bog region” according to the European mire typology (region IV; Tanneberger et al., 2021). The site has been listed as an EU Natura 2000 protected area since 2002 and is also designated as a Ramsar site. It is part of the French national peatland observatory (*SNO-TOURBIERES*) and the European Long-Term Ecosystem Research network (eLTER), equipped to monitor a range of environmental parameters (Buttler et al. 2023; Gogo et al. 2021).

The experimental site, originally described as a *Sphagnum*-dominated ombrotrophic peatland, encompasses two hydrologically distinct microhabitats (hereafter “WET” and “DRY”, Appendix S2) differing in water table depth, microtopography, and vegetation composition (V. E. Jassey et al. 2023). The WET microhabitat, a transitional poor fen area, is characterized by a flat surface with a mixed plant community comprising *Sphagnum fallax* (occasionally with *S. flexuosum*) and vascular plants (e.g., *Andromeda polifolia*, *Vaccinium oxycoccos, Scheuchzeria palustris*). The DRY microhabitat exhibits typical ombrotrophic bog microtopography (i.e., hummock-hollow) with *Sphagnum magellanicum s.l.* (i.e., corresponding to either *S. medium* or *S. divinum*, formerly reported as *Sphagnum magellanicum s.s.*; Hassel et al., 2018) and vascular plants, including *Eriophorum vaginatum, Andromeda polifolia*, *Vaccinium oxycoccos, Calluna vulgaris*). Within these contrasting hydrological conditions, WET and DRY, a long-term passive experimental warming through Open Top Chambers (OTCs) manipulation was established in 2008.

In April 2008, twelve 3 × 3 m plots were established within the long-term monitoring platform across the WET and DRY microhabitats, with six plots in each hydrological condition. In each plot, a permanent 50 x 50 cm subplot was defined in homogeneous areas to ensure consistency over time. Plots were randomly allocated to warming treatments, with three plots per hydrological condition assigned to passive warming using Open Top Chambers (OTCs) and three plots serving as controls. The OTCs followed the International Tundra Experiment (ITEX) protocol (Hollister et al. 2023) and consisted of transparent hexagonal polycarbonate chambers (50 cm high, 1.7 m top width, 2.4 m base width) raised 10 cm above the peat surface to allow air circulation. In this site, OTCs produced modest but significant near-surface warming, approximately 1 °C increase in average air temperature (Binet et al. 2017; V. E. J. Jassey et al. 2011). This resulted in a factorial design (2 hydrological conditions × 2 warming treatments × 3 replicates = 12 plots).

2.2 Data collection

Vegetation survey

Species abundances were measured as relative cover using the point-intercept method at peak biomass in July for each survey year of 2008, 2009, 2010, 2012, 2024, 2025. A transparent Plexiglas frame with adjustable legs was placed over each 50 × 50 cm subplot. A ruler with 20 holes was placed at 20 locations across the frame, generating a grid of 400 evenly-spaced sampling points. At each point, a 1 mm diameter metal pin was lowered vertically, and all vegetation contacts were recorded by taxon, from the top leaf layer down to the moss layer. The 2024 and 2025 surveys were conducted with a total of 200 points due to equipment constraints, but this was accounted for in the calculation of relative frequencies to obtain comparable results throughout the survey period. This survey method provided relative frequencies by taxon and considers the stratification of plant communities. *S. fallax* and *S. rubellum* were pooled under *S. fallax* for analyses, consistent with previous work at the site (Buttler et al. 2015). To analyze plant community dynamics, we used relative abundance (i.e., cover) of each species per year and per plot, following Buttler et al. (2015, 2023), to ensure comparability across studies. Species with mean relative abundance < 0.1 % across the dataset (n = 2: *Carex limosa* 0.004 %, *Pinus sylvestris* 0.006 %) were excluded from all following analyses.

Before subsequent analyses, species matrices were renormalized after removing litter and excluded species, except for stability and asynchrony calculations. The vascular species subset was then used for diversity, trait-based, stability and asynchrony analyses, whereas whole-community data were retained for compositional and descriptive analyses.

Functional trait data

Functional traits were used to describe ecological strategies and functions of species in their ecosystems (Garnier et al. 2016; Lavorel and Garnier 2002; Violle et al. 2007). A subset of four functional traits were selected: (1) root depth, related to belowground resource acquisition and hydrological niche, previously identified as a potential key driver of species responses in this peatland (Buttler et al. 2015); (2) specific leaf area (SLA), a proxy of leaf economics and resource acquisition efficiency (Wright et al. 2004); (3) plant height, reflecting the competitive ability for light and vertical stratification (Violle et al. 2009); and (4) seed mass, representing dispersal and colonization/establishment trade-offs (Westoby et al. 2002). Trait data were obtained from the TRY database (v.6.0, downloaded 24 June 2025, Kattge et al., 2020).

A complete trait matrix (i.e., with no missing values) was required for subsequent analyses. Root depth was missing for two of the ten vascular species (*Carex pauciflora* and *Scheuchzeria palustris*). For both species, root depth was set to 0.10 m based on published information (Chytrý et al. 2021). For *Vaccinium oxycoccos*, only qualitative information was available (i.e., “shallow”); this value was converted into a quantitative value (0.10 m) based on its shallow root systems in peatlands. Next, the collinearity among traits was examined on the trait matrix to ensure trait independence (all Spearman $|\rho| < 0.7$), and all traits were log-transformed prior to functional metrics calculation.

Phylogenetic tree

To compute phylogenetic diversity metrics, a phylogenetic tree was constructed from rbcL chloroplast sequences (1428 bp) obtained from NCBI GenBank. Sequences were aligned using MAFFT and analyzed with PhyML via ngphylogeny.fr. The resulting tree was ultrametricized using penalized likelihood. Details on sequences, alignment, and tree calibration are provided in Appendix S3.

2.3 Diversity metrics

Taxonomic diversity was characterized using species richness (N_0) and Hill numbers (Hill 1973; Jost 2006): Shannon diversity (N_1, Eq. 1) and Shannon evenness (E_{10}, Eq. 2). Shannon diversity (N_1) is the exponential of the Shannon's entropy index, with the order q = 1 in the framework of Hill numbers (Chao, Gotelli, et al. 2014):

$$N_1 = exp\left(-\sum_{i=1}^{S} p_\mathrm{i}\, ln(p_\mathrm{i})\right) \tag{1}$$

where S is the number of species and p_i the relative abundance of species i.

$$E_{10} = N_1 / N_0 \tag{2}$$

Community-weighted mean (CWM, Eq. 3) matrix was calculated to analyze the dominant trait strategy in every community. CWM was calculated as the mean raw trait value weighted by each species' relative abundance within plots:

$$CWM = \sum_{i=1}^{S} p_i x_i \tag{3}$$

where pi is the relative abundance of species i and xi its trait value.

Functional diversity was also quantified using Hill numbers (Chao et al. 2019), with functional diversity and functional redundancy. These metrics were computed on a Euclidean distance matrix of standardized traits (z-scores), and with the order q = 1 and τ set to the mean pairwise distance (Chao et al., 2019). Functional diversity (FD1) represents the effective number of functionally distinct species:

$$FD_1 = exp\left(-\sum_{i=1}^{S} p_i\, log\left(\sum_{j=1}^{S}\left[1 - f\left(d_{ij}(\tau)\right)\right] p_j\right)\right) \tag{4}$$

where d_{ij} represents the Euclidean distance between each pairwise species *i* and *j* in the functional space.

Functional redundancy (FR_1) represents the proportion of species that could theoretically be removed without affecting functional diversity (Dick 2023; Mahaut et al. 2025):

$$FR_1 = 1 - FD_1 / N_1 \tag{5}$$

Phylogenetic diversity was estimated using Hill numbers (q defined as above): phylogenetic diversity of order q = 1 (PD_1, Eq. 6), which represents the effective number of phylogenetically distinct species (Chao, Chiu, et al. 2014; Chao et al. 2010):

$$PD_1(T) = T\ exp\left(-\sum_{i \in B_T} \frac{L_i}{T} a_i ln a_i\right) \tag{6}$$

where B_T is the set of all branches in the tree, L_i is the length of branch i, a_i is the total relative abundance of all descendant species on branch i, and T is the abundance-weighted total branch length.

Faith’s PD (Faith 1992), which extends the concept of species richness to the phylogenetic dimension by capturing the evolutionary history of the community (Chao et al. 2010), which is equivalent to PD for q = 0 in Hill numbers framework (Eq. 7):

$$Faith'sPD = \sum_{i \in B_T} L_i \tag{7}$$

2.4 Stability and asynchrony

Stability and asynchrony were quantified from the same species subset as diversity metrics to ensure taxonomic comparability. Community-wide temporal stability (S_c, Eq. 8), also referred to as invariability or constancy (Kéfi et al. 2019), was quantified for each plot as the inverse of the coefficient of variation of total abundance across the survey time series (Tilman 1996). Thus, stability was calculated for an aggregate community property, not for a diversity index:

$$S_c = \frac{1}{CV_c} = \frac{\mu_c}{\sigma_c} \tag{8}$$

where μ_c is the mean total abundance and σ_c its temporal standard deviation across the survey time series. Higher values indicate greater temporal stability.

