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RESEARCH ARTICLE

Retention forestry enhances the resilience of the moss *Hylocomium splendens* to extreme drought in boreal forests

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Abstract

1. Understorey biodiversity is increasingly impacted by extreme climate events. Retention forestry, which involves preserving small patches of live and dead trees from preharvest forests within clearcuts, can help mitigate these extremes by creating more favourable microclimates than traditional clearcutting practices. Despite their importance in buffering climate extremes, it remains unclear whether, and to what extent, the microclimates in retention patches enhance the growth response and recovery of the understorey after extreme droughts in boreal managed forests.
2. We retrospectively investigated the annual growth response from 2016 **to** 2022 of the mat-forming understorey moss *Hylocomium splendens*, in relation to micro- and macroclimate, including an extreme drought in 2018, in retention patches relative to clearcuts and mature forests, across 130 plots distributed across 30 forest sites in a boreal landscape in Sweden.
3. The 2018 summer drought reduced the annual growth rates of *H. splendens*. Clearcuts experienced the greatest climatic impact from the 2018 drought and exhibited the lowest growth rates, followed by retention patches, while mature forests maintained the highest growth rates. This pattern persisted subsequent two post-drought years. Closer alignment of below-canopy temperature and vapour pressure deficits (VPDs) with those of mature forests enhanced moss growth in retention patches, bringing it closer to the levels observed in mature forests.
4. In clearcuts and mature forests, where variation in forest canopy and microclimate was minimal, biological legacies did not influence annual moss growth. In retention patches, however, a greater basal area of large living trees and the presence of standing deadwood contributed to higher canopy closure, which reduced microclimate VPDs and increased *H. splendens* growth. Increasing volumes of lying deadwood positively contributed to *H. splendens* growth, likely by creating favourable microhabitats and microclimates near the logs.
5. *Synthesis and applications*. This study demonstrates that drought reduced the growth of mat-forming understorey *H. splendens* in boreal forest ecosystems, but

drought effects in clearcuts are mitigated in retention patches. By preserving large living trees, standing and lying deadwood, retention patches can be further optimized. Foresters and policymakers can use these findings to minimize the impact of drought after clearcutting on understorey biodiversity and functionality.

KEYWORDS
biological legacy, climate change, deadwood, drought, microclimate, moss growth, retention forestry

1 | INTRODUCTION

With future extreme events, specifically warming and the increasing frequency and intensity of droughts and heatwaves (IPCC, 2021), it is crucial to understand to what extent these climate extremes will threaten ecosystem functionality and biodiversity (Roe, 2019). Boreal forests, which cover approximately 29% of the global forest area and support a diverse array of species across various taxonomic groups in climatically challenging environments (Kayes & Mallik, 2020), are likely to be more adversely impacted by global climate change because of the anticipated accelerated temperature rise at higher latitudes, coupled with the above-average occurrence of extreme climatic events (IPCC, 2021). The recent massive die-off of Norway spruce in Central and Northern Europe, attributed to the long-term effects of the 2018 drought in Europe (Kunert, 2020), underscores the urgency of developing conservation strategies to enhance climate resilience in boreal forests (Hylander et al., 2022).

To achieve this, the EU Forest Strategy for 2030 proposes Closer-to-Nature Forest Management to enhance conservation values and climate resilience in multifunctional, managed forests across Europe (Larsen et al., 2022). This management approach emphasizes principles, such as retaining habitat trees, preserving special habitats and deadwood, encouraging natural tree regeneration, implementing partial harvests, promoting structural heterogeneity within stands, fostering tree species mixtures and genetic diversity, and minimizing intensive management practices (Larsen et al., 2022). Retention forestry, which preserves biological legacies, such as live and dead trees and small patches of intact forests, is widely used in northern Europe's boreal forests to maintain structural and compositional complexity from preharvest to postharvest (Gustafsson et al., 2012). This approach creates small, isolated patches within harvested areas, fostering biodiversity and maintaining a more complex forest structure in the regenerating stand compared with clearcutting alone (Gustafsson et al., 2012). Additionally, retention forestry more effectively buffers solar radiation and creates favourable microclimates for shade-tolerant forest species (Zhang et al., 2024). As a result, it has been identified as crucial for conservation planning, climate adaptation and mitigation strategies within boreal forest landscapes (Gustafsson et al., 2012; Hylander et al., 2022; Larsen et al., 2022; Zhang et al., 2024). Although isolated retention patches have been shown to have a thermal buffering effect (Zhang et al., 2024), it remains uncertain to what extent the mitigated microclimates in such retention patches have a positive impact on understorey vegetation under extreme climate events. Studies in exposed forest environments, such as edges and clearcuts, suggest that boreal forest understorey species are sensitive to microclimatic changes (Hylander, 2005; Rudolphi et al., 2014; Schmalholz & Hylander, 2011). These effects can be intensified during drought, particularly at forest edges (Koelemeijer et al., 2022, 2023). Accordingly, detailed comparisons of understorey responses in retention patches versus open to semi-open clearcuts and larger, closed-canopy mature forests are still needed. Furthermore, responses to extreme climates vary by species and environment, and studies of understorey vegetation extending beyond 1 year post-event across different forest management practices are still scarce (Maxwell et al., 2019). This is driven by the infrequency of extreme climatic events and the unclear mechanisms by which different forest management practices support species under such conditions.

In 2018, Europe experienced record-breaking heatwaves, marked in Sweden by the highest temperature (over the past 120 years) and drought (the lowest precipitation levels in the last 20 years) anomalies during the summer season (Peters et al., 2020). This extreme drought event presents a distinctive opportunity to evaluate the effectiveness of retention forestry in mitigating potential negative effects arising from forest clearcutting and elevated climatic pressures on forest species. In this study, we conducted a retrospective analysis by quantifying the annual growth of *Hylocomium splendens* to assess the efficacy of retention forestry in preserving the understorey during the 2018 drought. This method, initially proposed by Koelemeijer et al. (2023) to study drought effects on understorey responses in boreal forests, identified *H. splendens* as a promising bioindicator due to its unique growth pattern, life strategy and role in ecosystem functioning. The study found that higher levels of forest canopy closure and tree height mitigated the impact of edge effects during drought conditions. *H. splendens* is a perennial, clonal moss that forms new growth segments annually on top of the previous year's segments (Økland, 1995). Its growth increments are closely linked to its poikilohydric strategy, which relies on ambient moisture levels and narrow temperature ranges for optimal photosynthesis (He et al., 2016). Perennial mat-forming mosses, such as *Hylocomium* spp., contribute significantly to biodiversity and forest ecosystem services in northern boreal regions (Eldridge et al., 2023). Furthermore, the growth response of *H. splendens* can potentially signal declines of more sensitive understorey species (Hylander, 2005; Koelemeijer et al., 2022).

