


RESEARCH ARTICLE

Rapid shifts in bryophyte phenology revealed by airborne eDNA

Fia Bengtsson^{1,2}  | Nils Cronberg¹ | Jose Antonio Lozano Villegas³ |
 Abu Bakar Siddique⁴ | Per Stenberg³ | Johan Ekroos^{5,6,7}

¹Department of Biology, Lund University, Lund, Sweden; ²Norwegian Institute for Nature Research, Trondheim, Norway; ³Department of Ecology and Environmental Sciences, Umeå University, Umeå, Sweden; ⁴Department of Plant Biology, Swedish University of Agricultural Science, Uppsala, Sweden; ⁵Centre for Environmental and Climate Science, Lund University, Lund, Sweden; ⁶Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland and ⁷Helsinki Institute of Sustainability Science, HELSUS, University of Helsinki, Helsinki, Finland

Correspondence

Fia Bengtsson

Email: fia.aurelia@gmail.com

Funding information

Bolencentret för klimatforskning, Stockholms Universitet; Svenska Forskningsrådet Formas, Grant/Award Number: 2016-01371, 2019-00579 and 2021-02155; BECC (Biodiversity and Ecosystem services in a Changing Climate)

Handling Editor: Jianyang Xia

Abstract

1. Bryophytes constitute a diverse plant group with important roles in ecosystem functioning, in particular in arctic and subarctic environments. As they are physiologically strongly dependent on climatic conditions bryophytes could serve as indicators of ongoing climatic change. Their spores are generally dispersed by wind, and because of contrasting phenologies among species, the composition of the spore cloud changes throughout the year. Unlike vascular plant pollen, airborne bryophyte spores have few specific morphological characteristics, and therefore spore dispersal phenology has, until now, relied on highly laborious in situ observations.
2. Here, we report on multi-decadal shifts in the phenology of spore dispersal in 16 bryophyte taxa using a unique 35-year time series of environmental DNA (eDNA) data collected in Kiruna, northern Sweden. We used shotgun sequencing data from air filters and matched reads to all major organism groups, of which a high proportion were bryophyte reads.
3. We found consistent shifts in bryophyte phenology, such that most bryophyte taxa advanced their (i) start of season with 4 weeks on average, and (ii) mid-season with 6 weeks, ranging between 4 and 7 weeks. Changes at the season end were less consistent across the 16 bryophyte taxa, although seven of them showed phenological delays over time. Rising temperatures during the third and fourth quarters of the year preceding spore release were correlated with phenological shifts, suggesting that bryophytes may enter hibernation at later stages of sporophyte development, with warmer conditions promoting more advanced sporophyte maturation by the onset of spring. As a consequence of the phenological shifts, seasons during which spores were observed became several weeks longer over the studied time period for most taxa.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

4. *Synthesis.* We conclude that the phenological shifts in our study suggest strong perturbations in bryophyte phenology, consistent with ongoing climate change. Our results demonstrate that studying airborne particles using eDNA methodology is a valuable complement to other monitoring methods, not the least in bryophytes and other less well-surveyed taxa.

KEYWORDS

subarctic, bryophytes, eDNA, global warming, monitoring, phenological shifts, phenology, sporophyte development

1 | INTRODUCTION

Global warming has accelerated in recent decades, especially in northern latitudes (IPCC, 2021). Several species and entire biotic communities have responded to the changing climate, for example through shifts in their phenology, which is the altered timing of recurring biological events (Fenner, 1998; Piao et al., 2019; Rosenzweig et al., 2008). On the one hand, phenological shifts related to vernal temperatures, such as the earlier onset of flowering, have been observed, not the least in arctic and subarctic environments (Bjorkman et al., 2020; MacDougall et al., 2021; Prevey et al., 2017). On the other hand, senescence and growing season length (SL) are less affected by the changing climate in vascular plant studies (MacDougall et al., 2021). In addition, phenological shifts have been found to be stronger for vascular plants compared to organisms at higher trophic levels (Roslin et al., 2021).

Notably, climatic effects on bryophyte phenology are understudied, even though specific characteristics in bryophyte physiology would predict strong and rapid responses to changes in temperature and precipitation. First, since bryophytes lack advanced vascular systems, they rely on water uptake through vegetative tissue and cease to grow without ambient moisture. Second, sexual reproduction critically depends on water availability; the motile male gametes need a water surface to reach the females before sporophyte formation (Longton & Schuster, 1983). Also, specific vapour levels regulate spore release from sporophytes (Zanatta et al., 2018) and spore germination relies on substrate humidity (Wiklund & Rydin, 2004). Third, bryophytes have lower temperature thresholds for growth than many vascular plants (Proctor, 1990).

Shifts in the timing of phenological events, such as when reproduction and spore dispersal take place, could provide early indications to suggest that bryophyte biomass or diversity is changing. Consistently sampled long-term data are required to detect phenological changes in ecosystems (Roslin et al., 2021). However, such data are often lacking altogether. Monitoring plant reproduction requires extensive fieldwork over multiple seasons, or if such data are unavailable, time series can be obtained from large herbarium collections (Song et al., 2021). In bryophytes, the timing of phenological events is rarely systematically documented (but see Arnell, 1875; Arnell, 1905; Grimme, 1903; Hagerup, 1935; Lackner, 1939). Despite sporadic later efforts to document bryophyte phenology (as

reviewed in Stark, 2002), no long-term studies have focused on phenological stages. Regarding angiosperms, pollen collected from the air has been used to identify flowering phenology (Rojo et al., 2021), but given that bryophyte species are rarely identifiable based on spore morphology, air samples for bryophyte species identification have hitherto not been an option, even though bryophyte spores are mostly wind-dispersed and thereby readily present in the air. However, environmental DNA (eDNA) from air samples should be particularly well-suited for monitoring changes in bryophyte spore composition, because these are primarily wind-dispersed.

A great variety of organisms can be detected using eDNA, that is DNA suspended in non-biological substrates such as water, soil and air. The interest in eDNA is surging as an alternative method for biodiversity screening when access to monitoring data is hard to obtain or requires limited and expensive expert input for taxonomic determination. In addition, eDNA monitoring can reveal the presence of organisms that go undetected with traditional methods (Abrego et al., 2018; Johnson et al., 2021; Karlsson et al., 2020; Roger et al., 2022). In this study, we analyse a globally unique shotgun-sequenced aerial eDNA time series from Kiruna, northern Sweden, spanning 1974–2008, assembled by the project Swedish Biodiversity In Time and Space (Karlsson et al., 2020; Sullivan et al., 2023). The Kiruna time series is a unique archive that provides a glimpse back in time for phenological studies, especially of bryophytes, which are particularly well represented in the database (Sullivan et al., 2023). As bryophyte spores are predominantly wind dispersed, peaks in the abundance of DNA reads can be interpreted to represent spore release events.

From the large dataset in Sullivan et al. (2023), we assess the relative abundance distribution of 16 bryophyte genera, including both mosses and liverworts, aiming to uncover long-term patterns in their phenology. The first objective of this study is to provide a unique description of the regional spore dispersal phenology in bryophytes across the 35-year time series, to describe the mainly unknown spore dispersal phenology, that is, when the selected taxa disperse their spores and when the peak, or mid-season, of spore dispersal occurs.

The second objective is to establish whether temporal shifts in the spore dispersal phenology have occurred over time. A shift is expected, given the changing climatic conditions during the sampled period, during which the average temperature has been rising by c.

2°C in Kiruna (Länsstyrelsen i Norrbottens län, 2017). We further investigate whether there are such changes in phenological timing and if they are related to climatic conditions. Finally, we ask whether the lengths of spore dispersal seasons changed during the time series. Based on results from phenological studies in other plant groups and climatic data, we hypothesize that the onset of spring events will have advanced and that the sporulation season has been extended.

2 | MATERIALS AND METHODS

2.1 | Sample collection

The dataset used in our analysis is a subset of an analysis-ready dataset generated by Sullivan et al. (2023), where, in total, 380 filter samples representing each week throughout the growing seasons of every second year during 1974–2008 were sampled. In Sullivan et al. (2023), the airborne eDNA was sampled by a permanent radionuclide monitoring station in the boreal forest of northern Sweden, outside Kiruna (67.84°N, 20.42°E; Figure 1). These air monitoring stations filter >100,000 m³ of air per week through 0.2-µm silica base filters. Filters were collected weekly and stored in long-term airtight containers. For further details about the sampling procedure, see Söderström et al. (2007). DNA was isolated from filters installed during weeks with a mean temperature above 0°C, every second year between 1974 and 2008; this translated to sampling between April and October at most. DNA extraction was performed in three steps with different degrees of bead-beating intensity to allow DNA extraction from a wide range of particle types. Five per cent of each filter was used for extraction; on average, 230 ng of DNA was obtained. Libraries from extracted DNA were sequenced on Illumina NovaSeq 6000 S4 flow cells using 2 × 150 bp output. In

total, ca. 30 terabases of high-quality metagenomic sequences were generated. In brief, reads were assigned to genera using Kraken 2 (Wood et al., 2019) on a custom database (4.2 TB), a gradient boosting machine was trained to identify true positive taxa (resulting in a precision of 93% and a recall of 72%), and proportions of reads assigned to each genus were log-ratio-transformed.