Community synchrony (φ, Eq. 9), reflecting temporal compensation mechanisms between species, was estimated using the Loreau and de Mazancourt (2008) framework:

$$\varphi = \frac{\sigma_c^2}{\left(\sum_{i=1}^{S} \sigma_i\right)^2} \tag{9}$$

where σ_c^2 is the temporal variance of total community abundance, σ_i is the temporal standard deviation of species i, and S is the number of species in the plot. By construction, $0 \leq \varphi \leq 1$. Asynchrony was then calculated as 1 - φ, with values closer to 1 indicating stronger asynchrony.

Using the same community subset for diversity, stability and asynchrony ensured direct comparability among metrics, while preserving distinct ecological meanings, as commonly done in plant community stability studies (Y. Meng et al. 2023; Valencia et al. 2020; Zhao et al. 2022). Diversity metrics describe compositional structure, stability describes temporal variability in aggregate abundance, and asynchrony describes the degree of temporal compensation among species.

2.5 Statistical analyses

Compositional gradients were explored through a principal component analysis (PCA), which was done on a Hellinger-transformed species abundance matrix to address the double-zero problem (Borcard et al. 2018; Legendre and Gallagher 2001). Next, relationships between community composition and experimental factors (i.e., year, hydrological condition, warming treatment) were analyzed using redundancy analysis (RDA), with Hellinger-transformed data. This method selection was validated through detrended correspondence analysis (DCA; gradient length < 1.6). To control for collinearity among predictors, variance inflation factors (VIF) were checked: VIF values were < 1.7 for all predictors. The relative importance of the different explanatory variables was quantified through hierarchical partitioning (Lai et al. 2022).

Taxonomic, functional and phylogenetic diversity metrics were tested for responses to experimental factors using linear mixed models (LMMs). We used a fixed model structure defined *a priori* based on the experimental design, rather than data-driven model selection, as our goal was to test specific effects of experimental warming and hydrology rather than to maximize explanatory power. The following fixed and random effect's structure was used for each metric: *metric ~ year* × *hydrology* + *year* × *treatment* + *hydrology* × *treatment* + *(1|plot)*. This model included all two-way interactions but excluded the three-way interaction to preserve degrees of freedom given the limited sample size. Final models and significant effects are detailed in Table 1, along with marginal and conditional R^2 values, R^2_m and R^2_c, respectively giving the proportion of variance explained by fixed effects alone and by the full model (both fixed and random effects) (Nakagawa and Schielzeth 2013).

We compared community temporal stability and species asynchrony (computed for each of the 12 plots across the six survey years) across hydrological and warming treatment using permutation-based ANOVAs with 9,999 permutations, to account for the limited sample size (Anderson and Braak 2003). Effect sizes were quantified using partial eta-squared ($\eta^2 p$).

We assessed the relationships between stability, asynchrony, and diversity metrics using Spearman partial correlations. Since diversity indices were calculated for each plot and year ($n = 72$ values for each metric), whereas stability and asynchrony were calculated over the entire time series ($n = 12$ for each), we averaged diversity indices per plot. We computed Spearman partial correlations following a three-step procedure: (1) rank-transforming all variables, (2) extracting residuals from linear models fit to the ranked variables to adjust for hydrological conditions × warming treatment effects, and (3) calculating Pearson correlations on these residuals. Given the small sample size of 12 plots, we focused on effect sizes (ρ) rather than significance testing, as effect sizes have greater ecological relevance (Popovic et al. 2024; Wasserstein et al. 2019).

We investigated residual-value correlations between diversity metrics using Spearman correlations on LMM residuals (controlling for year, hydrology, and warming effects; model structure as above) and visualized these relationships using Principal Component Analysis (PCA) on standardized residuals.

2.6 Reproducibility and transparency

We performed the analyses using R v4.4.1 (R Core Team 2024), in RStudio v2025.9.1.401 (Posit team 2025). For details on package names and versions, see Appendix S4. We checked validity conditions and model assumptions where relevant (e.g., for correlation coefficients and LMMs); where these conditions were not met, non-parametric tests were used. We assessed the risk of bias following the ROBITT framework (Boyd et al. 2022), a standardized tool for evaluating internal validity and potential bias in ecological studies (Culina et al. 2025); full details are provided in Appendix S5.

3. RESULTS

3.1 Community composition along the hydrological gradient

Redundancy analysis explained 57.8 % of total variance (R^2adj = 0.53; $P = 0.001$; Fig. 1A). RDA1 explained 47.8 % of total variance ($P = 0.001$) and represented the hydrological gradient, with DRY and WET communities occupying very distinct positions in the ordination space throughout the study period (2008-2025). RDA2 explained 7.5 % ($P = 0.001$) and captured temporal trajectories, with DRY and WET plots showing similar directional shifts over time. While hydrology ($F = 64.8$, $P = 0.001$) and year ($F = 4.1$, $P = 0.001$) effects were both significant, warming treatment showed a weak relationship ($F = 2.1$, $P = 0.085$). Hydrological separation persisted in unconstrained ordination, where control and heated plots overlapped within each hydrological condition, while overall DRY and WET communities remained distinct (PCA; Appendix S6). Hierarchical partitioning (Fig. 1B) revealed that hydrology alone explained 46 % of total community variance (86.5 % of the explained variance), year explained 10.7 % (20.1 %), and warming treatment explained only 0.77 % (1.45 %). Shared fractions were all small and close to zero.

Relative abundance trajectories for the three major plant functional groups (Fig. 1C) were consistent with these compositional gradients (see Table 1 for LMM results). Graminoid abundances increased over time ($P = 0.031$). Ericoid abundances also increased over time ($P < 0.001$) and differed between hydrological conditions ($P = 0.027$), with their temporal trajectories varying across hydrological conditions ($P < 0.001$): the increase was more pronounced in WET, but both groups converged in later years. By contrast, bryophyte abundances declined strongly over time ($P < 0.001$) and significantly differed between DRY and WET ($P < 0.001$). This decline was stronger in WET conditions, consistent with the significant year × hydrology interaction ($P < 0.001$). Artificial warming had no significant effect on any functional group (all $P > 0.22$). Overall, hydrology explained the largest independent fraction of variance, whereas warming explained a negligible fraction.

3.2 Metrics variation between hydrological conditions

We next examined how multifaceted diversity metrics responded to experimental conditions over time in the vascular plant community (Fig. 2; Table 1). At the taxonomic level (Fig. 2A-C), vascular species richness (N_0) varied with year ($P = 0.03$) but showed no evidence of hydrological or warming effects, with similar mean richness between DRY and WET plots across the study period. Effective diversity (N_1) and evenness (E_{10}) tended to be higher in WET than DRY ($P = 0.12$ and $P = 0.053$, respectively), and showed limited temporal dynamics (all year × hydrology/warming, $P > 0.07$). Functional diversity (FD_1, Fig. 2D) showed no clear responses to hydrology, warming, or their interaction. Functional redundancy (FR_1, Fig. 2E) showed significant temporal dynamics and divergence between hydrological conditions (year: $P = 0.005$; year × hydrology: $P = 0.031$). Conversely, phylogenetic diversity (PD_1, Fig. 2F) exhibited a strong and consistent hydrological separation with a higher diversity in WET than DRY communities (hydrology: $p < 0.001$).

CWM showed contrasting patterns across traits (Fig. 2 G-J). CWM root depth and CWM seed mass both showed strong hydrological differentiation (both $p < 0.001$) and significant year × hydrology interactions ($P = 0.008$ and $P = 0.006$, respectively), with root depth being higher in DRY and seed mass being higher in WET. CWM height decreased over time across all conditions ($P = 0.006$), with no significant hydrological or warming effect. CWM specific leaf area showed no detectable response to either factor (all $p > 0.28$). Given these contrasting responses across diversity facets, we next examined whether these metrics covaried independently of experimental structure.

3.3 Diversity facets covariation along a shared axis

Residual correlations (Fig. 3A) revealed that effective diversity (N_1) correlated strongly with functional diversity (FD_1; $\rho = 0.96$), and both were positively associated with phylogenetic diversity (PD_1; $\rho = 0.81$ and 0.76, respectively). By contrast, CWM root depth showed negative correlations with nearly all diversity metrics, most strongly with PD_1 ($\rho = -0.75$) and FD_1 ($\rho =$

−0.57). FR_1 showed moderate positive correlation with CWM root depth (ρ = 0.41) and negative correlation with CWM SLA (ρ = -0.49), but showed weak correlations with most other metrics (all $|\rho| \leq 0.37$). Consistent with these patterns, PCA (Fig. 3B) showed that PC1 (52.9%) contrasted CWM root depth with the N_1–FD_1–PD_1 covariation axis, while PC2 (15.6%) captured additional variation associated with CWM seed mass, and E_{10}.

3.4 Temporal stability linkage to diversity facets

Community temporal stability differed between hydrological conditions, with higher values in DRY than in WET plots (permutation ANOVA: F = 6.54, P = 0.035, η^2p = 0.45; Fig. 4A), while warming had no effect alone (F = 0.22, P = 0.7, η^2p = 0.03) or in interaction with hydrology (F = 0.39, P = 0.59, η^2p = 0.05). Similarly, species asynchrony was significantly higher in DRY than in WET plots (F = 11.86, P = 0.015, η^2p = 0.60; Fig. 4B), and warming had no effect either by itself (F = 0.1, P = 0.75, η^2p = 0.01) or in interaction with hydrology (F = 2.48, P = 0.15, η^2p = 0.24). Stability was positively correlated with asynchrony (Spearman's correlation ρ = 0.72, P = 0.011).