In this study, we utilize *H. splendens* as a bioindicator of forest understorey responses to drought by analysing growth patterns in both segment length and width in response to detailed forest macro- and microclimate variables. Additionally, we examine both the growth response and recovery of *H. splendens* following the extreme drought of 2018, comparing retention patches with clearcuts and mature forests in a boreal forest landscape in central Sweden. Økland (1995) developed a model that combines segment length, width and branch number to provide a comprehensive measure of dry weight. Hylander (2005) and Koelemeijer et al. (2023) used individual segment length measurements as a key metric to investigate growth relationships with drought, macroclimate and forest structural proxies for microclimate in forest-edge environments. Developing comparable models following Økland (1995) in clearcut environments would require significantly more effort, as drought and other stressors in these settings increase the prevalence of a unique growth pattern, that is monopodial growth. Instead, we focused our analysis on branch width, choosing it as a practical and reliable alternative due to time constraints and its strong correlation with other growth measures (see Section 2.4 for details). By quantifying the annual growth of *H. splendens* from 2016 to 2022, we evaluated the following hypotheses: (i) the extreme drought event in 2018 leads to a significant reduction in the annual growth of *H. splendens* compared with both pre- and post-drought growth periods, and (ii) clearcut experience the most significant impact, followed by retention patches, with the least impact observed in mature forests. Since the annual growth of new segments of *H. splendens* partly depends on water and nutrients supplied from its mother segment (Økland, 1995; Tamm, 1953), the 2018 drought event is likely to exert prolonged effects in subsequent years. We measured understorey moss growth and forest microclimates (temperature and humidity) 1–2 years after the drought (i.e. 2019 and 2020) to evaluate whether retention practices support understorey recovery following drought through microclimate modifications. Specifically, we hypothesized that (iii) the understorey growth of *H. splendens* would remain the lowest in clearcuts, followed by retention patches, and highest in mature forests post-drought. Furthermore, we hypothesized (iv) that retention patches with microclimates closely resembling those of mature 'reference' forests would exhibit moss growth levels closer to that in mature forests. Finally, we hypothesized that (v) the understorey moss growth in retention patches can be enhanced by increasing macroclimate buffering from biological legacies. Retention practices, through the preservation of biological legacies, including live and dead trees, as well as overstorey tree diversity, thus directly or indirectly influence the growth rate of *H. splendens*, given their influence on forest canopy and microclimates (cf. Zhang et al., 2024).

2 | MATERIALS AND METHODS

2.1 | Study area

Data collection and measurements took place across 130 plots within 30 research sites situated in a boreal forest landscape in Ånge Municipality, central Sweden. These locations spanned the coordinates 62°24′23.9″ N–62°27′54.7″ N and 15°28′55.7″ E–15°39′36.3″ E (Figure 1a,b). Necessary permission for the field studies was obtained from Västernorrland County Administrative Board (permit number: 521-5189-2020). The forest composition was primarily dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with smaller proportions of birch (*Betula* spp.), aspen (*Populus tremula*), alder (*Alnus* spp.) and goat willow (*Salix caprea*). The understorey was characterized by dwarf shrubs, such as *Vaccinium myrtillus* and *V. vitis-idaea*, while the forest floor featured moss species like *Hylocomium splendens* and *Pleurozium schreberi*. The research sites were located at elevations ranging from 256 to 425 m a.s.l., with a mean annual temperature of 3.48°C and an average annual precipitation of 552 mm, based on data from the nearest weather stations of the Swedish Meteorological and Hydrological Institute (SMHI) during 2000–2023. Central Sweden's forests have undergone over 70 years of intensive management, resulting in a mosaic of various-aged managed forests and clearcuts (Jönsson et al., 2009). Consequently, few older mature forests remain, isolated within a landscape dominated by younger, intensively managed forest stands (Jönsson et al., 2009).

2.2 | Study design

In this study, the 130 plots were situated within a variety of forest conditions, including stands of mature/old forests (spanning 4.0–11.0 ha), clearcuts aged 3–20 years where planted tree saplings were regenerating, and smaller retention patches (0.02–0.56 ha) preserved during the final harvesting process. The mature forests in our study area, which have likely been selectively cut historically and undergone long-term (90–150 years) natural regeneration without clearcutting and recent human management interventions (e.g. no thinning in the most recent decades), were located nearby (within 11.1 km) the clearcuts with retention patches. Therefore, we have 10 sites for mature forests, and 20 sites for both retention plots and clearcut plots in the same sites (Figure 1). Within each retention patch, the sampling design consisted of a transect starting with Plot R1 centred at *c.* 1.5 m distance from the southern edge, followed by Plot R2 centred within the retention patch, and ending with Plot R3 centred at *c.* 1.5 m distance from the northern edge (Figure 1c). Additionally, we established plots in clearcuts located approximately 30 m from both the south- and north-facing edges of the retention patches (plot CC1 and CC2 in Figure 1c). In the interior of mature forests, we set up three plots across a *c.* 30 m transect (similar to the average diameter of retention patches) (plot MF1–MF3 in Figure 1d). Data from clearcuts reflect intensive forest management and recent human disturbance, while data from mature forests serve as 'reference' sites with no recent human disturbance and located at least 50 m from any forest edge.