Previously, it was found that eDNA can be preserved for decades under these conditions with limited degradation (Karlsson et al., 2020). To investigate if there was any detectable degradation of bryophyte DNA over time in the archived samples analysed here, we calculated the yearly average summed pair-end read length (Figure S1). For full details on sampling, database assembly and processing, see Sullivan et al. (2023).

The permanent sampling station is situated in a relatively flat lowland surrounded by spruce forests and mixed mires. Mountains with snowbeds and rock outcrops in the vicinity contribute to heterogeneity in habitats and topography suitable for various bryophyte species. The average annual temperature at the station averaged over the sampled years was −1°C, where the warmest month was typically July, and the average monthly temperature in the warmest month each year was 12°C. The total average annual precipitation for the sampled years was 522 mm per year, and the average monthly precipitation of the warmest quarter was 225 mm (data from SMHI 2024).

2.2 | Selected taxa

Sullivan et al. (2023) estimated that 5%–10% of the data were bryophyte reads, which were assigned to taxa at the genus level using the best available genomic reference data at the time of analysis (December 2019) in GenBank. We selected 16 bryophyte genera



FIGURE 1 Location of the sampling site (red point) in Northern Scandinavia, close to Kiruna in Sweden (67.84°N, 20.42°E). At the sampling site, there was weekly sampling, and data from every second year were collected during the time series from 1974 to 2008.

that were well represented by the number of reads (140 million reads of 100 billion reads, i.e. 0.14%) and well characterized by available genomic data. One of the authors (Nils Cronberg) visited the site and surroundings in late August 2020, and the observations were used to ensure that the selected genera matched the species present in the vicinity of the filter collection point. We selected the studied taxa based on the interpretability of the classified sequencing data according to the following procedure: we first selected genera that were monospecific in the study area. These species included *Ceratodon purpureus*, *Funaria hygrometrica* and *Pleurozium schreberi*. Second, we selected genera that were represented by one or more species locally, but for which only one species was, to the best of our knowledge, the predominant spore disperser in the region. This group of species included most of the selected taxa: *Bartramia pomiformis*, *Tritomaria quinquentata*, *Sanionia uncinata*, *Andreaea rupestris*, *Ptilidium pulcherrimum*, *Tetraplodon mnioides*, *Pogonatum urnigerum* and *Pohlia nutans*. Additionally, we included a few genera that we expected to comprise several species, as these constitute a large part of the signal being locally abundant and sporulating, such as *Bryum*, *Dicranum*, *Polytrichum* and *Sphagnum*. Finally, we selected *Marchantia polymorpha*, which includes three subspecies with differing ecology, of which one or two are present in the study region (subsp. *montivagans*; possibly also subsp. *ruderalis*).

Species-specific traits can affect the strength of the relationship between changes in phenology and climate change (Williams et al., 2008). To this end, we summarize the life history traits of the studied taxa in Table 1, including life strategy, time of year of fertilization, spore capsule maturity and spore sizes. The data presented in Table 1 are mostly based on older and less accessible literature. We also summarize the lengths of reproductive cycles for the studied taxa based on reports from Lackner (1939 in Table S2).

2.3 | Data processing and statistical analyses

First, to illustrate phenology and general changes in phenology over time, we produced heatmaps for each taxon, using pivot coordinates to show the relative abundance (scaled to vary between 0 and 1, using $(x - \min(x))/(\max(x) - \min(x))$) of classified reads for each week during each sampling year across the time series (see Sullivan et al., 2023 for details). In addition, we plotted smoothed regressions onto the heatmaps to describe the weekly relative abundance using generalized additive models (GAMs), based on the function *gam* from the *mgcv* package (v1.8-42) (Wood, 2011).

Second, we analysed two aspects of the spore-spreading phenology: the timing and the length of the season. Regarding the timing, we quantified changes in the start of season (SS), mid-season (MS) and end of season (ES) for each study year, based on the seasonal distribution of relative spore abundance (following Lehtikoinen et al., 2019). Because of a low but continuous presence of reads for most taxa, the presence of taxon-specific reads could not alone signify the onset of spring (start of season). Instead, we used two phenological thresholds to define the start of the season: the time

points (weeks) when the cumulative annual relative abundance of reads reached the 10th and 20th percentiles of the total annual relative abundance (SS_{10} and SS_{20} , respectively). Similarly, to define the end of season, we used the timepoints when the cumulative annual relative abundance reached the 80th and 90th percentiles (ES_{80} and ES_{90} , respectively). We chose to analyse both the 10th and 20th percentiles for SS, and the 80th and 90th percentiles for ES to test for the sensitivity in the choice of thresholds. High and low ends of a frequency distribution can be sensitive to extreme values late or early in the season (but see Pearse et al., 2017), whereas percentiles describing SS and ES will be relatively robust towards skewed distributions caused by occurrence peaks or multinomial distributions. In addition, we used the median (50%) of the cumulative annual relative abundance distribution to describe the occurrence of the mid-period of spore dispersal across the time period (MS; following Lehtikoinen et al., 2019). We then tested the effect of year on each of these phenological variables, using separate quasi-Poisson regressions (using function *gls* available in library *nlme*; Pinheiro et al., 2022) for each phenology descriptor and taxon. In each model, we used the number of weeks sampled each year (on a \log_e -scale) as an offset to control for the effect of different sampling efforts between years.

We thereafter calculated SL as the number of weeks between the cumulative relative abundance percentiles from early and late seasons using the same descriptors of start of the season and end of the season as above, that is between the 10th and 90th (SL_{10-90}) and between the 20th and 80th (SL_{20-80}) percentiles. Then, we tested relationships between these variables and year using quasi-Poisson regression models, including the number of sampled weeks as an offset (as above) to control for the effect of different sampling efforts between years. We considered a change significant if the regression was significant at $p < 0.05$.

To visualize the model results, we extracted the phenological event time points from the first and the last years in the time series from the model fits and calculated the changes between these time points (number of weeks) over the time series. Also, for visualization, we calculated the change in SL over the time series from the fitted models.

For the taxa that showed significant changes in phenological timing at the start of the season, we tested if there was a correlation between the week that a taxon reached SS_{10} and SS_{20} , respectively, with climatic data from the closest weather station (SMHI, 2024). We tested correlations (Spearman) with mean annual temperature and summed annual precipitation, as well as with the previous year's mean annual temperature and the mean for the 3rd and 4th quarters, respectively.

3 | RESULTS AND DISCUSSION

Our novel use of airborne eDNA data reveals substantial changes in bryophyte phenology, including several weeks' (3–6 weeks) advance since the 1970s in seasonal timing of spore dispersal for 15 of the 16 taxa. All taxa, except two of those 15, showed significant

TABLE 1 Life history traits relating to sporulation in the studied taxa.