To examine the relationships between diversity, stability and asynchrony while accounting for experimental effects, we used partial correlations (Fig. 4C; see Appendix S7 for full uncorrected and FDR-corrected p-values and Appendix S8-S9 for individual scatterplots). This revealed a weaker stability-asynchrony relationship (ρ = 0.40) than the raw correlation. Stability showed strong ($|\rho| \geq 0.60$) negative correlations with phylogenetic diversity (PD_1, ρ = −0.79) and taxonomic richness (N_0, ρ = −0.66), and a strong positive correlation with CWM root depth (ρ = 0.79). Moderate negative correlations ($0.40 \leq | \rho | < 0.60$) were observed with functional diversity (FD_1, ρ = −0.54), CWM seed mass (ρ = −0.50), effective diversity (N_1, ρ = −0.41), and CWM SLA (ρ = −0.41). In contrast, functional redundancy (FR_1) showed a moderate positive correlation with stability (ρ = 0.47). All other correlations between stability and the remaining community metrics were weak ($\rho \leq 0.29$). Species asynchrony showed generally weak associations with diversity and trait metrics, with a moderate positive correlation with CWM height (ρ = 0.40) and a weak negative correlation with functional redundancy (FR_1, ρ = −0.38). All other correlations between asynchrony and the remaining metrics were weak (ρ ranging from −0.30 to 0.25).

4. DISCUSSION

Understanding how multifaceted diversity relates to stability remains a central challenge in ecology, especially in strongly constrained ecosystems such as peatlands. We assessed these relationships using a 17-year field experiment combining a hydrological gradient and experimental warming (open-top chambers, OTCs). Across the study period, hydrology dominated community assembly and trajectories, while OTC-induced warming had only a very weak community-scale effect within this system and time window. Community temporal stability and species asynchrony were structured by this same hydrological gradient. Multiple diversity facets (notably phylogenetic and taxonomic metrics) were negatively associated with stability. These negative associations persisted after accounting for experimental effects (i.e., hydrology and warming) using partial correlations. These patterns contradict classical expectations of positive diversity-stability relationships and raise questions when higher diversity does not translate into higher temporal stability in plant communities. This discrepancy is increasingly recognized as reflecting the multidimensional and context-dependent nature of ecological stability (I. Donohue et al. 2016; Kéfi et al. 2019). We interpret these patterns below.

Hydrology, contrasting two conditions in water table depth (WTD; Appendix S2), explained most of the compositional variance, with a 60-fold stronger effect than experimental warming, which had only a weak community-scale impact. In peatlands, WTD is a major environmental filter (Wheeler and Proctor 2000) which imposes direct physiological constraints on plants (e.g., limiting oxygen availability, altering redox conditions, and controlling root-zone saturation), and soil biota in the rooting zone (Buttler et al. 2023; V. E. Jassey et al. 2023), thereby selecting for unique tolerance strategies (Rydin et al. 2013). Over long timescales, peatland vegetation dynamics are primarily structured by hydrological conditions (Andrews et al. 2021), and long-term WTD changes reshape functional composition and vegetation trajectories (Buttler et al., 2023; Köster et al., 2023; Laine et al., 2021). Accordingly, CWM root depth and seed mass reflected distinct trait trajectories under persistent hydrological constraints. Seed mass showed strong hydrological differentiation (higher in WET), whereas root depth was consistently higher in DRY, reflecting contrasting belowground strategies along the hydrological gradient. Both traits also varied through time. This trait alignment suggests that communities are constrained into differentiated strategies set by the hydrology. Alongside these trajectories, ericoid shrubs and graminoids increased while bryophytes (i.e., living *Sphagnum* spp. layer) declined, shifts broadly consistent with shrub encroachment documented across peatlands (Buttler et al. 2023; Dieleman et al. 2015). Consistent with recent syntheses, peatland vegetation can shift over decadal timescales when hydrological and nutrient constraints change (Pinceloup et al. 2020). More generally, peatland warming responses are frequently context-dependent and can remain subordinate when WTD constraints dominate (Buttler et al. 2015, 2023; Górecki et al. 2021); the weak OTC effect here at this timescale is informative, not evidence that warming is ecologically irrelevant, as climate change can alter water-table dynamics. At larger spatial scales, temperature gradients may override hydrological controls on species turnover, but within this peatland system and time window hydrology remained the dominant driver of community structure and dynamics.

These hydrological constraints also structured how diversity facets covary. Multifaceted diversity indices are often treated as complementary descriptors (Chao, Chiu, et al. 2014), yet strong abiotic filtering may align them along dominant gradients. After accounting for experimental structure, effective (N_1), functional (FD_1) and phylogenetic diversity (PD_1) covaried tightly and loaded opposite to CWM root depth, consistent with a single hydrology-linked strategy axis. These results contrast with broader evidence that functional and phylogenetic diversity are often decoupled and only weakly related, supporting the idea that strong abiotic constraints can compress viable strategies and thereby couple multiple diversity facets along a dominant gradient (Hähn et al. 2025). In contrast, functional redundancy showed weaker and partly distinct correlations relative to the N_1-FD_1-PD_1 cluster, including a positive association with CWM root depth and negative associations with FD_1, PD_1 and specific leaf area, suggesting that redundancy may capture a partly distinct facet of community structure.

Community temporal stability and species asynchrony were both higher in DRY (i.e., the bog, deeper WTD) than WET (i.e., the transitional poor fen, shallower WTD) conditions, while experimental warming had no detectable effect on either metric. This is consistent with studies showing that moderate relative warming (ca. 1 °C) does not significantly alter plant community stability in other constrained systems (Quan et al. 2021), and it has been previously shown that the OTC on this experimental site produced only limited warming (ca. 1 °C, Binet et al., 2017). The higher stability in DRY conditions likely reflects contrasting environmental constraints: deeper WTD, lower pH and increased soil biological activity select for specialist, slow-growing and persistent strategies whose dynamics are buffered against hydrological fluctuations; whereas WET communities, despite experiencing less water limitation under average conditions, experience greater exposure to root-zone WTD fluctuations. This matches long-term drawdown evidence that bog functioning can be more predictable, whereas fen responses are more stochastic and turnover-driven under water-table change (Laine et al., 2021). This pattern aligns with recent continental-scale evidence from United States wetlands, where shallow WTD were also associated with reduced stability (Liu et al. 2025). The strong positive correlation between stability and asynchrony ($\rho = 0.72$) is consistent with the insurance hypothesis (Michel Loreau and de Mazancourt 2008, 2013; Thibaut et al. 2013), although recent work shows that asynchrony can arise predominantly from statistical averaging rather than true compensatory dynamics (Zhao et al. 2022). Global syntheses further show that community stability is more strongly linked to species synchrony than to species richness *per se* (Valencia et al. 2020). However, this relationship weakened substantially after controlling for hydrology and warming (partial $\rho = 0.40$), indicating that environmental constraints structure both stability and asynchrony beyond their direct association (Ian Donohue et al. 2013). This is consistent with recent evidence that compensatory dynamics often contribute to community stability without being directly positively linked with diversity, particularly when environmental filters dominate community dynamics (Zhao et al. 2022). Together, the strong raw stability-asynchrony correlation and its attenuation after controlling for hydrology suggest that their association reflects both shared hydrological forcing and, potentially, compensatory dynamics.

After controlling for experimental effects, stability decreased with phylogenetic diversity and species richness, and was also negatively associated with functional diversity and effective diversity, while increasing with deeper-rooted community strategies (CWM root depth). Because these diversity facets covaried tightly and opposed CWM root depth along the dominant residual gradient, these associations likely reflect a shared strategy axis rather than independent effects of each facet. The negative PD-stability association was robust to the phylogenetic metrics used: Faith's PD, which captures total branch length without abundance weighting, showed a similarly strong negative correlation with stability ($\rho = -0.63$, Appendix S7). This contrasts with studies where higher phylogenetic diversity enhanced temporal stability (Cadotte et al. 2012; Zhang et al. 2026), and suggests that PD-stability relationship may be contingent on ecosystem context. Interestingly, a recent large-scale grassland study also found a negative association between local functional diversity and local community stability, consistent with the view that diversity-stability relationships can vary with the diversity facet considered and the ecological context (Huang et al. 2026). Importantly, evenness (E_{10}) showed no clear association with stability, suggesting that the pattern is not simply a dominance/evenness effect in abundance distribution. Rather, greater diversity may coincide with higher temporal variance in aggregate cover, whereas lower-diversity communities dominated by deeper-rooted species (whose belowground strategies match persistent hydrological constraints of peatlands) show more buffered dynamics. In strongly filtered, species-poor ecosystems like peatlands, increases in local diversity may therefore not signal enhanced buffering capacity and may be a poor proxy for insurance-based expectations of community stabilization.

Beyond root depth, seed mass and specific leaf area also showed moderate negative correlations with stability. Seed mass, related to establishment-dispersal strategies, was the most strongly differentiated trait between hydrological conditions (higher in WET), suggesting that it may track the same hydrological gradient that structures stability. Similarly, higher specific leaf area (i.e., associated with faster resource acquisition) may reflect more acquisitive strategies in WET communities, as expected under less resource-limited fen-like conditions, although responses were weaker than predicted (Laine, et al., 2021; Lin et al., 2020). This hydrology-related strategy contrast is consistent with peatland drawdown results showing fen (WET) communities become more productive, whereas bog (DRY) responses are more conservative (A. Laine et al. 2021). In contrast, height showed no clear relationship with stability, despite being identified as a key stabilizing trait in continental-scale wetland analyses (Liu et al. 2025). Similarly, long-term drawdown experiments show that community-weighted mean height can decline across peatland types (Laine et al., 2021). This difference may reflect the primacy of belowground constraints in peatlands: whereas height captures competitive ability for light (a filter that may be dominant in many wetlands), hydrological access and waterlogging tolerance may override aboveground competition in this system. Because our trait set focuses on widely available ‘global’ traits, it likely under-represents peatland-specific tolerance traits (e.g., tolerance to waterlogging/anoxia and belowground aeration capacity), which could partly explain the comparatively weak relationships observed for specific leaf area and height.