2.3 | Micro- and macroclimate

At all 130 plots, climate loggers (Lascar Easylog EL-USB-2; accuracy ±0.5°C for temperatures ranging from −35 to +80°C) were installed

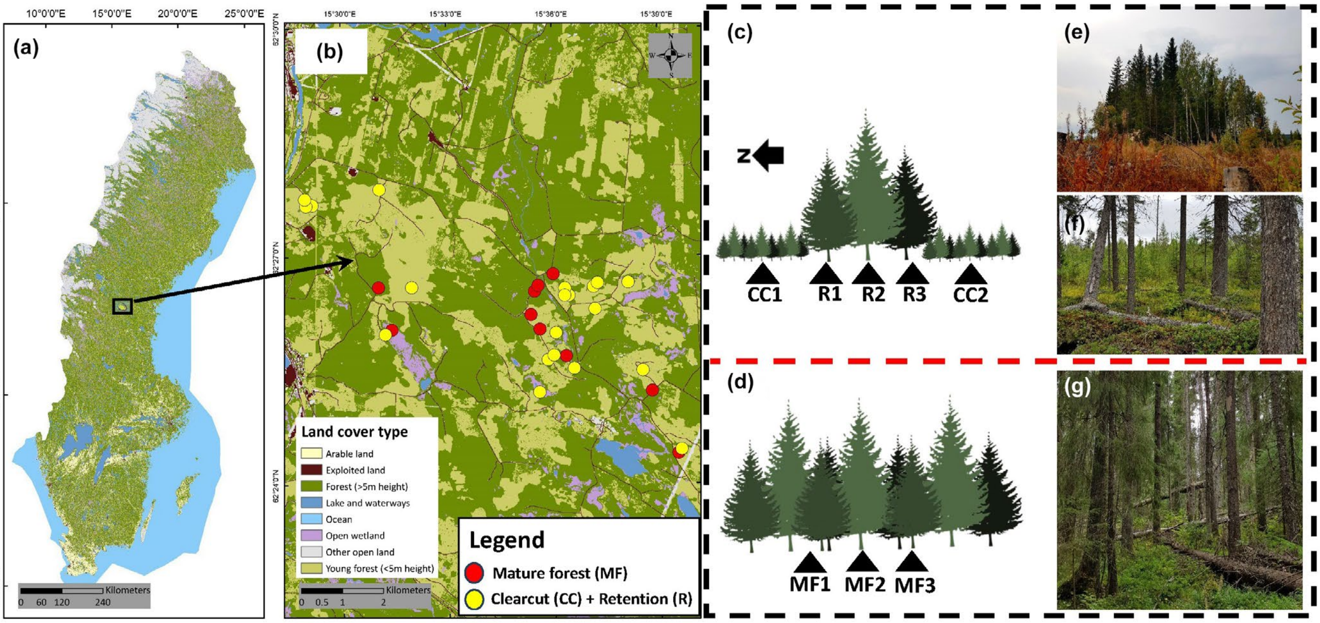

FIGURE 1 Location of the study area (a) and distribution of the 30 research sites (Site ID, b) in central Sweden, modified after Zhang et al. (2024). The map (b) shows the location of the 10 mature forests (marked in red circles) and 20 clearcut sites with associated retention patches (marked in yellow circles). The sampling design for the plots in the clearcuts and retention patches is detailed in (c), while the sampling in mature forests is outlined in (d). In panel (c), the black triangles labelled CC1 and CC2 represent the northern and southern clearcut areas, respectively, while R1, R2 and R3 mark plot arrangements within retention patches. Panel (d) shows MF1, MF2 and MF3, which denote plot setups located in mature forests. Black triangles in both panels (c) and (d) indicate positions where climate data loggers were installed, as well as locations for collecting moss and forest structural data. Field photographs depict various site features, including a dense retention patch with mixed tree species visible from the adjacent clearcut area (e), a retention patch characterized by reduced canopy closure, lower basal area and a less diverse tree composition from within the patch (f) and an image of a mature forest (g). The maps in panels (a) and (b) are based on data from the Swedish National Land Cover Database (2018), supplied by the Swedish Environmental Protection Agency.

to monitor air temperature (*T*) and relative humidity. Data were recorded at 6-h intervals during June, July and August in 2019, and at hourly intervals during the same months in 2020. The loggers were positioned approximately 75 cm above the ground on wooden poles or trees, mounted on wooden boards and protected by small white plastic cups that served as radiation shields, minimizing direct sunlight and rain exposure while allowing airflow. To reduce solar interference, the loggers were installed on the north-facing side of trees or poles. Below-canopy microclimatic moisture conditions were quantified using vapour pressure deficit (VPD), calculated from the observed temperature and humidity values following Zhang et al. (2024) (details provided in Method S1). Data were processed into daily averages and then further condensed into seasonal means for each plot in 2019 and 2020.

2.4 | *H. splendens* sampling and measurement

We collected *H. splendens* from 8 to 14 May 2023. The sampling and survey of *H. splendens* took place in quadrats centred on the sensors' locations (depicted by plot locations in Figure 1). At each quadrat, we placed a 0.5 × 0.5 m sub-square on the ground in each cardinal direction, 0.75 m from the logger station. We selected three random 0.5 × 0.5 m sub-squares. In each sub-square, we randomly collected a small tuft of *H. splendens* shoots (~4 × 4 cm) directly from the soil, as close to the sub-square centre as possible. If only a few scattered shoots were present, we sampled the three shoots closest to the centre. Each sample consisted of at least three mature, intact shoots of varying sizes (both small and large), ensuring representation of the available segment size range, with a minimum of nine shoots collected per plot. In the event that *H. splendens* was absent within a quadrat, we endeavoured to locate the nearest moss along the corresponding cardinal direction and recorded its distance from the data loggers (7 out of 130 plots). After being collected, the samples were air-dried in paper bags and rehydrated prior to measurement. The mean ground cover of *H. splendens* in sub-squares was 12.2% in clearcuts, 35.7% in retention patches and 69.8% in mature forests.