Taxon	Bryophyte group	Species	Habitat	Life strategy (During, 1979)	Reproductive system	Fertilization	Spore capsule maturity	Spore capsule frequency	Spore size (µm)	Spore capsule hibernating
<i>Andreaea</i>	Moss	<i>Andreaea rupestris</i>	On stone in varying environments	Short-lived shuttle (s)	Monoicous	Spring	Spring	Frequent	33	Hibernating
<i>Bartramia</i>	Moss	<i>Bartramia pomiformis</i>	On stone or soil in shaded environments	Long-lived shuttle (l)	Monoicous	Summer*2	Summer*2	Common	23	
<i>Bryum</i>	Moss	Several species	Dep. on species	Dependant on species: c/p/s	Dep. on species	Dep. on species	Dep. on species	Dep. on species	10–30 dep. on species	Within season for many species
<i>Ceratodon</i>	Moss	<i>Ceratodon purpureus</i>	On disturbed, thin soils	Colonist (c)	Dioicous	Summer	Summer	Common	12	Hibernating
<i>Dicranum</i>	Moss	Several species: <i>D. majus</i> , <i>D. polysetum</i> , <i>D. fuscescens</i> , <i>D. scoparium</i>	Mainly in forest on moist soil, stone, preferably shaded, <i>D. polysetum</i> also drier pine forest, <i>D. scoparium</i> also in exposed habitats	Perennial stayers (p)	Dioicous	Summer	Autumn	Dep. on species: Occasional/rare	20/21/21/17	Hibernating
<i>Funaria</i>	Moss	<i>Funaria hygrometrica</i>	On disturbed soil in varying environments	Fugitive (f)	Monoicous	Late summer	Summer	Common	19	Hibernating
<i>Pleurozium</i>	Moss	<i>Pleurozium schreberi</i>	Forest floors, mainly relatively dry	Perennial stayers (p)	Dioicous	Summer	Spring	Very rare	15	Hibernating
<i>Pogonatum</i>	Moss	Likely <i>Pogonatum urnigerum</i>	On bare mineral, disturbed soil	Colonist (c)	Dioicous	Spring	Autumn	Common	12	Within season
<i>Pohlia</i>	Moss	Likely <i>Pohlia nutans</i>	On disturbed, thin soils	Colonist (c)	Dioicous	Summer	Summer	Frequent	19.5	Hibernating
<i>Polytrichum</i>	Moss	Several species: <i>P. commune</i> , <i>P. juniperum</i> , <i>P. piliferum</i>	<i>P. commune</i> in forest or mire edges, the others on relatively dry disturbed soil or peat	Dependant on species: p/s	Dioicous	Summer	Summer	Dep. on species: Common/frequent	10/9.5/43.5	Hibernating
<i>Sanionia</i>	Moss	<i>Sanionia uncinata</i>	On different substrates in forested and open moist areas	Perennial stayers (p)	Monoicous	Summer to autumn	Summer	Frequent to common	14	Hibernating
<i>Sphagnum</i>	Moss	Several species	Forest floor or mires, dep. on species	Long-lived shuttle (l)	Dependant on species	Summer*6	Summer/summer to autumn*4	Dep. on species	20–40 dep. on species	Within season*6
<i>Tetraplodon</i>	Moss	Likely <i>Tetraplodon mnioides</i>	On carcasses and faeces in open and forested, relatively dry areas	Short-lived shuttle (s)	Monoicous	Summer	Summer	Common	11	Hibernating
<i>Marchantia</i>	Liverwort	<i>Marchantia polymorpha</i> , mainly subsp. <i>montivagans</i>	On bare mineral, disturbed soil	Colonist (c)	Dioicous	Summer	Summer to autumn*4	Rare	13.5	Within season
<i>Ptilidium</i>	Liverwort	<i>Ptilidium pulcherrimum</i>	Forested areas on wood	Short-lived shuttle (s)	Dioicous	Spring*3	Spring*3	Common*3	28.5	Hibernating*3
<i>Tritomania</i>	Liverwort	<i>Tritomania quinquentata</i>	Forested areas on stone	Perennial stayers (p)	Dioicous	Summer*5	Summer*5	Rare	14	
Data source		Authors' field observations	*5	*4	*4	*1 unless otherwise stated	*1 unless otherwise stated	*4 unless otherwise stated	*4	*1 unless otherwise stated

Note: Data were derived from the following references: *1 = Arnell (1875); *2 = Arnell (1905); *3 = Jonsson and Söderström (1988); *4 = Bernhardt-Römermann et al. (2018); *5 = Artfakta, <https://artfakta.se/artbestamning>; *6 = Cronberg (1993).

changes in both the 10th and 20th percentiles of spore release. These phenological shifts constitute an overall prolonged spore release season, although the taxa showed less consistent changes in phenology at the mid-season and the end of the season. The shifts are consistent with ongoing climate change, as the mean annual temperature has increased by c. 1.7°C (calculated from the slope of the regression line) at the closest weather station in Kiruna over the surveyed period (linear regression, R^2 : 0.27, F -statistic: 12.17 on 1 and 33 DF, p -value: 0.0014, Figure S2a). The summed annual precipitation has not changed significantly (Figure S2b).

3.1 | Phenological shifts in the beginning and mid-season

For each taxon, we calculated which week represented the time point at which the cumulative annual relative abundance reached the 10th

and 20th percentiles each year (SS_{10} and SS_{20} , respectively) and used models to test whether there were statistically significant changes in these variables over time. The resulting models showed profound shifts in spore dispersal timing across most studied bryophyte taxa in our 35-year time series (Figure 2). Thus, SS_{10} was consistently reached earlier towards the end of the time series in all studied taxa, except the leafy liverwort *Tritomaria quinquedentata* (quasi-Poisson regressions significance level 0.05; statistical data shown in Table 2). Overall, the significant effects corresponded to spore spread reaching SS_{10} between 3 and 5 weeks earlier in 2008 than in 1974 based on model predictions (Figure 2). In addition, most taxa also reached SS_{20} significantly earlier with time (Table 2), except for *Tritomaria*, the three moss genera *Ceratodon*, *Pohlia* and *Polytrichum*, and the thalloid liverwort *Marchantia*, which did not show significant changes over time in this respect. Based on model predictions, the timing for SS_{20} varied slightly more than SS_{10} , advancing by 3–6 weeks (SL change for each taxon is shown in Figure 2).

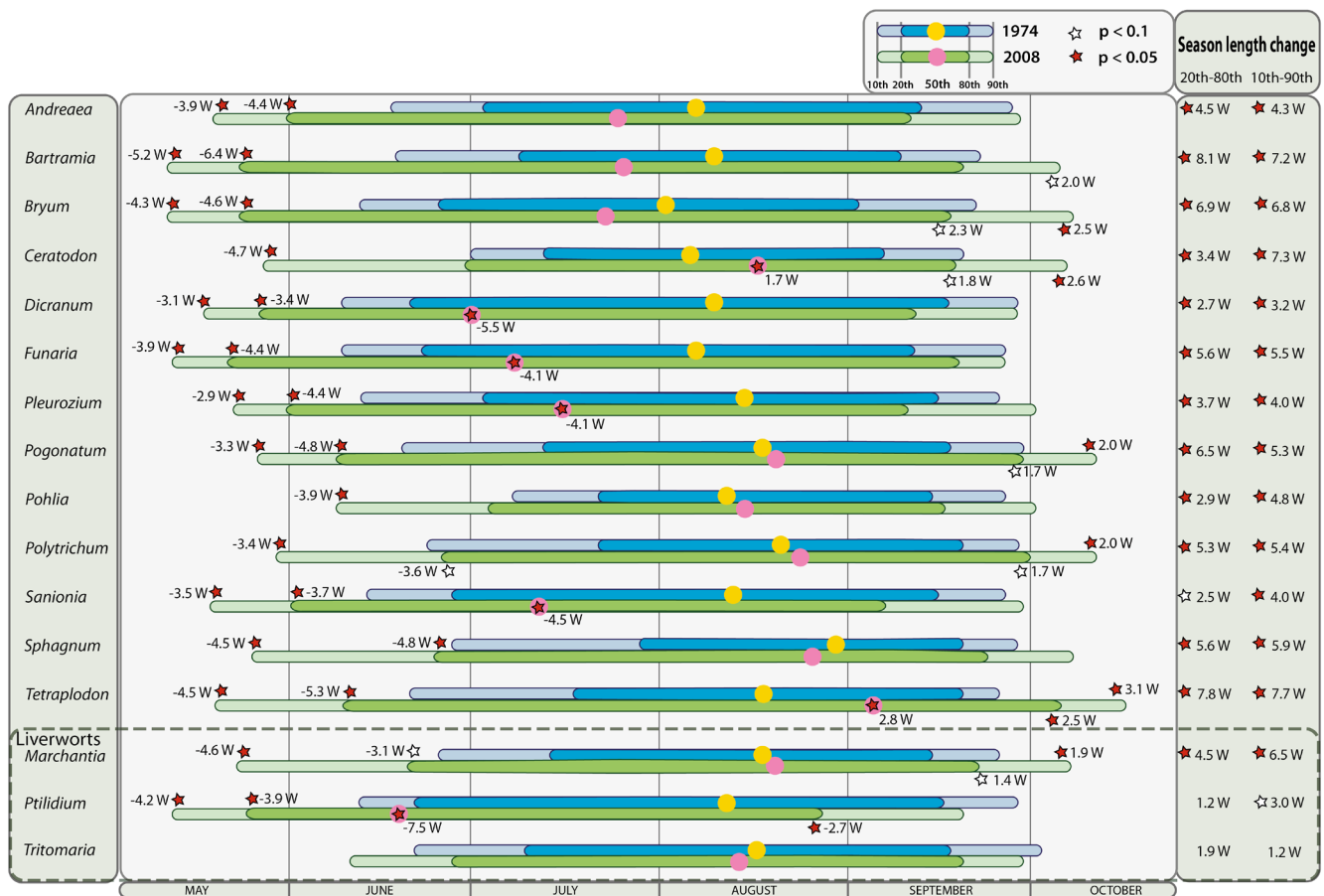


FIGURE 2 The spore dispersal timing and changes in timing between the years at the start (1974) and the end (2008) of the Kiruna time-series for each studied taxon, based on quasi-Poisson regression model estimates for each taxon, testing the relationships between year and each of the responses describing start of season (10th and 20th percentiles), mid-season (50th percentile) and end of season (80th and 90th percentiles). The percentiles describe the week when relative annual abundance reached that threshold. Model results are illustrated by comparing model-estimated phenology descriptors as week numbers (translated to dates using first day of the week) for the study years 1974 and 2008. The change in season length over the time series was also calculated from the fitted models for the purpose of visualization (blue and green bars for 1974 and 2008, respectively). The right column shows the number of weeks the changes correspond to, including the changes in season length, with significant models labelled with stars.