Diversity-asynchrony relationships were generally weak. Functional redundancy (FR_1) was associated with lower asynchrony and, after controlling for experimental effects, with moderately higher stability. These FR_1 associations suggest that redundancy may capture a partly distinct aspect of community structure, but that the links between redundancy, species covariance through time and community-level stability are not straightforward in this system. More broadly, these results align with recent work showing that diversity-stability linkages depend on stability decomposition and covariation among community properties, and that in strongly structured environments diversity metrics can track dominant strategy gradients, complicating mechanistic inference from diversity–stability correlations alone (De Bello et al. 2021; Zhao et al. 2022).

Several limitations warrant consideration. First, passive OTC warming captured moderate mean temperature increases but does not reproduce key dimensions of climate change such as extremes, altered seasonality, or the full range of warming-hydrology feedbacks. In this site specifically, climate projections suggest substantial changes in water table depth and seasonality through 2100 under warming scenarios (Bertrand et al. 2021), and such combined effects can dominate vegetation responses (Andrews et al. 2021; Kokkonen et al. 2024). Moreover, the warming intensity may be insufficient to trigger detectable community-level responses, or effects may require longer timescales to manifest in slow-responding ecosystems such as peatlands. Second, bryophytes exhibited a strong decline, yet stability metrics excluded them despite their functional importance; future work should explicitly integrate bryophyte dynamics to test whether diversity-stability patterns propagate across community compartments (Telgenkamp et al. 2025). To assess generality, tests across multiple peatlands would be valuable. Finally, we treated stability as a single facet (temporal stability/invariability of aggregate community cover), whereas recent frameworks emphasize ecological stability as multidimensional, with potentially decoupled components (Ian Donohue et al. 2013; I. Donohue et al. 2016; Kéfi et al. 2019), distinguishing, for instance, temporal stability (invariability) from resistance and resilience (Yan et al. 2025). Disentangling these components would refine our understanding of how filtering shapes different facets of temporal dynamics.

5. CONCLUSION

Our core result highlighting the inverse relationship between several diversity facets and community temporal stability suggests that diversity-stability relationships can be negative when diversity covaries with dominant strategy gradients in strongly structured environments. Multifaceted diversity is often expected to stabilize communities through buffering and compensatory dynamics, yet this prediction remains context-dependent. Because much of the evidence for diversity–stability relationships comes from grassland studies (Craven et al. 2018; Mahaut et al. 2023; Zhao et al. 2022), it remains unclear how general these expectations are in ecosystems where abiotic filtering is particularly strong and can align trait composition and temporal covariance among species. By bringing multifaceted diversity-stability inference to peatland communities, our study helps test the boundary conditions of diversity-stability expectations in a context that is common globally but comparatively less represented in the stability literature. More broadly, our results highlight that fine-scale hydrological heterogeneity within peatland complexes can generate contrasting community dynamics, supporting the need to consider peatlands as habitat mosaics when assessing and conserving their community stability. From a conservation perspective, this suggests that maintaining (or restoring) key functional strategies aligned with prevailing constraints may be as important as maximizing species richness for sustaining stability under intensifying global change pressures, consistent with calls to move beyond species richness as a primary conservation metric (Fletcher et al. 2025); and that increases in diversity alone, if decoupled from traits associated with higher stability, may not enhance and can even reduce community temporal stability in strongly constrained ecosystems.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section:

Appendix S1. Forbonnet peatland location and experimental platform.

Appendix S2. Long-term water table depth dynamics at Forbonnet peatland.

Appendix S3. Phylogenetic tree reconstruction.

Appendix S4. Package names and versions.

Appendix S5. Risk of bias assessment.

Appendix S6. Principal Component Analysis (PCA) of plant community composition.

Appendix S7. Size effects (ρ) and significance (p-values) of the residual correlations between the various facets of diversity, community temporal stability, and species asynchrony.

Appendix S8. Partial residual relationships between community stability and diversity metrics.

Appendix S9. Partial residual relationships between species asynchrony and diversity metrics.

TABLE

Table 1. Linear mixed-effects models testing effects of year (Y), hydrological condition (H: DRY/WET), and warming treatment (T: OTC/control) on plant community metrics. Models followed the structure *metric ~ Y × H + Y × T + H × T + (1*|*plot)*. Significance of fixed effects was assessed using Type III Wald χ^2 tests. All effects with $p \leq 0.10$ are reported. Marginal R^2 (R^2m; variance explained by fixed effects) and conditional R^2 (R^2c; variance explained by fixed and random effects) are shown. "–" indicates effects with $P > 0.10$.

Metric	Community	Effects	R^2m	R^2c
Functional group cover				
Ericoid cover	All	Y (*P* < 0.001); H (*P* = 0.027); Y×H (p < 0.001)	0.61	0.82
Graminoid cover	All	Y (*P* = 0.031)	0.33	0.66
Bryophyte cover	All	Y (*P* < 0.001); H (*P* < 0.001); Y×H (*P* < 0.001); H×T (*P* = 0.076)	0.81	0.87
Taxonomic diversity				
Species richness (N_0)	Vascular	Y (*P* = 0.030)	0.21	0.73
Effective diversity (N_1, q = 1)	Vascular	Y (*P* = 0.095)	0.45	0.69
Evenness (E_{10}, q = 1)	Vascular	H (*P* = 0.053); Y×H (*P* = 0.075)	0.43	0.68
Functional diversity				
Functional diversity (FD_1, q = 1)	Vascular	-	0.42	0.68
Functional redundancy (FR_1, q = 1)	Vascular	Y (*P* = 0.005); Y×H (*P* = 0.031)	0.18	0.58
Functional identity (CWM)				
Height	Vascular	Y (*P* = 0.006)	0.35	0.74
Specific leaf area	Vascular	-	0.29	0.50
Root depth	Vascular	H (*P* < 0.001); Y×H (*P* = 0.008)	0.49	0.64

Seed mass	Vascular	H ($P < 0.001$); Y×H ($P = 0.006$); Y×T ($P = 0.093$)	0.67	0.76
Phylogenetic diversity				
Phylogenetic diversity (PD_1, $q = 1$)	Vascular	H ($P < 0.001$)	0.60	0.73

FIGURES

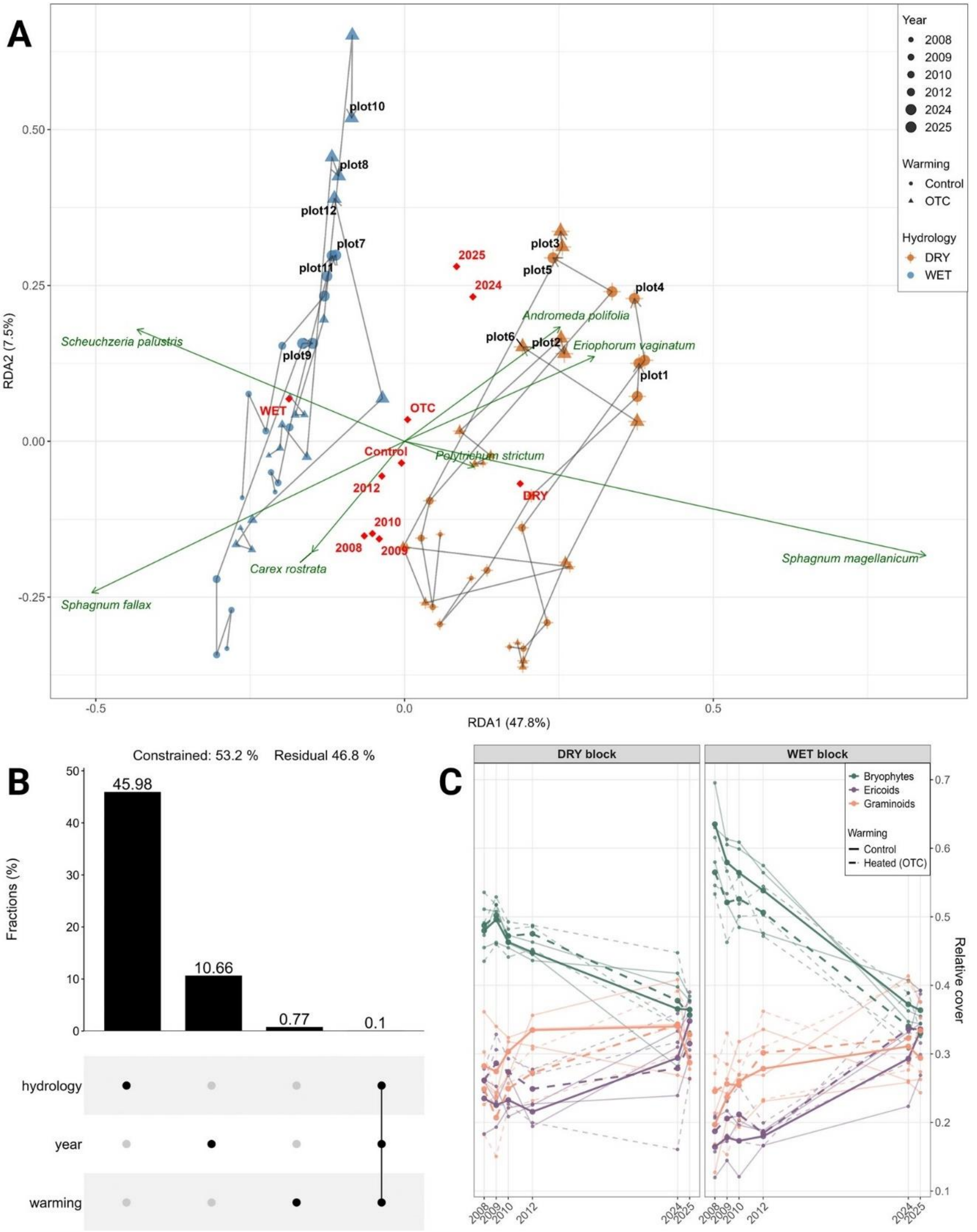

Figure 1. Redundancy Analysis (RDA), hierarchical partitioning, and relative cover temporal change of the three major plant functional groups. (A) RDA triplot showing the