We retrospectively quantified the annual growth of six randomly selected (out of a minimum of nine collected) *H. splendens* shoots per plot (Figure 1) and measured the segment length and maximum width from 2016 to 2022, resulting in a total of 3832 measurements for each variable. The annual segment length was measured from the base to the apical tip, along with the segment's widest point across the branching perpendicular to its length, using a digital calliper to the nearest 0.01 mm. When more than one segment was produced in a year ($n = 409$), a random segment was selected for measurement. Although a segment's 'production potential'—its capacity to produce biomass for daughter shoots—is proportional to its size and shared among multiple segments (Økland, 1995), we determined that branching segments did not significantly affect the overall growth measures. This conclusion is supported by the lack of a significant difference in the frequency of multiple segments across forest habitat types ($p=0.658$ based on ANOVA). Additionally, a previous study has shown that branching patterns are typically not influenced by edge effects (Koelemeijer et al., 2023), further supporting the robustness of our measurements. Previous research has shown that new growing points usually arise sympodially, where the apical main axis terminates and growth continues from one or more lateral branches. However, Økland (1995) found that, on average, 7.3% of new growing points originate monopodially, with the main axis continuing to grow with a slight curvature. Although the frequency of monopodial growth varies in complex and not fully understood ways, this uncommon growth pattern has been observed in association with certain environmental stressors (Økland, 1995; see also Figure S1). While monopodial growth can complicate yearly length measurements, it is important to note that such growth patterns do not preclude the use of length-based growth modelling, as demonstrated by Økland (1995). Nonetheless, in this study, we opted to use annual maximum width as the sole measure of growth due to time constraints and the strong positive relationship between segment maximum width and length. Regression analyses revealed significant correlations, with coefficients of 0.67, 0.85 and 0.98 in mature forests, retention patches and clearcuts, respectively (Figure S2), supporting the validity of our approach.

2.5 | Forest structure

To characterize forest structure and tree species composition, we surveyed all living large trees (a minimum diameter at breast height [DBH] of 10 cm) within 5-m radius plots (allowing three plots to fit in retention patches), around the installed climate data loggers (Figure 1). Tree DBH was measured using a calliper at 1.30 m above the ground in May 2023. The basal area (BA, $m^2\ ha^{-1}$) for each tree species was then calculated using the measured DBH values. Tree species diversity was represented by the Shannon diversity index (denoted as H index; Method S2), based on species relative proportions from basal area (Zhang et al., 2024). Canopy closure, defined as the percentage of the sky covered by the branches and crowns of trees, was measured at the same locations as the climate loggers using photographs taken with a standard-angle camera lens and analysed digitally using ImageJ (see also Zhang et al., 2024). Measurements were conducted under cloudy conditions in August 2020 to reflect canopy conditions during the growing season. All standing and lying dead trees, with a DBH greater than 2 cm or a large-end diameter exceeding 2 cm, originating within the plot, were recorded. We calculated the basal area of standing deadwood ($m^2 ha^{-1}$) and the volume of lying deadwood ($m^3 ha^{-1}$) (Method S3). The small size of our 5-m radius sampling plots likely led to an underestimation of the volume of lying deadwood in the interior of mature forests, as larger, dispersed substrates (compared with retention patches) may have originated outside this limited sampling area (only 7/27 mature forest plots contained lying deadwood). Larger plots, such as 10-m radius plots of the Swedish National Forest Inventory, typically provide a more representative sample. This could explain the lower values observed in our study compared with larger-scale inventories (Nilsson et al., 2020). The multiple sampling plots within mature forests were nonetheless useful for comparing smaller-scale structural differences and relations to microclimate in our study. Detailed structural attributes of clearcuts, retention patches and mature forests (hereafter referred to as 'habitat types') are reported in Table S1.

2.6 | Data analyses

We applied linear mixed models (LMMs) with 'habitat type' as a fixed effect and '1|Site ID' as a random effect to test whether the mean annual maximum width differed between the habitat types (i.e. clearcut vs. retention vs. mature forest) for each recorded year (2016–2022). Additionally, model results for growth differences between years (including 'year' as a fixed effect) for all habitat types individually and pooled were included in the Supporting Information, but should be viewed cautiously due to declining segment vitality of older parts. Mean annual maximum moss widths were calculated from the measurements of the sampled six shoots and were analysed in all models (hereafter referred to as 'annual maximum widths' or 'annual growth'), although older parts of the shoots generally had fewer intact years to measure (Table S2).

We applied LMMs to analyse moss growth in retention patches during the 2 years following the drought (2019 and 2020), in relation to detailed microclimate measurements. Since mature forests were identified as optimal reference conditions for moss growth recovery following drought (see Section 3.1), we calculated the mean microclimate values (T and VPD) and annual maximum widths in these forests as reference values, for each respective year. Delta (Δ) was introduced to represent the differences between retention patches and these mean reference values, treating them as both dependent (growth differences) and independent (microclimate differences) variables in the models. This method allowed us to assess whether minimizing microclimate differences towards reference values could enhance moss growth in retention patches to levels resembling mature forests. Given the high correlation between ΔT and ΔVPD ($r=0.96$), we modelled Δ annual moss growth as a function of either ΔT or ΔVPD in separate models to avoid multicollinearity. Each model included either ΔT or ΔVPD as a fixed effect, with nested terms ('1|Year/Site ID/Plot ID') as random effects. All LMMs were fitted by applying the lme function from the nlme package (Zuur et al., 2007).

Finally, we applied piecewise structural equation models (SEMs) to evaluate whether biological legacies (including large living trees, H index, standing deadwood and lying deadwood) impacted the growth of *H. splendens* following drought (2019 and 2020) directly, and/or indirectly via their impacts on the forest canopy closure and modified microclimates. Given the high correlation between T and VPD ($r=0.89$), we included only VPD in the SEMs to avoid multicollinearity. This is because VPD integrates both temperature and humidity and is more closely related to drought-induced plant physiological responses (Grossiord et al., 2020). We additionally included results for SEMs based on temperature in the Supporting Information. In this study, three SEMs were constructed separately for each habitat type. The setups of each pathway in the SEMs were reported in Method S4. The SEMs were implemented with the piecewiseSEM-package (Lefcheck, 2016). All analyses were performed using R version 4.2.3.

3 | RESULTS

3.1 | Drought effects on the annual growth of *H. splendens*

Differences in the annual growth of *H. splendens* between retention patches and clearcuts were year-specific (Figure 2; Table S3), while mature forests consistently exhibited the highest growth rates over the entire recording period (2016–2022). Notably, the annual growth of *H. splendens* was significantly higher in retention patches (19.4 ± 0.48 mm; mean ± SE) than in clearcuts (17.6 ± 0.56 mm) during 2018, a year characterized by extreme drought with low precipitation and high maximum temperatures (Figure 2; Table S2) throughout the main growing seasons (June, July and August). This pronounced difference persisted in the subsequent 2 years (2019 and 2020), with retention patches showing greater growth than clearcuts: 20.7 ± 0.47 mm vs. 18.5 ± 0.53 mm in 2019, and 21.4 ± 0.45 mm vs. 20.3 ± 0.50 mm in 2020 (both $p < 0.05$). In the pre-drought years 2016–2017 and post-drought years 2021–2022, no significant differences were observed in the annual growth of *H. splendens* between retention patches and clearcuts. Contrasting different years within habitat types, the moss *H. splendens* experienced its lowest recorded growth level in the 2018 drought year, especially in clearcuts (Figure S3).