TABLE 2 Model estimates on phenological shifts in 16 bryophyte taxa during the start of season, based on the time by which the annual cumulative, relative abundance reached the 10th or 20th percentiles out of the entire distribution.

Genus	Week of 10th percentile				Week of 20th percentile			
	Deviance squared	Estimate (e [^] x)	Standard error	p-value	Deviance squared	Estimate (e [^] x)	Standard error	p-value
<i>Andreaea</i>	0.42	-0.0052	0.0016	0.005	0.57	-0.0054	0.0012	0.0004
<i>Bartramia</i>	0.54	-0.0070	0.0017	0.001	0.49	-0.0079	0.0021	0.002
<i>Bryum</i>	0.38	-0.0059	0.0020	0.009	0.41	-0.0058	0.0018	0.006
<i>Ceratodon</i>	0.36	-0.0058	0.0020	0.01	0.06	-0.0018	0.0018	0.3
<i>Dicranum</i>	0.35	-0.0042	0.0015	0.01	0.39	-0.0043	0.0014	0.007
<i>Funaria</i>	0.44	-0.0054	0.0016	0.004	0.49	-0.0058	0.0015	0.002
<i>Pleurozium</i>	0.38	-0.0038	0.0013	0.009	0.51	-0.0053	0.0013	0.001
<i>Pogonatum</i>	0.38	-0.0043	0.0014	0.009	0.45	-0.0055	0.0016	0.003
<i>Pohlia</i>	0.25	-0.0046	0.0021	0.04	0.14	-0.0026	0.0016	0.1
<i>Polytrichum</i>	0.24	-0.0043	0.0020	0.05	0.17	-0.0039	0.0022	0.10
<i>Sanionia</i>	0.41	-0.0047	0.0014	0.005	0.45	-0.0046	0.0013	0.003
<i>Sphagnum</i>	0.45	-0.0058	0.0016	0.003	0.35	-0.0051	0.0018	0.013
<i>Tetraplodon</i>	0.39	-0.0059	0.0019	0.007	0.25	-0.0061	0.0027	0.04
<i>Marchantia</i>	0.49	-0.0059	0.0016	0.002	0.20	-0.0035	0.0018	0.07
<i>Ptilidium</i>	0.45	-0.0058	0.0017	0.003	0.47	-0.0051	0.0014	0.003
<i>Tritomaria</i>	0.16	-0.0017	0.0010	0.1	0.13	-0.0017	0.0011	0.2

Note: Deviance squared is a measure of how well the model fits the data, with lower values indicating a better fit. The Estimate represents the predicted change in the response variable for a unit change in the predictor variable. The standard error (SE) reflects the variability in the estimate. The *p*-value indicates the probability of observing the results. We follow the convention of calling *p*-values <0.05 significant, but also take note of values <0.1, marked in orange. A clear or orange *p*-value is interpreted as evidence of or slightly less strong evidence of change in phenological timing for that taxon. *N* for each regression = 17. p>0.1 ; p>0.5

Our results on advancing biological spring align well with studies on vascular plant communities, showing an ongoing shift towards earlier phenological events during spring in arctic and subarctic regions (Bjorkman et al., 2020), including our study region (MacDougall et al., 2021). A meta-analysis of phenological records on plants and animals in Europe (Menzel et al., 2006) suggested that spring events advanced 2.5 days per decade (between 1970 and 2000). Our data on bryophytes suggest a more accelerated shift, translating to 8 days per decade, which is consistent with the notion that climate change is faster in northern regions (AMAP; Arctic Management and Assessment Programme, 2012), but also that bryophytes might be more sensitive to changes in climate. Such strong phenological shifts may have effects on the bryophyte flora through changed recruitment or indicate ongoing changes in community composition, with possible influence on associated grazers such as lemmings (Virtanen et al., 2002) and reindeer (Bernes et al., 2015).

The point when 50% of the annually observed spores were captured (M50) differed among taxa over time (Figure 2). It occurred significantly earlier over time in five of the studied taxa, showing dramatic phenological shifts ranging between 4.1 and 7.5 weeks earlier towards the end of the time series (Table 3). In nine taxa, we found no changes over time in M50, and in two taxa (*Tetraplodon* and *Ceratodon*), the effects were the opposite, with M50 occurring

1.7 and 2.8 weeks later, respectively, in 2008 compared to 1974 ($p < 0.05$). Heatmaps (Figure S2a–d) revealed that the peak in relative abundance in some taxa shifted from early to later, resulting in double peaks overall. Other taxa, such as *Polytrichum*, were characterized by two peaks over time, potentially because different species within the genera peak at different times. In contrast, *Tetraplodon* and *Ceratodon* reached 50% in their annual occurrence later than others. Both are colonizers, *Tetraplodon* growing on scats and *Ceratodon* on exposed bare soil (Table 1). In these cases, the peak dispersal might, for example, be controlled by a shift in the temporal abundance of the substrates or an ability to reproduce sexually in previously unsuitable areas, although somewhat delayed, potentially as such areas might still be suboptimal.

3.2 | Changes in the end of season and season length

In contrast to phenological changes at the start of the season and at M50, we found little evidence of phenological shifts towards an earlier ending of the season. Only the liverwort *Ptilidium* reached ES₈₀ (the timepoint when the cumulative annual relative abundance reached the 80th percentile) significantly earlier in the season towards the end of the time series ($p < 0.05$; Table 4), corresponding to 2.7 weeks earlier

TABLE 3 Model estimates on phenological shifts in 16 bryophyte taxa during the mid-season, based on the time by which the annual cumulative, relative abundance reached the median of the entire distribution.

Genus	Week of median			<i>p</i> -value
	Deviance squared	Estimate (e ^x)	Standard error	
<i>Andreaea</i>	0.16	-0.002	0.001	0.11
<i>Bartramia</i>	0.14	-0.002	0.001	0.14
<i>Bryum</i>	0.05	-0.001	0.001	0.38
<i>Ceratodon</i>	0.27	0.002	0.001	0.03
<i>Dicranum</i>	0.29	-0.006	0.002	0.02
<i>Funaria</i>	0.29	-0.004	0.002	0.03
<i>Pleurozium</i>	0.25	-0.004	0.002	0.04
<i>Pogonatum</i>	0.01	0.000	0.001	0.68
<i>Pohlia</i>	0.03	0.001	0.001	0.49
<i>Polytrichum</i>	0.03	0.001	0.001	0.52
<i>Sanionia</i>	0.28	-0.004	0.002	0.027
<i>Sphagnum</i>	0.02	-0.0003	0.001	0.62
<i>Tetraplodon</i>	0.38	0.002	0.001	0.009
<i>Marchantia</i>	0.02	0.000	0.001	0.58
<i>Ptilidium</i>	0.59	-0.008	0.002	0.0003
<i>Tritomaria</i>	0.01	0.000	0.001	0.66

Note: Deviance squared is a measure of how well the model fits the data, with lower values indicating a better fit. The estimate represents the predicted change in the response variable for a unit change in the predictor variable. The standard error (SE) reflects the variability in the estimate. The *p*-value indicates the probability of observing the results. We follow the convention of calling *p*-values <0.05 significant, but also take note of values <0.1, marked in orange. A clear or orange *p*-value is interpreted as evidence of or slightly less strong evidence of change in phenological timing for that taxon. *N* for each regression = 17. p>0.1 ; p>0.5

based on model predictions (Figure 2). However, in seven taxa, either ES₈₀ or ES₉₀ occurred significantly or marginally non-significantly later (*p* < 0.1; Table 4), corresponding to c. 2 weeks (Figure 2).

The period of spore dispersal, that is SL, was significantly extended for nearly all taxa over time (quasi-Poisson regressions, *p* < 0.05; Table 5). SL₁₀₋₉₀ was extended between three and 8 weeks, whereas SL₂₀₋₈₀ was extended between two and a half to seven and a half weeks. The exceptions were two liverworts, *Tritomaria* and *Ptilidium*, showing no significant changes in SL, although the latter showed a marginally, non-significantly longer SL corresponding to 3 weeks based on predicted values for SL₁₀₋₉₀ (*p* < 0.1; Table 5, Figure 2). The lengths of reproductive cycles range from 10.5 to 24.5 months, according to Lackner (1939; Table S2). No systematic survey exists for liverworts, but *Marchantia polymorpha* has a short cycle of 3 months under artificial cultivation (Ishizaki et al., 2016) and is known to complete fertilization, capsule maturation and spore release in one season. The leafy liverwort *Lophozia silvicola* (related to *Ptilidium* and *Tritomaria*) has a

2-year cycle with gametangial development during the first year and sporophyte formation during the second (Laaka-Lindberg, 2005).