ordination of the twelve plots across hydrological conditions (DRY/WET) and warming treatment (OTC-heated/Control) and survey years, in species ordination space. Red vectors represent experimental variables, green vectors show species loadings. Axis percentages indicate the proportion of total variance explained by each canonical axis (i.e., RDA1 and RDA2). (B) Hierarchical partitioning of constrained variance showing the relative contribution of each experimental factor. Values represent the percentage of explained variance attributable to each factor after accounting for shared effects. (C) Relative cover dynamics of major plant functional groups (bryophytes, ericoids, and graminoids). Thick lines represent mean trajectories by experimental condition; thin lines show individual plot trajectories.

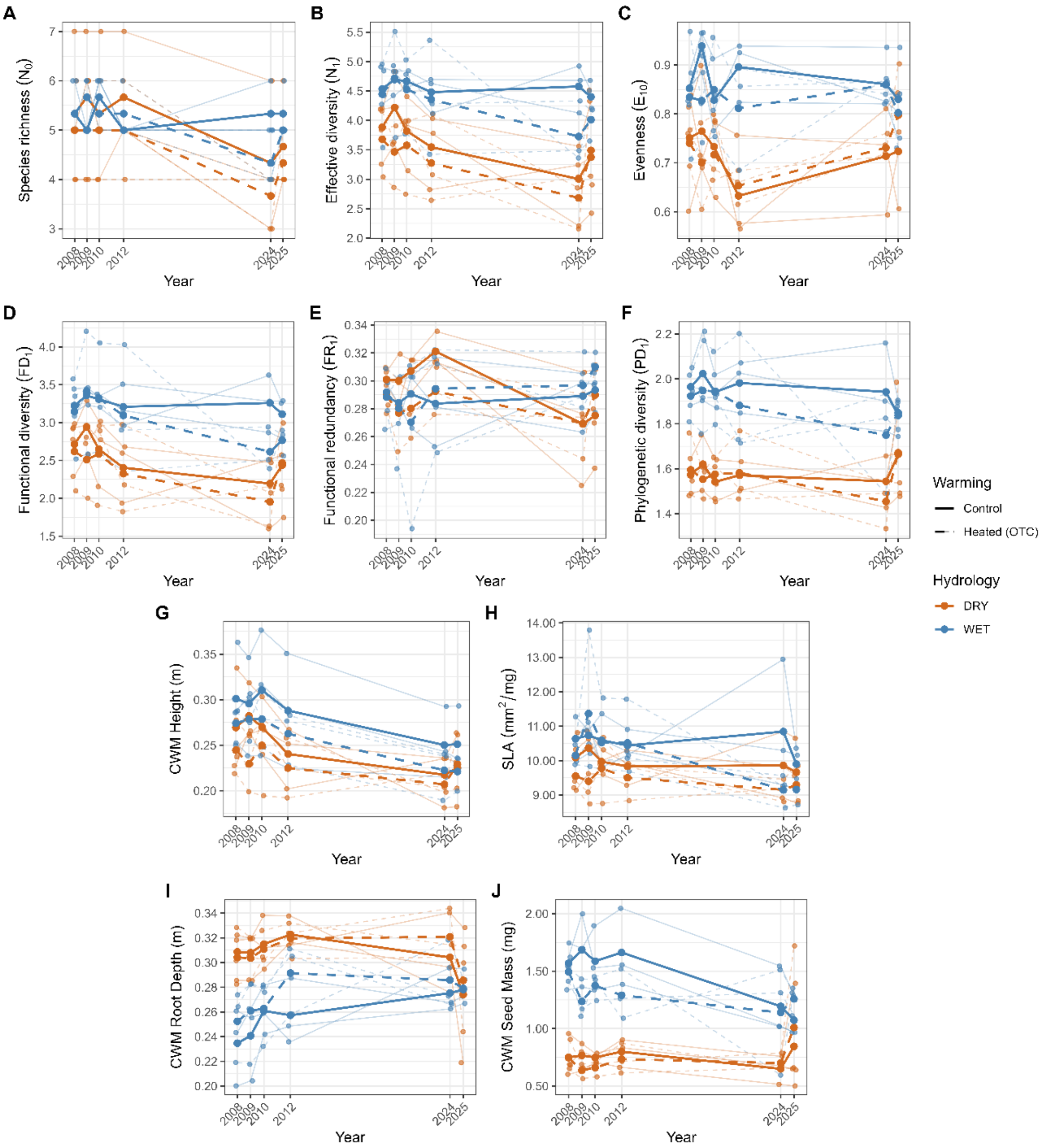

Figure 2. Temporal dynamics of multifaceted diversity and community-weighted mean (CWM) traits in the vascular plant community across experimental conditions. (A-F) **Diversity metrics**: (A) Species richness (N_0). (B) Effective diversity (N_1). (C) Evenness (E_{10}). (D) Functional diversity (FD_1), representing the effective number of functionally distinct species. (E) Functional redundancy (FR_1), representing the proportion of species that could theoretically be removed without affecting functional diversity. (F) Phylogenetic diversity (PD_1), representing the effective number of phylogenetically distinct species. (G-J) **Community-weighted mean traits**:

(G) Plant height. (H) Specific leaf area (SLA). (I) Root depth. (J) Seed mass. All traits were log-transformed prior to CWM calculation (see Methods). Thick lines represent mean trajectories per experimental condition; thin lines show individual plot trajectories. Lines connect survey years only for visualization and do not imply continuous annual trajectories between 2012 and 2024.

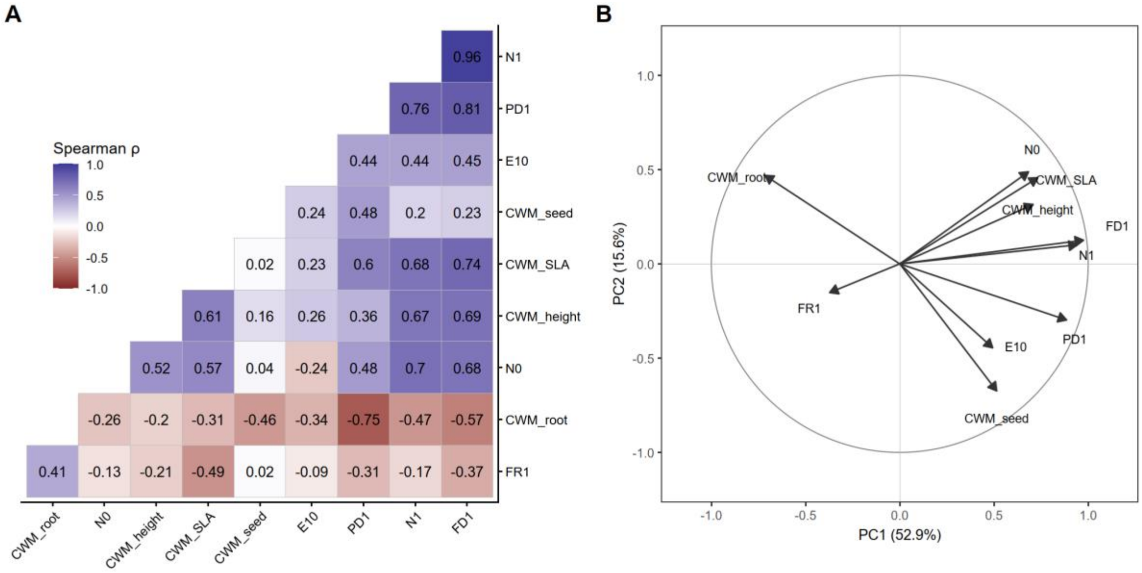

Figure 3. Relationships among diversity metrics after controlling for experimental effects. (A) Spearman correlation matrix computed on LMM residuals (*n* = 72 plot-year combinations). (B) PCA correlation circle based on LMM residuals, showing the first two principal components (68.5% of variance). Models followed the structure *metric ~ Y × H + Y × T + H × T + (1|plot)*. See abbreviations of diversity metrics and traits in figure 2.