3.2 | Effect of microclimates on annual moss growth in retention patches versus mature forests

Moss growth in retention patches increased when below-canopy temperatures and VPDs more closely resembled those of mature forests (smaller ΔT and ΔVPD), narrowing the gap in growth between them. This was shown by negative relationships between Δ maximum width and increasing microclimates differences (ΔT and ΔVPD) between retention patches and mature forests in the 2 years following the drought (Figure 3; Table S4). Specifically, a 1°C increase in Δ temperature reduced the Δ maximum width by approximately 0.80 mm ($p = 0.015$), while a 0.1 kPa increase in ΔVPD (indicating drier conditions) reduced it by approximately 0.46 mm ($p = 0.010$). However, even with similar microclimates, annual maximum widths in retention patches were generally lower than in mature forests.

3.3 | Effects of biological legacies on the annual moss growth

In the two summer growth seasons following the drought (2019 and 2020), we found that biological legacies contributed positively to the annual growth of *H. splendens* in retention patches, while they exhibited no significant relationships with growth in clearcuts and mature forests (Figure 4). In retention patches, a greater basal area of large living trees contributed positively to increased canopy closure, which, in turn, had a negative relationship with VPD and indirectly contributed to the higher annual growth of *H. splendens* (Figure 4). Similarly, increasing volumes of standing deadwood in retention patches also decreased VPD, indirectly contributing to the increased annual growth of *H. splendens*. Notably, the volume of lying deadwood directly contributed to the increased annual growth of *H. splendens* in retention patches, despite potentially indirectly

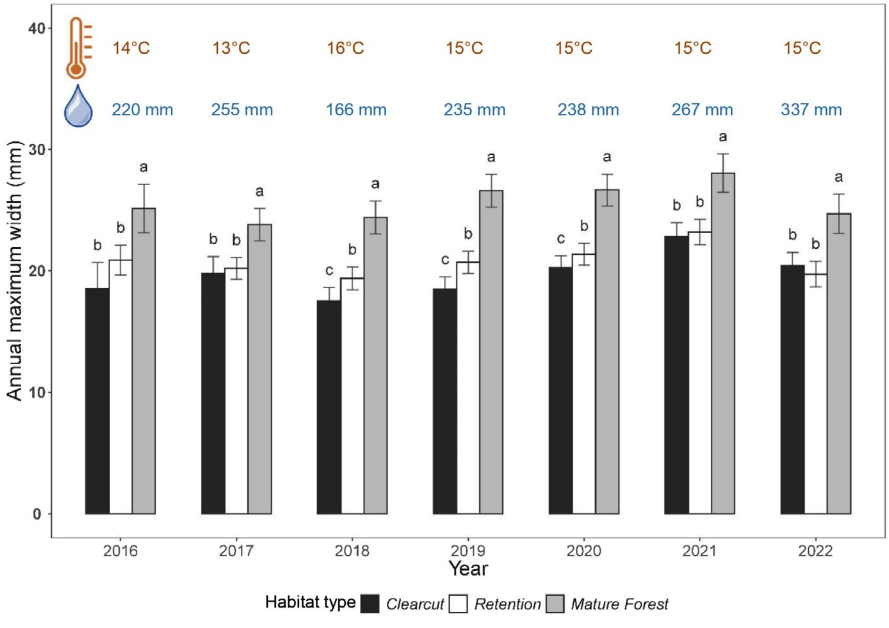

FIGURE 2 Moss growth (2016–2022) across different habitat types. Annual maximum width (mm) of *H. splendens* moss in clearcuts, retention patches and mature forests from 2016 to 2022. Bars depict the mean values, and error bars represent 95% confidence intervals (mean ± 1.96 × SE). Different letters denote statistically significant differences in growth rates of *H. splendens* among the three habitat types. The overlaid numbers show mean summer (June–August) macroclimate temperatures (orange) and precipitation (blue) for each year, sourced from the ERA5-land reanalysis database (mean ± SD in Table S2).