These results are consistent with research on vascular plants, revealing that late-season phenostages, such as leaf senescence, tend to show less pronounced shifts compared to spring events (Menzel et al., 2006). For example, MacDougall et al. (2021) did not find clear changes in either senescence or SL, suggesting a dependence on the timing of flowering/fertilization or pollinator availability, rather than climatic conditions late in the season.

3.3 | Variation in peak spore release and dispersal

In Figure S2a-d, we observed interannual variations in peak spore dispersal, matching what we know about bryophyte biology. Once bryophyte spores reach maturity, their dispersal relies on weather conditions and species employ alternative strategies (Zanatta et al., 2018). Most mosses prevent spore release in high humidity through hygroscopic capsule teeth that shut the capsule opening. Such mechanisms ensure a gradual spore release under optimal conditions but turn off dispersal during unsuitable weather conditions, such as prolonged rain periods.

Heatmap analyses revealed clusters of bryophyte taxa showing markedly similar fluctuations over time (left panel Figure S3a-d). First, a cluster of seven taxa with consistent advances in early-season phenologies (the mosses *Andreaea*, *Bartramia*, *Bryum*, *Funaria*, *Pleurozium*, *Sanionia* and the liverwort *Ptilidium*) had higher relative abundances spread over the season in the first part of the time series, followed by a slightly more concentrated occurrence in the middle of the season (around week 30) until 1990, after which a shift occurred towards a concentrated high relative abundance in the early season from the 90s and onwards (right panel Figure S3a-d). A clear shift towards concentrated high relative abundances earlier in the season also characterized *Dicranum*, showing two peaks (around week 20 and week 35, respectively) until around 1985 (Figure S1a-d). These taxa also showed significant advances in mid-season phenology (except for *Andreaea* and *Bartramia*; see above).

Second, a cluster of three taxa (*Ceratodon*, *Pohlia* and *Sphagnum*) all had one clear peak during the late summer period but showed no visible shifts in the occurrence of high annual relative abundances (and showed no signs of advances in mid-season phenology; see Figure S3a-d and Table 3). High annual relative abundance concentrated around week 30 for *Ceratodon* and *Pohlia*, and around week 35 for *Sphagnum*. In our study, *Sphagnum* showed a distinct, short-lasting peak, although variation in the timing of spore maturation occurs among *Sphagnum* subgenera, possibly due to photoperiodic control (Cronberg, 1993). Individual *Sphagnum* spore capsules disperse all the spores at once in an explosive event when the capsules are dry enough for the lids to pop off (Sundberg, 2010). Although there may still be individual or species variation in the timing of spore capsule maturation, suitable weather conditions could synchronize spore release.

Third, one cluster of species showed multiple peaks across the season. Among these, *Pogonatum* and *Polytrichum* showed two clear peaks

TABLE 4 Model estimates on phenological shifts in 16 bryophyte taxa during the end of the season, based on the time by which the annual cumulative, relative abundance reached the 10th or 20th percentiles.

Genus	Week of 80th percentile				Week of 90th percentile			
	Deviance squared	Estimate (e ^{^x})	Standard error	p-value	Deviance squared	Estimate (e ^{^x})	Standard error	p-value
<i>Andreaea</i>	0.00	0.0000	0.0009	0.99	0.01	0.0003	0.0010	0.78
<i>Bartramia</i>	0.15	0.0013	0.0008	0.12	0.17	0.0002	0.0008	0.095
<i>Ceratodon</i>	0.21	0.0014	0.0007	0.06	0.31	0.0020	0.0007	0.02
<i>Funaria</i>	0.04	0.0009	0.0012	0.44	0.09	0.0012	0.0010	0.24
<i>Pleurozium</i>	0.03	-0.0005	0.0008	0.53	0.06	0.0008	0.0009	0.34
<i>Sanionia</i>	0.06	-0.0010	0.0010	0.33	0.01	0.0004	0.0009	0.66
<i>Pogonatum</i>	0.20	0.0013	0.0007	0.07	0.26	0.0014	0.0006	0.03
<i>Pohlia</i>	0.02	0.0003	0.0006	0.62	0.05	0.0006	0.0007	0.37
<i>Tetraplodon</i>	0.46	0.0019	0.0005	0.003	0.52	0.0023	0.0006	0.001
<i>Bryum</i>	0.21	0.0018	0.0009	0.07	0.25	0.0019	0.0008	0.04
<i>Dicranum</i>	0.02	-0.0006	0.0010	0.59	0.00	0.0001	0.0009	0.92
<i>Polytrichum</i>	0.22	0.0013	0.0006	0.06	0.28	0.0015	0.0006	0.03
<i>Sphagnum</i>	0.08	0.0006	0.0005	0.29	0.12	0.0010	0.0007	0.18
<i>Marchantia</i>	0.23	0.0011	0.0005	0.05	0.29	0.0014	0.0006	0.03
<i>Ptilidium</i>	0.30	-0.0023	0.0009	0.02	0.08	-0.0009	0.0008	0.28
<i>Tritomaria</i>	0.03	0.0003	0.0004	0.52	0.00	-0.0002	0.0007	0.83

Note: Deviance squared is a measure of how well the model fits the data, with lower values indicating a better fit. The estimate represents the predicted change in the response variable for a unit change in the predictor variable. The standard error (SE) reflects the variability in the estimate. The *p*-value indicates the probability of observing the results. We follow the convention of calling *p*-values <0.05 significant, but also take note of values <0.1, marked in orange. A clear or orange *p*-value is interpreted as evidence of, or slightly less strong evidence of change in phenological timing for that taxon. *N* for each regression = 17. p>0.1 ; p>0.5

in relative abundance, of which the second was taller (Figure S3b,c). *Tetraplodon* and *Marchantia* were, in turn, characterized by a high initial relative abundance, indicating that some early-season dispersal activity was missed (Figure S3d). *Tritomaria* had low initial relative abundances followed by diffuse peaks across the season (Figure S3a–d).

Given the lack of knowledge about bryophyte responses to global change, it is hard to point out the mechanisms contributing to the differences between the taxa. As bryophytes represent a highly diverse group of plants, it is hardly surprising that their climatic responses differ. In general, research on bryophyte phenology is overall scarce, and although our study significantly advances the knowledge base, more research is needed, particularly to understand the underlying mechanisms that cause different responses between bryophyte species and potential consequences for population persistence under climate change.

3.4 | Environmental drivers

In general, the understanding of environmental control of bryophyte reproductive phenology is limited. Bryophytes display similarities, as well as fundamental differences in physiology compared to vascular plants, for example in water regulation (Proctor, 1990) and circadian clocks (Linde et al., 2017). Water availability is vital to bryophyte

growth, and growth ensues even at relatively low temperatures and light intensities, provided the water is not frozen (Proctor, 1990). Gene complexes controlling the circadian clocks are simpler than those of vascular plants but might contribute to the timing of phenological responses.

Our study did not extensively analyse environmental drivers of the phenological changes, which we identify as a critical knowledge gap for future research. Nevertheless, we tested the correlation between average annual temperature and precipitation versus the week number that the 10th and 20th percentiles of relative abundance (SS_{10} and SS_{20} , respectively) were reached every year. We found no significant correlations for precipitation and next to no significant correlations for temperature during the present year, but for the average temperature of the previous year, most correlations were significant (Table S1). Autumn conditions may determine the stage of sporophyte maturation reached by the time of hibernation, affecting the timing of spore release in the subsequent spring. Therefore, we followed up by testing the correlation of SS_{10} and SS_{20} mean temperatures of the previous years' 3rd and 4th quarters. Most of these correlations were significant, indicating that autumn temperature is indeed a major driver for bryophyte spring phenology.

We hypothesize that climatic factors are primary cues for spore capsule ripening and spore release for most taxa. For example, earlier snowmelt removes the physical barrier of snow but also,

TABLE 5 Model estimates on phenological season length changes in 16 bryophyte taxa, based on the number of weeks between the time by which the 10th and the 90th percentiles were reached, or the number of weeks between the time by which the 20th and 80th percentiles were reached.