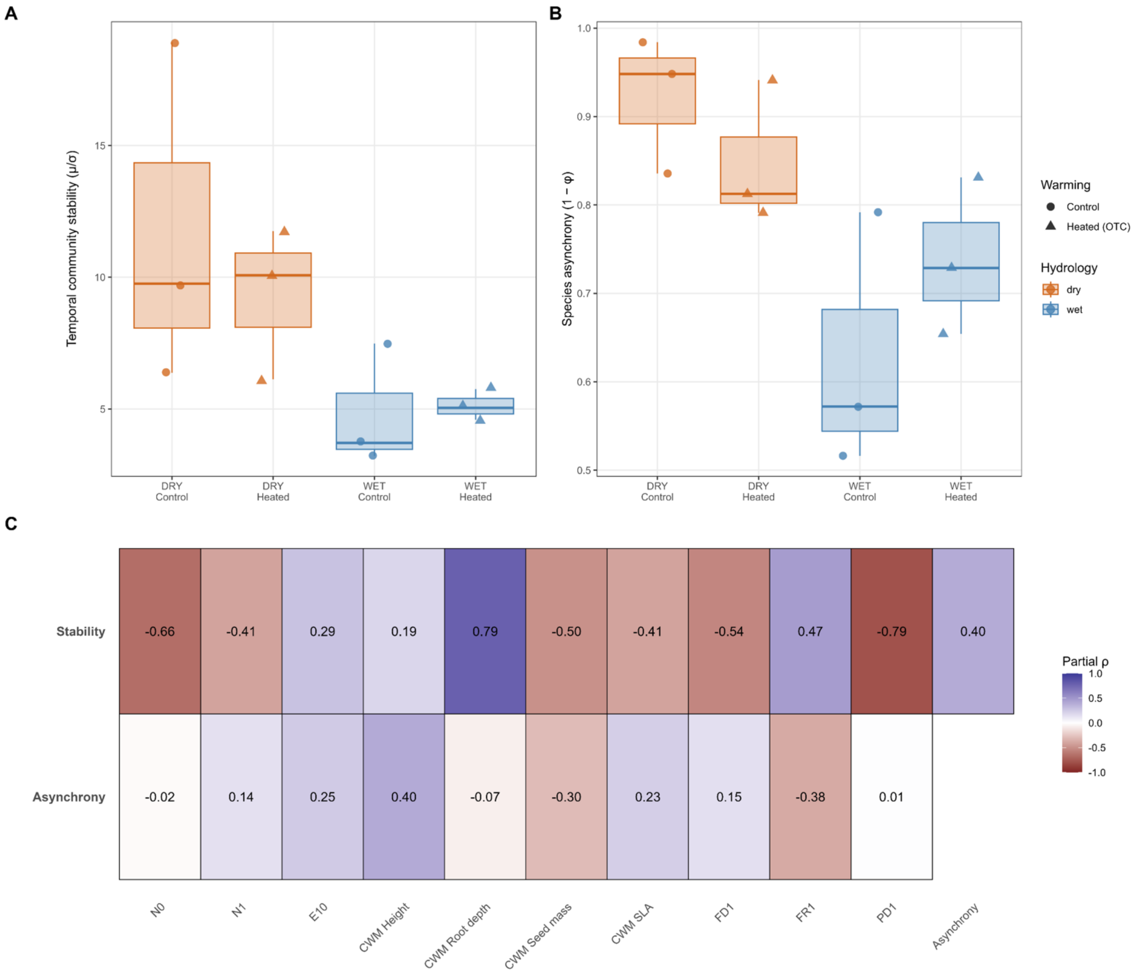

Figure 4. Community temporal stability and species asynchrony of the vascular plant community across experimental conditions, with partial Spearman correlations. (A) Community temporal stability across experimental conditions. (B) Species asynchrony across experimental conditions. (C) Heatmap of partial Spearman correlations (*ρ*) among community stability, species asynchrony, diversity facets, and trait metrics based on residuals after accounting for experimental structure (see Methods section). Each cell reports *ρ* (see Appendix S7 for full uncorrected and FDR-corrected p-values). Boxplots show median, quartiles, and individual data points (*n* = 3 plots per condition). Abbreviations: N_0 = species richness; N_1 = effective diversity; E_{10} = evenness; FD_1 = functional diversity; FR_1 = functional redundancy; PD_1 = phylogenetic diversity; CWM = community-weighted mean. See Appendix S8-S9 for individual scatterplots.

Supporting Information to the paper

Diversity comes at a cost: multifaceted diversity reduces plant community stability in peatlands

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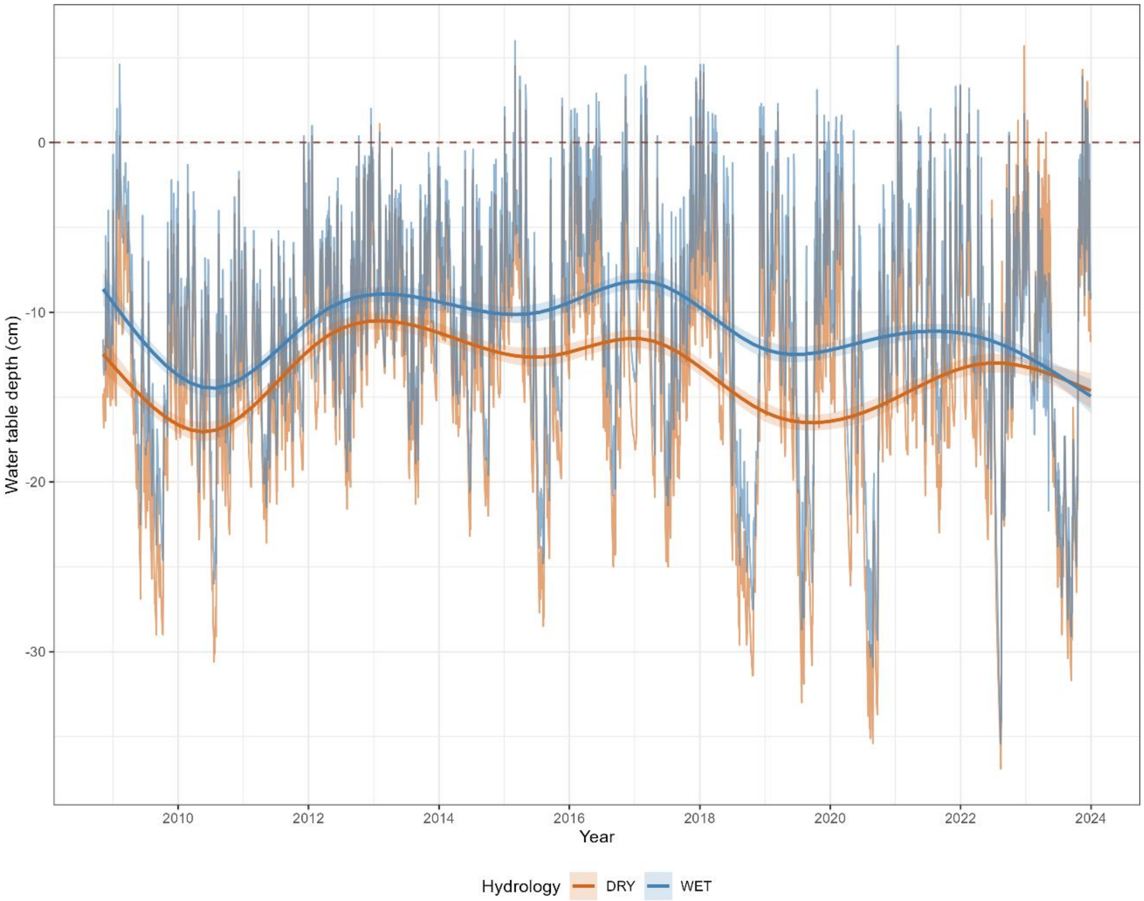
Appendix S1. Forbonnet peatland location and experimental platform.

(A) Geographic location of the site with aerial orthophotograph (coordinates in WGS84, decimal degrees, IGN 2021 BD Ortho raster and Natural Earth vector); (B) Photograph of the experimental platform (photo credit: OPEN-Lab DREAM); (C) Photograph of an Open Top Chamber (OTC) at the site (photo credit: Noémie Poteaux).

Appendix S2. Long-term water table depth dynamics at Forbonnet peatland.

Daily water table depth (WTD) measurements (2008–2023) for the two hydrological blocks, with GAM smoothing trends ± SE (shaded areas). WTD was measured using floating piezometers, so values are referenced to the local peat surface at the time of measurement (dashed line). Data from 2024 onwards were excluded due to sensor malfunction.



Appendix S3. Phylogenetic tree reconstruction

The phylogenetic tree was constructed from the sequences of the chloroplast gene rbcL (ribulose-1,5-bisphosphate carboxylase/oxygenase) extracted from the NCBI Genbank database for each of the species present in the base vegetation matrix (see Table bellow for the corresponding accession numbers).

For species without available sequences or with sequences that were too short, the sequence of the closest species was used as a proxy (also detailed in Table bellow). The longest rbcL sequence available for *Vaccinium oxycoccos* (longest available sequence = 552 bp) was substituted with *V. uliginosum* (longest available sequence = 1398), its closest extant sister lineage based on a recent phylogeny of the *Vaccinieae* (Becker et al. 2024). A substitution was also made for *Polytrichum strictum* (longest available sequence = 684 bp), which was substituted with *P. commune* (longest available sequence = 1428, see Table below), a close congeneric species with a complete rbcL sequence.