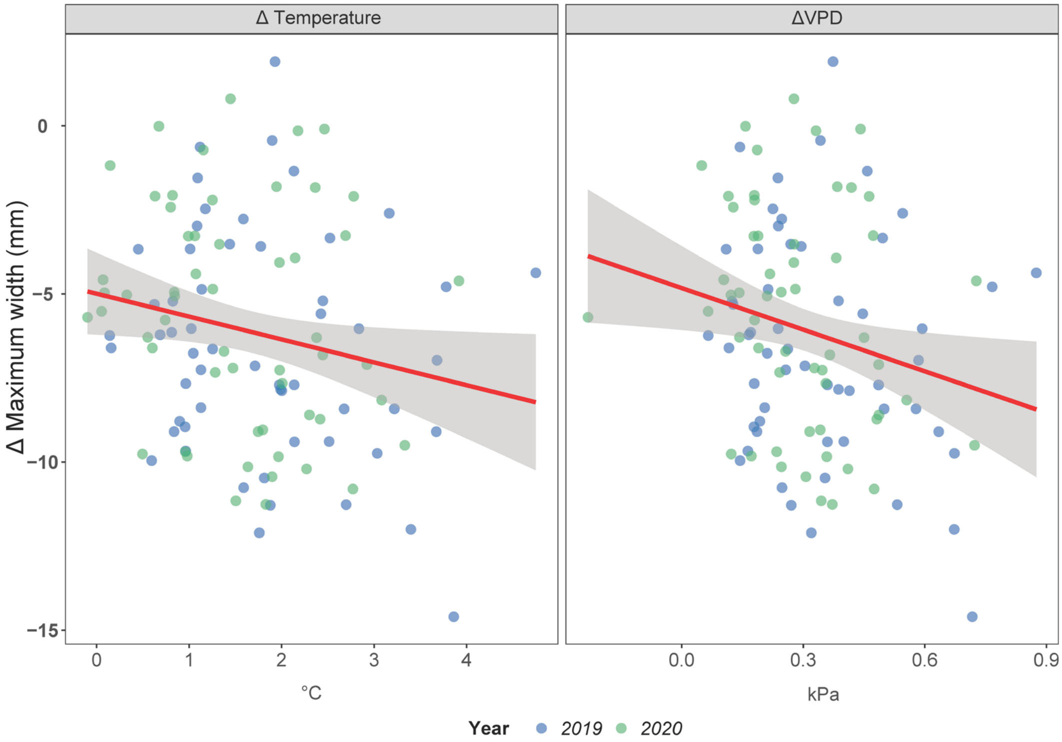

FIGURE 3 Relationship between moss *H. splendens* maximum width differences (Δ Maximum width) and microclimate differences (ΔTemperature and ΔVPD, respectively) in retention patches relative to mature forests in 2019 and 2020. Each dot represents the difference in moss growth (generally lower in retention) relative to differences in temperature and VPD (higher in retention, although one plot had lower VPD in retention in 2020) between the two habitat types. The red line shows the fitted regression, with a 95% confidence interval shaded in dark grey.

impacting the annual moss growth by lowering canopy closure and enhancing VPD (the overall slope was +0.22). In clearcuts and mature forests, although we indeed detected that biological legacies may potentially impact VPD, the annual moss growth was not impacted, given that no relationship was established between VPD and the annual moss growth in both habitat types. See Figure S4 for SEMs that include temperature, and Table S5 for detailed microclimate attributes across different habitat types.

4 | DISCUSSION

Numerous studies have projected that drought events will become more frequent and severe due to climate warming (Spinoni et al., 2018). In boreal forest ecosystems, it is crucial to understand the response and functionality of understories to climate warming and drought (Eldridge et al., 2023; He et al., 2016), particularly in extensive clearcuts practised with retention forestry. In this study, we applied a retrospective approach by quantifying the annual growth of *H. splendens* to reflect understorey moss growth in small retention patches under varying macroclimate conditions from 2016 to 2022, including a summer drought in 2018. Our experimental setups revealed that retention forestry can effectively mitigate the negative effect on understorey moss growth from extreme drought when compared to clearcuts, and this mitigation persists in the subsequent 2 years. Relative to mature forest conditions, however, the moss growth in retention patches was reduced and the recovery of the understorey moss growth following drought was dependent on the biological legacies and microclimate of retention patches. Our results showed that retaining large living trees and maintaining the volume of standing and lying deadwood in smaller patches during harvests can foster buffered microclimates that better support the growth of *H. splendens*, promoting healthier understories in managed boreal forests.

4.1 | Drought effect on *H. splendens* growth

In agreement with our first hypothesis (i), we demonstrated that the extreme drought in 2018 significantly impaired the understorey growth of the mat-forming *H. splendens* in boreal forests. This finding aligns with previous research showing that extreme climate events, such as drought and heatwaves, substantially impact the persistence (e.g. population size and mortality) and performance (e.g. changes in metabolic activity and growth) of diverse organism groups (Maxwell et al., 2019; Orsenigo et al., 2014). Specifically, significant declines in growth and population stability under extreme climate conditions have been documented for *H. splendens*, with notable effects from drought years, such as 1994 and 2018 (Halvorsen, 2019; Økland, 1997). The results also align with Koelemeijer et al. (2023), who highlighted that