Genus	Weeks between 10th and 90th percentile				Weeks between 20th and 80th percentile			
	Deviance squared	Estimate (e ^x)	Standard error	p-value	Deviance squared	Estimate (e ^x)	Standard error	p-value
<i>Andreaea</i>	0.32	0.008	0.003	0.019	0.39	0.010	0.003	0.007
<i>Bartramia</i>	0.67	0.012	0.002	0.0001	0.55	0.018	0.004	0.001
<i>Ceratodon</i>	0.60	0.014	0.003	0.0002	0.27	0.010	0.004	0.030
<i>Funaria</i>	0.48	0.009	0.002	0.002	0.44	0.011	0.003	0.004
<i>Pleurozium</i>	0.40	0.007	0.002	0.007	0.35	0.009	0.003	0.012
<i>Ptilidium</i>	0.20	0.005	0.003	0.074	0.10	0.003	0.002	0.23
<i>Sanionia</i>	0.38	0.007	0.002	0.009	0.20	0.006	0.003	0.070
<i>Tritomaria</i>	0.06	0.002	0.002	0.37	0.17	0.005	0.003	0.11
<i>Pogonatum</i>	0.55	0.009	0.002	0.001	0.56	0.015	0.003	0.001
<i>Pohlia</i>	0.28	0.010	0.004	0.029	0.26	0.009	0.004	0.043
<i>Tetraplodon</i>	0.63	0.013	0.003	0.0001	0.46	0.018	0.005	0.003
<i>Bryum</i>	0.51	0.011	0.003	0.001	0.58	0.015	0.003	0.000
<i>Dicranum</i>	0.41	0.005	0.002	0.007	0.29	0.006	0.002	0.025
<i>Marchantia</i>	0.65	0.012	0.002	0.000	0.38	0.012	0.004	0.007
<i>Polytrichum</i>	0.41	0.010	0.003	0.005	0.34	0.014	0.005	0.011
<i>Sphagnum</i>	0.63	0.011	0.002	0.0001	0.42	0.016	0.005	0.003

Note: Deviance squared is a measure of how well the model fits the data, with lower values indicating a better fit. The estimate represents the predicted change in the response variable for a unit change in the predictor variable. The standard error (SE) reflects the variability in the estimate. The *p*-value indicates the probability of observing the results. We follow the convention of calling *p*-values <0.05 significant, but also take note of values <0.1, marked in orange. A clear or orange *p*-value is interpreted as evidence of or slightly less strong evidence of change in phenological timing for that taxon. *N* for each regression = 17. p>0.1 ; p>0.5

importantly, increases light availability and the risk of frost damage (van Zuijlen et al., 2024). Our data suggest that sporophyte development is more flexible concerning the winter resting period than previously perceived. For bryophytes, we know little about the mechanisms that regulate seasonal allocation to growth versus sexual reproduction. Hagerup (1935) states that vegetative development is paused before winter at different intrinsically controlled stages depending on species. Lackner (1939) indicates that many bryophytes halt sporophyte development or gamete production before the end of the growing season. For example, *Sphagnum* species initiate antheridia—a sensitive stage (Sundberg, 2002)—before winter, followed by fertilization in the subsequent spring or summer and spore production later in the same season (Cronberg, 1993). It is thus unclear whether reproductive organs or sporophytes are programmed to hibernate in a specific stage. Notably, our data indicate that sporophyte maturation could proceed further in a milder climate, resulting in more developed spore capsules at the onset of winter and earlier spore release in spring. This is comparable to vascular plant resilience to climate warming (Prevey et al., 2017) by the initiation of flower buds in the autumn that develop and flower early in the next season. Such adaptations may carry risks, like delays in autumn temperature decline or more unpredictable weather that could affect preparedness for winter

(Taulavouri, 2013). Unexpected weather may also prematurely break winter and freeze tolerance or interrupt dormancy during warm spells (Taulavouri, 2013), potentially jeopardizing the production of viable spores in bryophyte spore capsules.

Our results are consistent with studies on other organisms, such as Menzel et al. (2006), that found temperature to be the primary driver of phenological change in reproductive traits among 542 vascular plant species and 19 animal species. Environmental factors and conditions other than temperature also affect plant phenology. For example, photoperiod has an impact on arctic vascular plants (Bjorkman et al., 2017), while lichens may depend more on precipitation and snow regime (Björk & Molau, 2007). MacDougall et al. (2021) concluded that snowmelt timing may be more critical than temperature for phenological events in vascular plants.

The phenology of the leafy liverwort *Tritomaria quinquedentata* differs from all other species in this study by showing no phenological changes over time, indicating spore dispersal primarily controlled by photoperiod rather than temperature. Regarding late successional tree species, Körner and Basler (2010) noted a photoperiod threshold for winter dormancy to break, while opportunistic tree species are solely affected by temperature. In this respect, many of our taxa could be considered opportunists, better equipped to adapt to warming, contrasting with species with conservative responses to

warming (Körner & Basler, 2010). Despite this, phenological shifts pose a risk of mismatches with substrate availability and water requirements needed for successful establishment (Wiklund & Rydin, 2004).

Our study shows clear changes in relative spore abundances within the seasons (Figure S3a–d). A milder climate, coupled with an extended season and more favourable microclimatic niches, could allow species to colonize new sites or initiate spore production for a species in habitats where it was previously reliant on vegetative reproduction (De Frenne et al., 2021). Although many bryophytes primarily propagate vegetatively (Newton & Mishler, 1994), sexual reproduction and spore dispersal play crucial roles in ensuring the ability to colonize new sites and generate potentially adaptive genotypes.

The effects of environmental changes on arctic and subarctic bryophyte communities are still poorly understood. Bjorkman et al. (2020) found that the abundance and biomass of most plant species in northern habitats were unaffected by experimental warming and did not increase during monitoring. Their meta-study reported bryophytes as one functional group with a stable abundance, without considering species turnover or whether declining species were replaced by other species. Studies from alpine Finse, central Norway, over three decades suggest that bryophytes expand under ambient warming with some species turnover (summarized in Roos et al., 2023). Experimental transplantations of bryophytes at their warm range margin in boreal forest show that they can stand increased temperatures but suffer from indirect effects such as competition, herbivory, leaf litter shading, and water scarcity (Greiser et al., 2021). Transplanting experiments have also demonstrated differential responses indicative of adaptation to specific microclimates (Merinero et al., 2020).

3.5 | Dispersal ranges and spore viability

The dispersal ranges and viability of the spores after deposition are crucial points in interpreting our results. Bryophyte spore release is strongly leptokurtic, with most spores deposited close to the sporulating individual (Lönnell et al., 2012; McQueen, 1985). However, bryophyte spores (ranging 10–40 µm in diameter among our taxa) can readily become airborne, and genetic data suggest a generally high dispersal capacity (Fichant et al., 2023). Long-distance dispersal can be enhanced by turbulent weather (Lönnell et al., 2015), but modelling of particles of 22 µm in the region suggests that the catchment area is roughly 50 km (Sullivan et al., 2023). This aligns with experimental data from Canada indicating that the bryophyte spore cloud is dominated by spores dispersed in a range of 1.5–10 km (Barbé et al., 2016). We cannot exclude that our data is influenced by long-distance dispersal, but relatively late peaks (compared to conditions in southern Sweden) indicate deposition from regional sources.

Experiments with liverwort spores carried in specially designed containers on the outside of aircrafts demonstrate a varying survival capacity under UV radiation, drought, and low temperatures

at high elevations, correlating with distribution patterns (van Zanten & Gradstein, 1988). Moss spores have variable lifespans in drought, ranging from 1 to over 6 months (Dalen & Söderström, 1999; Wiklund & Rydin, 2004). Genomic data, especially for some species of *Sphagnum*, show that they can travel far and still be viable (Sundberg et al., 2006). To conclude, regional sources most likely dominate our data, but long-range dispersal is possible, and most spores retain viability for some time in the air column.

Finally, one cluster was characterized by three taxa (*Bartramia*, *Bryum* and *Funaria*) with relative abundances either showing two peaks, the first taller than the second, or high initial relative abundances, indicating that the sampling period did not fully capture the entire season (Figure S3a–d). This relates to a general concern with the passively collected air-filter data; the ‘everything is everywhere’-problem (Clare et al., 2021), illustrated by Sullivan et al. (2023) that found all types of organisms in their material, including taxa that do not occur in the study area. Relevant to our study, we observed bryophyte reads outside of the sporulation season. These reads may have originated from more or less viable spores floating in the air column for extended time periods, from spores attached to aerosols of different kinds, or from spores re-suspended from the ground by turbulence. We nevertheless believe that using quantiles to reflect phenological events early and late in the season is a relatively robust method to capture phenological shifts, as has been done in research on birds (cf. Knudsen et al., 2011; Lehikoinen et al., 2019).

Another source of uncertainty in our study related to the relative abundance starting comparatively high in spring is introduced by the fact that DNA was only extracted from filters collected when temperatures exceeded 0°C, because initial studies revealed low levels of DNA in the air during winter (Karlsson et al., 2020), although this was not directly assessed for bryophytes. While we accounted for the length of the sampling season in the analyses by including the number of weeks as an offset variable, we note that this effect could still cause heterogeneity in the within-season phenology (see Figure S3a–d). In Kiruna, temperatures below 0°C typically mean that the snow cover effectively blocks the dispersal of any kind of bryophyte fragments from the ground. Elevated surfaces such as tree trunks and rock ledges may be free from snow, which could explain why the rock-wall specialist genus *Bartramia* often reached high relative abundance at the beginning of the spring. We also observed early relative abundance of reads for *Funaria*, which might be attributed to its habit of colonizing fireplaces where high salt concentration in the charcoal, along with low albedo, accelerates snowmelt in the spring (Gleason & Nolin, 2016).