The sequences were aligned on the NGPhylogeny.fr platform (Frédéric Lemoine et al. 2019) using the “PhyML/OneClick” tool. The workflow selection was as follows: multiple alignment with MAFFT (Katoh and Standley 2013), alignment curation with BMGE (Criscuolo and Gribaldo 2010), tree inference with PhyML (Guindon et al. 2010), bootstrap values were computed using TBE (F. Lemoine et al. 2018) and finally tree rendering with Newick display (Junier and Zdobnov 2010). Next, on R Studio, we imported the resulting Newick tree and processed it as follows: (i) midpoint rooting, (ii) ultrametric transformation using the *chronos*() function from ape package (see S4), and (iii) matching of species labels with the vegetation matrix using *match.phylo.comm*() from picante package. The final tree, which was an ultrametric tree, was used for computing phylogenetic diversity metrics.

Sequences accession numbers

GenBank accession numbers for rbcL sequences used in the phylogenetic analyses. Length indicates aligned sequence lengths. Notes column indicates proxy species used when target species sequences were inadequate.

Species	**Accession number**	**Length (bp)**	**Notes**
Andromeda polifolia	AF124572.1	1355	
Calluna vulgaris	ON684482.1	1428	
Carex limosa	JX644630.1	1295	
Carex pauciflora	GQ469850.1	1408	
Carex rostrata	GQ469851.1	1408	
Drosera rotundifolia	KM360758.1	1352	
Eriophorum vaginatum	AB369971.1	1408	
Pinus sylvestris	OQ184488.1	1428	
Scheuchzeria palustris	HQ901572.1	1344	*Zannichellia palustris* used as proxy (the only acceptable sequence for *Scheuchzeria palustris* was not grouped with *Carex* species
Vaccinium oxycoccos	AF421107.1	1398	*V. uliginosum* used as proxy
Polytrichum strictum	LC702108.1	1428	*P. commune* used as proxy
Sphagnum fallax	AB013673.1	1305	
Sphagnum magellanicum	MF362295.1	961	

Appendix S4. Package names and versions

The following table lists all R packages used in the analyses, with their version and citations.

Package	Version	Reference
ape	5.8.1	(Paradis and Schliep 2019)
car	3.1.3	(Fox and Weisberg 2019)
conflicted	1.2.0	(Wickham 2023)
DHARMa	0.4.7	(Hartig 2024)
effectsize	1.0.1	(Ben-Shachar et al. 2020)
factoextra	1.0.7	(Kassambara and Mundt 2020)
FactoMineR	2.12	(Lê et al. 2008)
FD	1.0.12.3	(Laliberté and Legendre 2010)
funrar	1.5.0	(Grenié et al. 2017)
fuzzySim	4.38	(Barbosa 2015)
ggcorrplot	0.1.4.1	(Kassambara 2023)
ggrepel	0.9.6	(Slowikowski et al. 2024)
hillR	0.5.2	(Li 2018)
janitor	2.2.1	(Firke et al. 2024)
lme4	1.1.37	(Bates et al. 2015)
mFD	1.0.7	(Magneville et al. 2022)
patchwork	1.3.2	(Pedersen 2025)
performance	0.15.3	(Lüdecke et al. 2025)
permuco	1.1.3	(Frossard and Renaud 2021)
phytools	2.5.2	(Revell 2024)
picante	1.8.2	(Kembel et al. 2010)
randomForest	4.7.1.2	(Liaw and Wiener 2002)
rdacca.hp	1.1.1	(Lai et al. 2022)
tidyverse	2.0.0	(Wickham et al. 2019)
UpSetVP	1.0.0	(Liu 2022)
vegan	2.7.2	(Oksanen et al. 2025)

Appendix S5. Risk of Bias assessment

This Risk of Bias assessment is adapted from ROBITT framework (Boyd et al. 2022).

1. ROBITT iteration number: 1

2. Statistical population of interest

2.1 Define the statistical target population about which you intend to make inferences.

Detailed in the methods.

2.2 What are your inferential goals?

Detailed in the methods.

2.3 From where were your data acquired (please provide citations, including a DOI, wherever possible)? What are their key features in respect of the inferential aims of your study (see the guidance document for examples)?

Detailed in the methods and Appendix (S3).

2.4 Provide details of, and the justification for, all of the steps that you have taken to clean the data described above prior to analyses.

Detailed in the methods.

3. Bias assessment and mitigation

3.1 At what geographic, temporal and taxonomic resolutions (i.e. scales or grain sizes) will you conduct your bias assessment?

Geographic level: plot level (12 fixed plots). Temporal: annual surveys in July, and 6 years per plot. Taxonomic/organismal level: community (vascular + bryophytes, including litter for a part of first question) and vascular-only subsets (for remaining analyses).

3.2 Are the data sampled from a representative portion of geographical space in the domain of interest?

Yes, our site (111 ha) is a transitional peatland. Within our site, the 2 microhabitats (WET/DRY) cover the typical hydrological gradient of raised bog/poor fen mosaics in region IV (region IV; Tanneberger et al., 2021; see methods). However, this is a single-site study: inference is intended for peatlands with similar characteristics (bogs and fens similar to ours).

3.3 Are your data sampled from the same portions of geographic space across time periods?

Yes, plots are permanent, and were installed in 2008, as well as OTCs. Same plot locations sampled every year. See methods.

3.4 If the answers to the above questions revealed any potential geographic biases, or temporal variation in geographic coverage, please explain, in detail, how you plan to mitigate them.

No potential biases. Models we used include plot random intercepts (i.e., “(1|plot)”) to account for within plot temporal dependencies. No major geographic coverage variation is expected because plots are permanent.

3.5 Are your data sampled from a representative portion of environmental space in the domain of interest?

Yes, **the WET/DRY contrast captures a water table depth (WTD) gradient central to our inferential aims.**

3.6 Are your data sampled from the same portion of environmental space across time periods?

Vegetation sampling occurred in July. Interannual coverage is not homogeneously distributed (2008, 2009, 2010, 2012, 2024, 2025). But intrannual coverage survey are (all done in July). See methods.

3.7 If the answers to the above questions revealed any potential environmental biases, or temporal variation in environmental coverage, please explain, in detail, how you plan to mitigate them.

Inferences cannot be made from 2013 to 2023, we will focus on large temporal scale evolutions (especially for community temporal stability and species asynchrony).

3.8 Is the sampled portion of the taxonomic (or phylogenetic, trait or other space if more relevant) space representative of the taxonomic (or other) domain of interest?

Yes, within the study design. The same protocol was applied across all plots, and replication is balanced (3 plots per WET/DRY × experimental warming treatment combination).

3.9 Do your data pertain to the same taxa/taxonomic domain across time periods?

Yes.

3.10 If the answers to the above questions revealed any potential taxonomic biases, or temporal variation in taxonomic coverage, please explain, in detail, how you plan to mitigate them.

No potential bias.

3.11 Are there other potential temporal biases in your data that relate to variables other than ecological states?

Sampling intensity changed (400→200 points, see methods). Observer effect (one person did the vegetation survey from 2008 to 2012 and another from 2024 to 2025). Irregular time steps (gaps between 2012 and 2024).

3.12 Are you aware of any other potential biases not covered by the above questions that might cause problems for your inferences?

No.

3.13 If questions 3.11 or 3.12 revealed any important potential biases, please explain how you will mitigate them.

Sampling intensity changed (400→200 points, see methods): addressed by using relative cover. Observer effect (one person did the vegetation survey from 2008 to 2012 and another from 2024 to 2025): minimized with fixed protocol and with the fact that both scientists are well trained botanists and know very well this specific vegetation. Irregular time steps (gaps between 2012 and 2024): but time series lengths are the same across plots to compute community temporal stability and species asynchrony; the method that we choose are comparable given equal temporal cover.

Appendix S6. Principal Component Analysis (PCA) of plant community composition

PCA biplot based on Hellinger-transformed species abundance data. Convex hulls delimit the four experimental conditions (hydrology × warming). Control and heated plots largely overlap within each hydrological block, while DRY and WET communities remain clearly separated, consistent with the constrained ordination results (RDA; Fig. 1A).