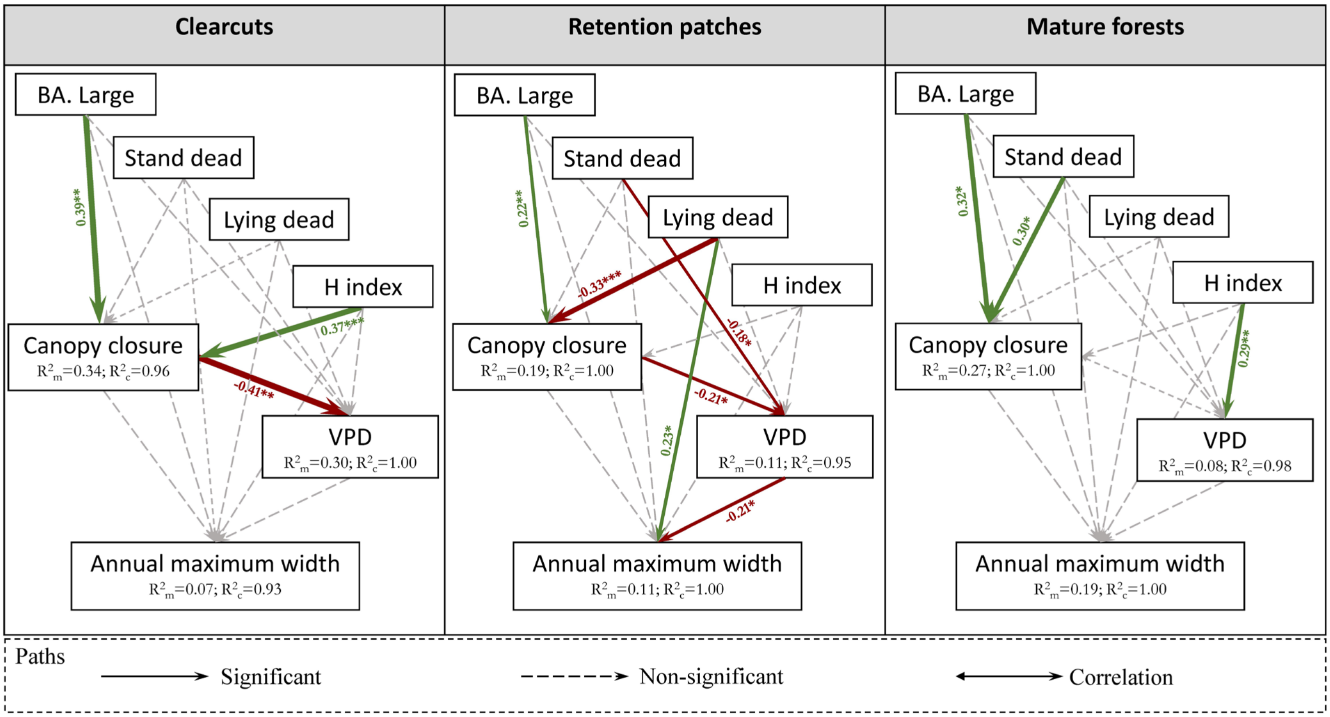

FIGURE 4 Piecewise structural equation model results of direct and indirect effects of the biological legacies (large living trees (BA. Large), standing and lying dead trees, and Shannon tree species diversity (H index)), forest canopy (canopy closure) and microclimate vapour pressure deficits (VPD) on the annual maximum width of *H. splendens* in respective clearcuts, retention and mature forests in 2019 and 2020. Marginal (R^2_m) and conditional (R^2_c) R^2 values for the fitted linear regression models are displayed below each estimator. Green arrows represent positive relationships, while red arrows indicate negative ones. Dashed arrows denote non-significant effects, and solid arrows signify significant effects, with the width of the solid arrows reflecting the strength of these effects. Asterisks (*, **, ***) denote significance levels at $p<0.05$, $p<0.01$ and $p<0.001$, respectively.

drought amplifies forest-edge effects on *H. splendens* growth in semi-natural boreal forest edges. Our study extends this knowledge in an applied forest management context by specifically evaluating the effectiveness of small, isolated retention patches—greatly affected by edge effects due to their size and isolation within harvested areas—in enhancing understorey resilience during drought.

Consistent with our second hypothesis (ii), we observed that the extreme drought in 2018 disproportionately impaired understorey moss growth in clearcuts compared with retention and mature forests. This suggests that while retention patches can mitigate some of the severe drought impacts seen in clearcuts, it does not fully replicate the buffering conditions and understorey growth of mature forests. Our findings are consistent with those of Tonteri et al. (2016), who reported that clearcutting poses a substantial threat to shade-tolerant species like *H. splendens*, leading to declines of over 70% following such disturbances. In contrast, thinning cuts can maintain or even increase the presence of *H. splendens* and other pleurocarpous mosses, such as *Pleurozium schreberi*. This is likely because thinning preserves partially shaded, moist microhabitats while allowing more light penetration and increasing the cumulative temperature, creating conditions that are beneficial for moss growth (Tonteri et al., 2016). Our results align with earlier research showing that bryophytes of conservation concern are often sensitive to clearcutting disturbances but can persist in managed retention patches, albeit at reduced rates compared with intact forests (Rudolphi et al., 2014). We demonstrate that a bioindicator bryophyte has the capacity to persist, albeit with reduced growth, in managed retention patches under drought conditions. Additionally, consistent with our third hypothesis (iii), the drought in 2018 induced a prolonged effect on moss growth in the two subsequent years (2019–2020), evident in a pronounced difference in moss growth among habitat types (clearcuts < retention < mature forests). This enduring drought impact on *H. splendens* growth can be attributed to the dependency of new segment production on the size of its mother segment (Table S6), corroborating the findings of Tamm (1953) and Økland (1995). Such legacy effects from severe disturbances and environmental stressors typically last 2–4 years, as growth curves indicate a gradual recovery in shoot size over time due to the slow increase in individual segment size following these events (Halvorsen, 2019; Økland, 1997). Long-term studies are generally important for improving predictions of species and understorey responses to extreme events, yet they remain rare (Maxwell et al., 2019). Retrospective annual measurements of *H. splendens* offer an alternative approach (Koelemeijer et al., 2023). However, retrospective approaches may not capture the full range of insights available from long-term demographic studies, such as those involving life cycle graphs and matrix modelling, which can offer a more comprehensive understanding of population dynamics over time (Rydgren & Økland, 2002). Our results suggest that if extreme droughts become more severe and recur every few years, even generalist species like *H.*

splendens can struggle to recover between events in clearcuts. More specialized understorey species, especially those found on convex substrates and in exposed microhabitats, could potentially experience more severe and prolonged negative effects (Koelemeijer et al., 2022; Schmalholz & Hylander, 2011). Combined with findings from studies of bryophytes in retention patches under normal climate conditions (Hylander, 2005; Jönsson et al., 2022; Rudolphi et al., 2014), our results underscore the importance of designing retention patches that mitigate diverse macroclimate conditions and promote forest understorey recovery following drought. Interestingly, we noticed that growth was generally low in all forest types in 2022, possibly due to the excessive rainfall recorded in the summer. Similar reductions in average size and population decline were also noted in southeastern Norway by Økland et al. (2023), suggesting this pattern may be more widespread. While these effects require further investigation, they could be due to the moss retaining excess external water, which increases resistance to air diffusion, hinders CO_2 exchange and reduces photosynthesis and other essential processes (Fan et al., 2022).

4.2 | Retention forestry to mitigate macroclimate and enhance understorey drought recovery

In line with our hypothesis (iv), reduced microclimate differences in retention patches enhanced moss growth to levels closer to those in mature forests. This aligns with Zellweger et al. (2020), who found that forest microclimates determine understorey plant responses to warming. Since macroclimate buffering is highly dependent on forest structural attributes (De Frenne et al., 2019) and edge effects (Koelemeijer et al., 2023), it can be expected that variations in microclimate was influential on the understorey in small and isolated retention patches. However, differences in daily mean temperature and VPD alone might not be able to fully account for the reduced growth rates in retention patches compared with mature forests. Future studies should explore a broader range of microclimate variables and variations (e.g. maximum and minimum values; Table S5) to better understand their impacts on understorey vegetation in retention patches. For instance, mature forests consistently exhibited superior VPD_{max} and T_{max} buffering capacities (Table S5), maintaining cool and humid conditions that are optimal for growth.