Additionally, other kinds of bryophyte tissues besides spores are possible sources for our dataset, similarly to studies on vascular plants, where pollen is not the sole source of air-borne eDNA (Johnson et al., 2019). In theory, detached fragments or vegetative dispersal agents can be caught in the air filters, although these sources likely represent a smaller part of the signal than the light bryophyte spores. Another potential source is male gametes dispersed through scattered raindrops (Clayton-Greene et al., 1977) or

carried by microarthropods (Cronberg et al., 2006). Similarly, small flies are believed to be the major dispersers of the sticky spores of *Tetraplodon* (Marino, 1991), which is abundant in the vicinity of the sample station. Although these factors may increase noise in our dataset, we see no reason why the likelihood of these sources of error would have changed over time to bias our main results.

eDNA preservation over time may raise concerns, as multi-decadal storage could lead to the gradual degradation of DNA. However, we have taken various measures to assess this problem (Sullivan et al., 2023), including removing trends correlated with DNA degradation over time. The sampled filters were stored in air-tight containers in the ambient temperature of an underground storage facility, resulting in the successful preservation of bryophyte DNA with minimal degradation (cf. Figure S1). Even if some degradation has occurred, this is unlikely to systematically affect the detection of spore release timing between years, which is the focus of this study. Furthermore, Karlsson et al. (2020) and Sullivan et al. (2023) showed that the phenological patterns of pollen and long-term trends in bird abundances can accurately be reconstructed from eDNA recovered from the archived filters.

4 | CONCLUSIONS AND FUTURE DIRECTIONS

Our study is the first to document phenological differences in spore dispersal of multiple bryophyte taxa, and to demonstrate substantial phenological shifts in spore phenology over time, consistent with climate change. We also refer to historical records across Europe (Arnell, 1875, 1905; Grimme, 1903; Lackner, 1939), which are relatively inaccessible (summarized in Table 1; Table S2). In contrast to the older data (based on field observations and herbarium specimens), we can quantify the annual spore dispersal phenology and analyse phenological changes over decades. While differences in data sampling techniques and study location complicate direct comparison between the datasets, we note that data from the later part of our sampling period tend to approach earlier reported spore release periods, derived from more southerly European regions. Importantly, we conclude that bryophyte phenology is more flexible and dynamic than earlier anticipated.

Modern metagenomic analysis on shotgun sequenced airborne eDNA samples (Sullivan et al., 2023) allowed us to undertake this study, demonstrating that eDNA could be used to monitor bryophyte phenology over time, and the same methodology would greatly advance our possibilities to detect temporal changes in bryophyte communities more broadly. However, it should be acknowledged that there are challenges involved in the extraction and quantification of DNA from samples of this kind, considering degradation over time, the compositional nature of the data and restrictions of available genomic data for classification of reads (Sullivan et al., 2023). Also, it should be noted that species that rarely produce sporophytes or other situations in which the abundance of a species is not correlated with sporophyte production, would lead to

mis-representation in such a monitoring scheme. Ideally, continuous field monitoring, coupled with eDNA collection, would be valuable for validating the relationship between spore release and eDNA capture (Roger et al., 2022).

As genomic resources covering more species become available, studies at lower taxonomic levels can be performed in the future. Further studies could elucidate how species-specific life history traits and habitat specificity affect the potential of bryophytes to adapt to changing environmental conditions. Another important research gap relates to understanding intra-annual variation in spore abundance depending on a range of environmental variables, including snowmelt and meteorological parameters. Finally, the surveys of bryophyte eDNA can be extended both in time and space as air samples stored as glass-fibre sheets have been collected from a handful of stations across Sweden since the 1960s.

The long-term consequences of altered bryophyte phenology are potentially strong. Regarding individual species, shifts in spore release timing may prove detrimental, for example if it causes a mismatch with the availability of colonization sites or a swamping of the spore cloud by certain species so that competitive exclusion occurs between species at spore germination (Cheng et al., 2024). Bryophytes comprise multiple functional groups and play crucial roles in ecosystems, such as N fixing (Rousk et al., 2013) and C sequestration (Yu, 2012), insulation of the soil (Blok et al., 2011) and albedo (Xiao & Bowker, 2020). Changes in bryophyte community composition may change these roles and impact other groups of organisms through direct or indirect interactions, highlighting a potential for bryophytes as 'canaries in the coal mine' for climate change using eDNA practices.

AUTHOR CONTRIBUTIONS

The original ideas for this research came from Nils Cronberg, Johan Ekroos and Per Stenberg, and all authors were involved in designing the methodology. Fia Bengtsson analysed the data and led the writing of the manuscript. Jose Antonio Lozano Villegas, Abu Bakar Siddique and Johan Ekroos analysed the data. All authors contributed critically to the data interpretation and revisions of the manuscript, and all authors gave final approval for submission.

ACKNOWLEDGEMENTS

This work was funded by the strategic research environment BECC (Biodiversity and Ecosystem services in a Changing Climate), hosted by the Centre for Environmental and Climate Research, Lund University, by the Bolin Centre for Climate Research, Stockholm University and by Formas (2016-01371, 2019-00579 and 2021-02155).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70180>.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.x95x69pxs> (Bengtsson et al., 2025).

ORCID

Fia Bengtsson  <https://orcid.org/0000-0003-0497-8316>

REFERENCES

- Abrego, N., Norros, V., Halme, P., Somervuo, P., Ali-Kovero, H., & Ovaskainen, O. (2018). Give me a sample of air and I will tell which species are found from your region: Molecular identification of fungi from airborne spore samples. *Molecular Ecology Resources*, 18, 511–524. <https://doi.org/10.1111/1755-0998.12755>
- AMAP (Arctic Management and Assessment Programme). (2012). Arctic Climate Issues 2011: Changes in Arctic snow, water, ice and permafrost. SWIPA 2011 Overview Report (amap.no).
- Arnell, W. H. (1875). *De skandinaviska lövmossornas kalendarium* (PhD thesis). Uppsala University.
- Arnell, W. H. (1905). Phenological observations on mosses. *The Bryologist*, 8, 41–44.
- Barbé, M., Fenton, N. J., & Bergeron, Y. (2016). So close and yet so far away: Long-distance dispersal events govern bryophyte metacommunity reassembly. *Journal of Ecology*, 104, 1707–1719. <https://doi.org/10.1111/1365-2745.12637>
- Bengtsson, F., Cronberg, N., Lozano Villegas, J. A., Siddique, A. B., Stenberg, P., & Ekroos, J. (2025). Data for “Rapid shifts in bryophyte phenology revealed by airborne eDNA”. *Dryad Digital Repository* <https://doi.org/10.5061/dryad.x95x69pxs>
- Bernes, C., Bråthen, K. A., Forbes, B. C., Speed, J. D. M., & Moen, J. (2015). What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence*, 4, 4.
- Bernhardt-Römermann, M., Poschlod, P., & Hentschel, J. (2018). BryForTrait – A life-history trait database of forest bryophytes. *Journal of Vegetation Science*, 29, 798–800. <https://doi.org/10.1111/jvs.12646>
- Björk, R. G., & Molau, U. (2007). Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic, and Alpine Research*, 39, 34–43.
- Bjorkman, A. D., García Criado, M., Myers-Smith, I. H., Ravolainen, V., Jónsdóttir, I. S., Westergaard, K. B., Lawler, J. P., Aronsson, M., Bennett, B., Gardfjell, H., Heiðmarsson, S., Stewart, L., & Normand, S. (2020). Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. *Ambio*, 49, 678–692. <https://doi.org/10.1007/s13280-019-01161-6>
- Bjorkman, A. D., Vellend, M., Frei, E. R., & Henry, G. H. R. (2017). Climate adaptation is not enough: Warming does not facilitate success of southern tundra plant populations in the High Arctic. *Global Change Biology*, 23, 1540–1551. <https://doi.org/10.1111/gcb.13417>
- Blok, D., Heijmans, M. M. P. D., Schaepman-Strub, G., van Ruijven, J., Parmentier, F. J. W., Maximov, T. C., & Berendse, F. (2011). The cooling capacity of mosses: Controls on water and energy fluxes in a Siberian tundra site. *Ecosystems*, 14(7), 1055–1065. <https://doi.org/10.1007/s10021-011-9463-5>
- Cheng, J., Lončarević, I., & Cronberg, N. (2024). Interspecific competition affects spore germination and gametophore development of mosses. *Open Research Europe*, 3, 91. <https://doi.org/10.12688/openreseurope.16004.2>
- Clare, E. L., Economou, C. K., Faulkes, C. G., Gilbert, J. D., Bennett, F., Drinkwater, R., & Littlefair, J. E. (2021). eDNAir: Proof of concept that animal DNA can be collected from air sampling. *PeerJ*, 9, e11030. <https://doi.org/10.7717/peerj.11030>
- Clayton-Greene, K. A., Green, T. G. A., & Staples, B. (1977). Studies of *Dawsonia superba*. 1. Antherozoid dispersal. *The Bryologist*, 80(3), 439–444. <https://doi.org/10.2307/3242019>
- Cronberg, N. (1993). Reproductive biology of *Sphagnum Lindbergia*, 17, 69–82.
- Cronberg, N., Natcheva, R., & Hedlund, K. (2006). Microarthropods mediate sperm transfer in mosses. *Science*, 313(5791), 1255. <https://doi.org/10.1126/science.1128707>
- Dalen, L., & Söderström, L. (1999). Survival ability of moss diaspores in water—An experimental study. *Lindbergia*, 24, 49–58.
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klings, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., ... Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, 27, 2279–2297. <https://doi.org/10.1111/gcb.15569>
- Fenner, M. (1998). The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, 1, 78–91. <https://doi.org/10.1078/1433-8319-00053>
- Fichant, T., Ledent, A., Collart, F., & Vanderpoorten, A. (2023). Dispersal capacities of pollen, seeds and spores: Insights from comparative analyses of spatial genetic structures in bryophytes and spermatophytes. *Frontiers in Plant Science*, 14, 1289240. <https://doi.org/10.3389/fpls.2023.1289240>
- Gleason, K. E., & Nolin, A. W. (2016). Charred forests accelerate snow albedo decay: Parameterizing the post-fire radiative forcing on snow for three years following fire. *Hydrological Processes*, 30, 3855–3870. <https://doi.org/10.1002/hyp.10897>
- Greiser, C., Ehrén, J., Luoto, M., Meineri, E., Merinero, S., Willman, B., & Hylander, K. (2021). Warm range margin of boreal bryophytes and lichens not directly limited by temperatures. *Journal of Ecology*, 109, 3724–3736.
- Grimme, A. (1903). Über die Blüthezeit deutscher Laubmoose. *Hedwigia*, 62, 1–75.
- Hagerup, O. (1935). Zur Periodizität im Laubwechsel der Moose. *Biologische Meddelelser*, 11(9), 1–88.
- IPCC. (2021). Climate change 2021: The physical science basis. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
- Ishizaki, K., Nishihama, R., Yamato, K. T., & Kohchi, T. (2016). Molecular genetic tools and techniques for *Marchantia polymorpha* research. *Plant Cell Physiology*, 57, 262–270.
- Johnson, M. D., Cox, R. D., & Barnes, M. A. (2019). The detection of a non-anemophilous plant species using airborne eDNA. *PLoS One*, 14(11), e0225262. <https://doi.org/10.1371/journal.pone.0225262>
- Johnson, M. D., Fokar, M., Cox, R. D., & Barnes, M. A. (2021). Airborne environmental DNA metabarcoding detects more diversity, with less sampling effort, than a traditional plant community survey. *BMC Ecology and Evolution*, 21, 218. <https://doi.org/10.1186/s12862-021-01947-x>
- Jonsson, B. G., & Söderström, L. (1988). Growth and reproduction in the leafy hepatic *Ptilidium pulcherrimum* (G. Web.) Vainio during a 4-year period. *Journal of Bryology*, 15, 315–325. <https://doi.org/10.1179/jbr.1988.15.2.315>
- Karlsson, E., Johansson, A., Ahlinder, J., Lundkvist, M. J., Singh, N. J., Brodin, T., Forsman, M., & Stenberg, P. (2020). Airborne microbial biodiversity and seasonality in northern and southern Sweden. *PeerJ*, 8, e8424. <https://doi.org/10.7717/peerj.8424>
- Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P. P., Möller, A. P., Nilsson, A. L. K., Péron, G., ... Stenseth, N. C. (2011). Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, 86, 928–946.
- Körner, C., & Basler, D. (2010). Phenology under global warming. *Science*, 327, 1461–1462. <https://doi.org/10.1126/science.118647>