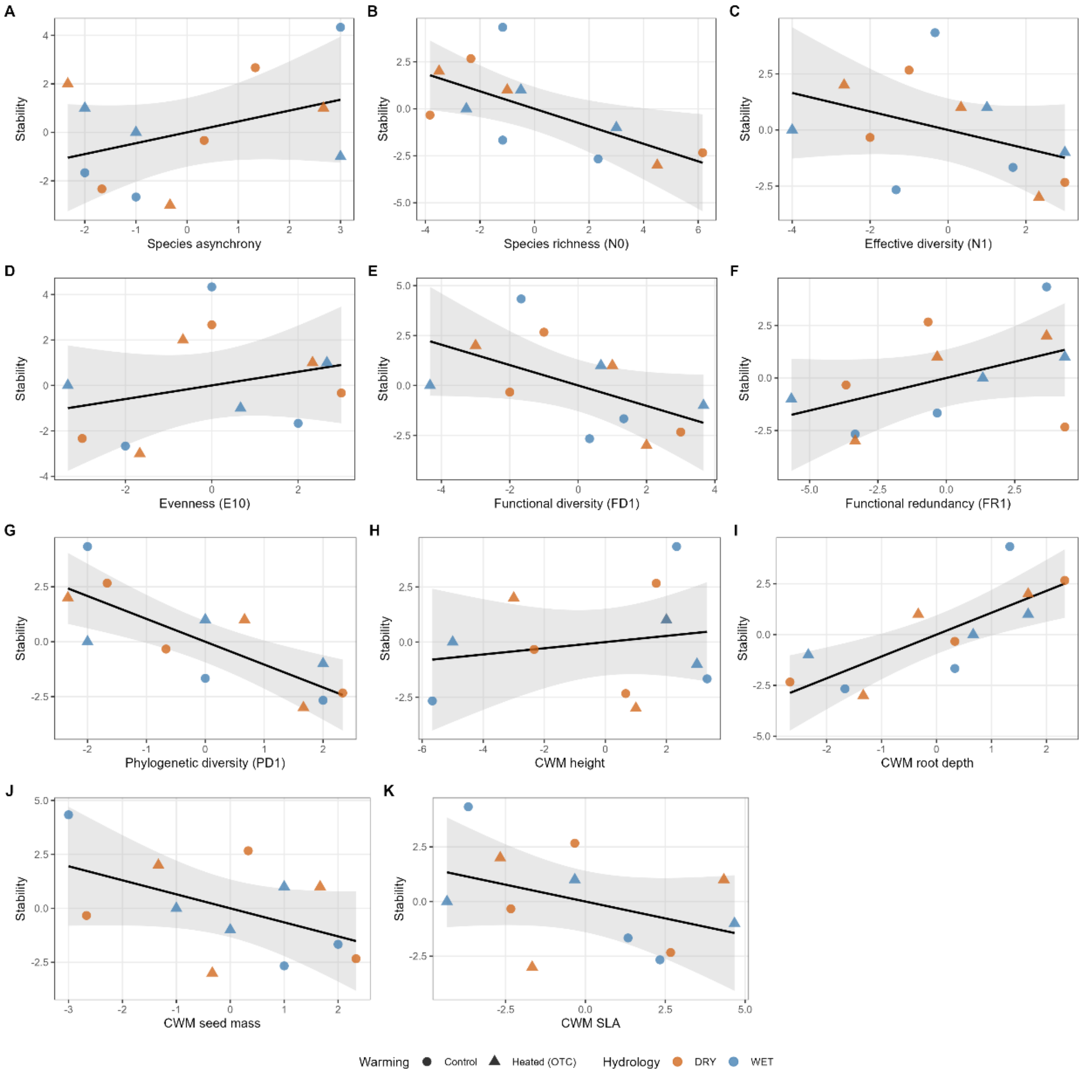
Appendix S7. Effect size (*ρ*) and significance (*p*-values) of the residual correlations between the various facets of diversity, community temporal stability, and species asynchrony

Correlations were computed on rank-transformed variables after extracting residuals from linear models controlling for experimental factors (see Methods section of the main manuscript). P-values are reported for transparency, but interpretation focuses on effect sizes (Popovic et al. 2024; Wasserstein et al. 2019). False discovery rate (FDR) correction was applied using the Benjamini-Hochberg procedure across all correlations. Abbreviations: N0 = species richness; N1 = Shannon diversity; E10 = Shannon evenness; FD1 = functional diversity; FR1 = functional redundancy; PD1 = phylogenetic diversity; Faith PD = Faith's phylogenetic diversity; CWM = community-weighted mean (of different traits).

Response	Predictor	ρ	p_uncorrected	p_FDR
Asynchrony	N_0	−0.02	0.9430	0.9790
Asynchrony	N_1	0.14	0.6560	0.7940
Asynchrony	E_{10}	0.25	0.4320	0.6620
Asynchrony	CWM Height	0.40	0.1950	0.4160
Asynchrony	CWM Root depth	−0.07	0.8250	0.9300
Asynchrony	CWM Seed mass	−0.30	0.3430	0.5940
Asynchrony	CWM SLA	0.23	0.4730	0.6800
Asynchrony	FD_1	0.15	0.6480	0.7940
Asynchrony	FR_1	−0.38	0.2240	0.4280
Asynchrony	PD_1	0.01	0.9790	0.9790
Asynchrony	Faith PD	−0.06	0.8490	0.9300
Stability	N_0	−0.66	0.0195	0.1500
Stability	N_1	−0.41	0.1820	0.4160
Stability	E_{10}	0.29	0.3620	0.5940
Stability	CWM Height	0.19	0.5460	0.7390
Stability	CWM Root depth	0.79	0.0024	0.0274
Stability	CWM Seed mass	−0.50	0.1010	0.3880
Stability	CWM SLA	−0.41	0.1820	0.4160
Stability	FD_1	−0.54	0.0671	0.3090
Stability	FR_1	0.47	0.1190	0.3920
Stability	PD_1	−0.79	0.0021	0.0274
Stability	Faith PD	−0.63	0.0278	0.1600
Stability	Asynchrony	0.40	0.1990	0.4160

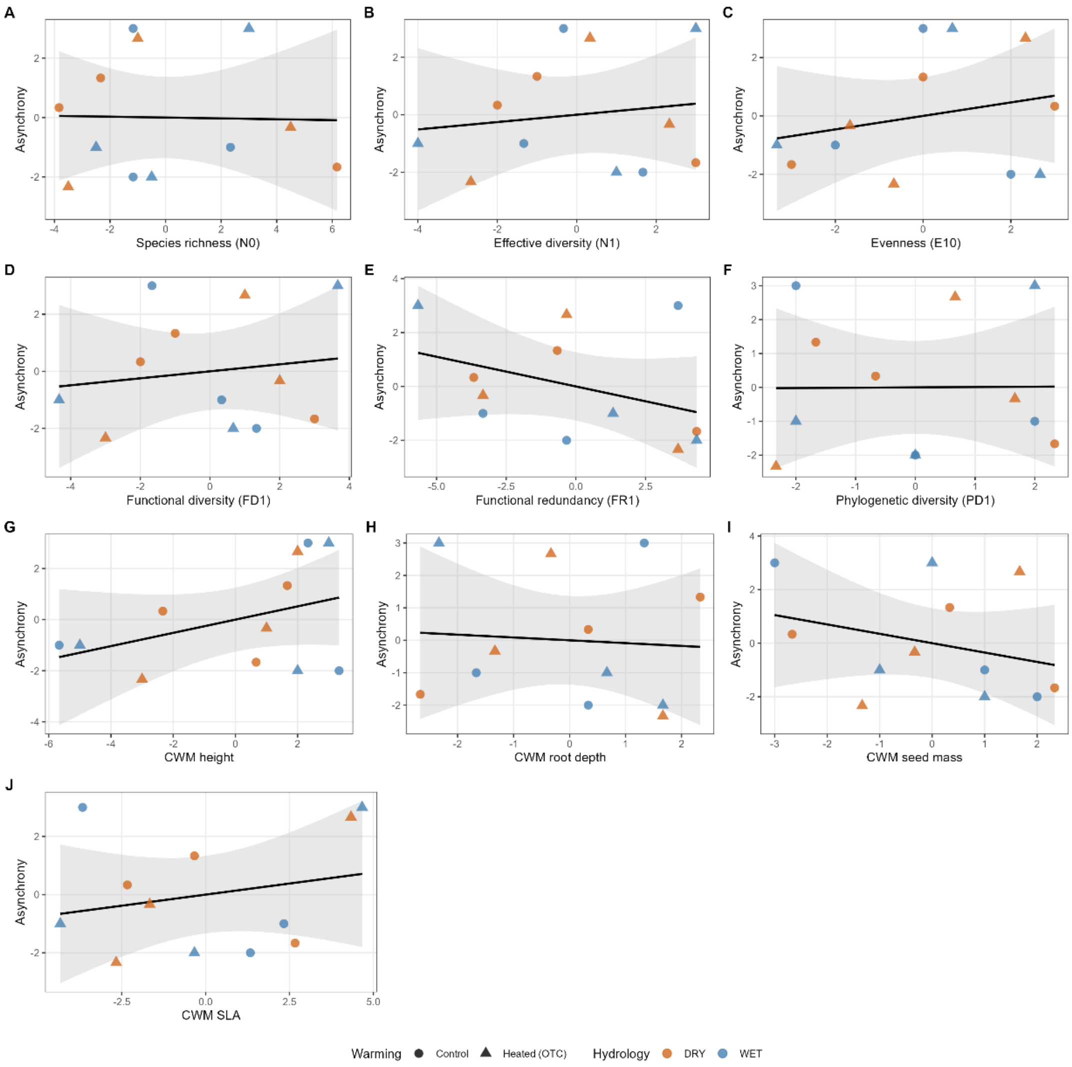
Appendix S8. Partial residual relationships between community stability and diversity metrics.

Scatterplots showing relationships between stability and (A) species asynchrony, (B) species richness (N_0), (C) effective diversity (N_1), (D) evenness (E_{10}), (E) functional diversity (FD_1), (F) functional redundancy (FR_1), (G) phylogenetic diversity (PD_1), (H) CWM height, (I) CWM root depth, (J) CWM seed mass, and (K) CWM SLA. All values are partial residuals after controlling for experimental conditions (hydrological × warming, n = 12 plots, see Methods section). Black lines show linear regression fits with 95% confidence intervals. Corresponding partial correlation coefficients are reported in Fig. 4C and Appendix S7.



Appendix S9. Partial residual relationships between species asynchrony and diversity metrics.

Scatterplots showing relationships between asynchrony and (A) species richness (N_0), (B) effective diversity (N_1), (C) evenness (E_{10}), (D) functional diversity (FD_1), (E) functional redundancy (FR_1), (F) phylogenetic diversity (PD_1), (G) CWM height, (H) CWM root depth, (I) CWM seed mass, and (J) CWM SLA. All values are partial residuals after controlling for experimental conditions (hydrological × warming, n = 12 plots, see Methods section). Black lines show linear regression fits with 95% confidence intervals. Corresponding partial correlation coefficients are reported in Fig. 4C and Appendix S7.



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