Although favourable microclimates significantly enhance moss growth in retention patches, their impact on annual moss growth in clearcuts and mature forests was minimal. This observation can be attributed to the limited variation in certain forest structural attributes and biological legacies present in these areas (refer to Table S1 for these attributes). As a result, no significant effect of biological legacies, forest canopy or microclimates on annual moss growth were found in clearcuts or mature forests when analysed individually. Therefore, our reporting and discussion focus on the findings observed in retention patches. Preserving biological legacies in retention patches influenced moss growth, in line with our hypothesis (v) and previous research (Schmalholz & Hylander, 2011). Our results support that deadwood legacies impact moss growth via modification of the microclimate, although the standing and lying deadwood contribute in different ways. The presence of standing deadwood potentially contributes to increased understorey moss growth by lowering VPDs in retention patches. Indeed, as an important structural component of forests, standing deadwood with bare crowns can still shield the ground from insolation, thereby contributing to more moist conditions (cf. Kovács et al., 2017; Zhang et al., 2024) and supporting understorey moss growth. On the other hand, presence of lying deadwood may negatively impact macroclimate buffering as a negative correlation was found between lying deadwood and canopy closure. Higher tree mortality and the resulting canopy gaps may have permitted increased heat penetration to the forest floor, reducing thermal buffering and exacerbating summer drought conditions (Schmidt et al., 2017; Thom et al., 2020). However, our findings simultaneously show that moss growth is directly amplified with higher amounts of lying deadwood in retention patches. This is indeed expected given that lying deadwood may create favourable microhabitats closer to the ground, such as beneficial light conditions, reduced wind, and increased humidity and nutrient availability very close to logs (Seibold et al., 2015).

Our results, combined with earlier studies (Hylander, 2005; Koelemeijer et al., 2023; Økland et al., 2023), suggest that *H. splendens* growth can serve as a bioindicator of forest understorey performance and biodiversity in response to land use and climate change. However, a limitation of the retrospective method is that we could only assess surviving shoots, with fewer segments available for measurement as shoots aged and decomposed. Given the differences in moss ground cover among habitat types, the measured shoots, especially those in clearcuts, likely represent individuals in more optimal microhabitats (Schmalholz & Hylander, 2011). Although we randomized sampling to mitigate this, our results likely underestimate clearcut effects by focusing on surviving shoots, as this approach potentially overlooks mortality among more vulnerable shoots and underrepresents the full impact of clearcut conditions. Unlike dendrochronology, where dead samples can be cross-dated, bryophytes deteriorate quickly, limiting growth estimates for pre-drought years (2016 and 2017) due to fewer segments and segment deterioration. Future studies should stratify moss sampling both immediately after drought and 4 years later to obtain robust pre- and post-drought growth estimates. Additionally, long-term monitoring through population data from permanent plots would be invaluable for capturing broader trends and recovery trajectories over time, enhancing our understanding of how repeated drought events affect understorey moss populations (Økland et al., 2023; Rydgren & Økland, 2002).

4.3 | Management implications

In boreal forest ecosystems, *H. splendens* is one of the most prevalent understorey moss species, occurring in over 75% of sampling plots across Fennoscandian forests (Pohjanmies et al., 2021), and is significantly impacted by forest cuttings of varying intensity

(Tonteri et al., 2016). Therefore, understanding how forest management practices can conserve forest understorey species is crucial, particularly in the context of more frequent and intense climate extremes. Our findings show that retention forestry better supports understorey moss growth during droughts compared with clearcuts, with benefits extending into the following 2 years. To further enhance these climate buffering benefits, which did not match those of intact mature forests, increasing the retention forest's ability to buffer macroclimatic conditions is key. While biological legacies like large living trees, standing and lying deadwood had minimal effects in clearcuts and mature forests, they significantly influenced microclimate and moss growth in retention patches. This highlights the dual importance of conserving large living trees and deadwood, not only as critical habitats for threatened boreal forest species (SLU Artdatabanken, 2020), but also for the growth of mosses like *H. splendens* and potentially other understorey species. Forest managers should, therefore, focus on retaining greater basal areas of large living trees to increase canopy closure within retention patches and maintain both standing and lying deadwood to improve the understorey growing conditions and functionality. Although more sensitive understorey species might still struggle in the warmer, drier conditions within retention patches, long-term studies, in line with our findings, indicate that increasing structural heterogeneity within patches supports the survival of many bryophytes of conservation concern (Jönsson et al., 2022; Rudolphi et al., 2014).

AUTHOR CONTRIBUTIONS

Shengmin Zhang, Jörgen Sjögren and Mari Jönsson contributed to the study conception and design. Shengmin Zhang led the data collection and data analysis, with contributions from Mari Jönsson. Shengmin Zhang wrote the first draft of the manuscript, while Jörgen Sjögren, Kristoffer Hylander, Irena A. Koelemeijer and Mari Jönsson provided comments on previous versions. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available via the Figshare Repository https://doi.org/10.6084/m9.figshare.27909654.v2 (Zhang, 2024).

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SUPPORTING INFORMATION

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

Figure S1: Photo of the growth pattern of a random *Hylocomium splendens* shoot from a mature forest plot (upper) respective a clearcut forest plot (lower) in our study.

Figure S2: Scatter plots of annual maximum width versus length for three habitat types: Clearcut, Retention, and Mature Forest.

Figure S3: The annual maximum width of *H. splendens* was assessed for each year (2016-2022) in clearcuts, retention forests, mature forests, and across the three habitat types pooled.

Figure S4: Piecewise structural equation model results of direct and indirect effects of the biological legacies (large living trees (BA. Large), standing and lying dead trees, and Shannon tree species diversity (H index)), forest canopy (canopy closure), and microclimate temperatures (T) on the annual maximum width of *H. splendens* in respective clearcuts, retention and mature forests in 2019 and 2020.

Table S1: Characteristics of each habitat type (Clearcuts vs Retention patch vs Mature forests).

Table S2: Macroclimate temperatures and precipitations (Mean ± SD) during the summer seasons (June, July and August) from 2016 to 2022.

Table S3: Model outputs for the linear mixed models (LMMs) with 'habitat type' as a fixed effect and '1|Site ID' as a random effect to test whether the mean annual maximum width differed between the habitat types (i.e. clearcut vs. retention vs. mature forest) for each recorded year (2016–2022).

Table S4: Model outputs for the linear mixed models (LMMs) for *H. splendens* Δ maximum width as a function of either Δ*T* or ΔVPD in two separate models.

Table S5: Air temperature and VPD in the different habitat types (i.e. clearcut vs retention vs old forest).

Table S6: Estimates of the mother segment size for the estimation of annual maximum width.

Method S1: Vapour pressure deficit (VPD) calculation.

Method S2: Forest diversity measure.

Method S3: Deadwood measures.

Method S4: Data analyses—piecewise structural equation models (SEMs).

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