- Laaka-Lindberg, S. (2005). Reproductive phenology in the leafy hepatic *Lophozia silvicola* Buch in southern Finland. *Journal of Bryology*, 27(3), 253–259. <https://doi.org/10.1179/174328205X70001>
- Lackner, L. (1939). Über die Jahresperiodizität in der Entwicklung der Laubmoose. *Planta*, 29, 534–616.
- Länsstyrelsen i Norrbottens län. (2017). Klimatförändringar i Norrbottens län—konsekvenser och anpassning för areella näringar och ekosystemtjänster. *Rapportserie*, nr 11/2017, 3–97. <https://www.lansstyrelsen.se/download/18.8cd5a1b19362fb4fc23e37/1732540214829/Klimatf%C3%B6r%C3%A4ndringar%20i%20Norrbottens%20l%C3%A4n%20-%20areella%20n%C3%A4ringar%20och%20ekosystemt%C3%A4nster.pdf>
- Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T. L., Dunn, E. H., Gregory, G., Karlsson, L., Kristiansen, V., Mackenzie, S., Newman, S., Røer, J. E., Sharpe, C., Sokolov, L. V., Steinholtz, Å., Stervander, M., Tirri, I.-S., & Tjørnløv, R. S. (2019). Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. *Ecological Indicators*, 101, 985–991. <https://doi.org/10.1016/j.ecoli.2019.01.083>
- Linde, A.-M., Eklund, D. M., Kubota, A., Pederson, E. R. A., Holm, K., Gyllenstrand, N., Nishihama, R., Cronberg, N., Muranaka, T., Oyama, T., Kohchi, T., & Lagercrantz, U. (2017). Early evolution of the land plant circadian clock. *New Phytologist*, 216(2), 576–590. <https://doi.org/10.1111/nph.14487>
- Longton, R. E., & Schuster, R. M. (1983). Reproductive biology. In R. M. Schuster (Ed.), *New manual of bryology* (pp. 386–462). Hattori Botanical Laboratory.
- Lönnell, N., Hylander, K., Jonsson, B. G., & Sundberg, S. (2012). The fate of the missing spores—Patterns of realized dispersal beyond the closest vicinity of a sporulating moss. *PLoS One*, 7(7), e41987. <https://doi.org/10.1371/journal.pone.0041987>
- Lönnell, N., Norros, V., Sundberg, S., Rannik, Ü., Johansson, V., Ovaskainen, O., & Hylander, K. (2015). Testing a mechanistic dispersal model against a dispersal experiment with a wind-dispersed moss. *Oikos*, 124(9), 1232–1240. <https://doi.org/10.1111/oik.01886>
- MacDougall, A. S., Caplat, P., Olofsson, J., Siewert, M. B., Bonner, C., Esch, E., Lessard-Therrien, M., Rosenzweig, H., Schäfer, A.-K., Raker, P., Ridha, H., Bolmgren, K., Fries, T. C. E., & Larson, K. (2021). Comparison of the distribution and phenology of Arctic Mountain plants between the early 20th and 21st centuries. *Global Change Biology*, 27(20), 5070–5083. <https://doi.org/10.1111/gcb.15767>
- Marino, P. C. (1991). Dispersal and coexistence of mosses (Splachnaceae) in patchy habitats. *Journal of Ecology*, 79(4), 1047–1060. <https://doi.org/10.2307/2261097>
- McQueen, C. B. (1985). Spatial patterns and gene flow distances in *Sphagnum subtile*. *The Bryologist*, 88(4), 333–336. <https://doi.org/10.2307/3242668>
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mäge, F., ... Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12(10), 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>
- Merinero, S., Dahlberg, C. J., Ehrlen, J., & Hylander, K. (2020). Intraspecific variation influences performance of moss transplants along microclimate gradients. *Ecology*, 101, e02999.
- Newton, A. E., & Mishler, B. D. (1994). The evolutionary significance of asexual reproduction in mosses. *Journal of the Hattori Botanical Laboratory*, 76, 127–145.
- Pearse, W. D., Davis, C. C., Inouye, D. W., Primack, R. B., & Davies, T. J. (2017). A statistical estimator for determining the limits of contemporary and historic phenology. *Nature Ecology & Evolution*, 1, 1876–1882.
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25, 1922–1940. <https://doi.org/10.1111/gcb.14619>
- Pinheiro, J., Bates, D., & R Core Team. (2022). nlme: Linear and nonlinear mixed effects models. R package version 3.1–160, <https://CRAN.R-project.org/package=nlme>
- Prevey, J., Vellend, M., Rüger, N., Hollister, R., Bjorkman, A., Myers-Smith, I., Elmendorf, S., Clark, K., Cooper, E., Elberling, B., Fosaa, A. M., Henry, G., Høye, T., Jónsdóttir, I., Klanderud, K., Lévesque, E., Mauritz, M., Molau, U., Natali, S., & Rixen, C. (2017). Greater temperature sensitivity of plant phenology at colder sites: Implications for convergence across northern latitudes. *Global Change Biology*, 23, 2660–2671. <https://doi.org/10.1111/gcb.13619>
- Proctor, M. C. F. (1990). The physiological basis of bryophyte production. *Botanical Journal of the Linnean Society*, 104, 61–77.
- Roger, F., Ghanavi, H. R., Danielsson, N., Wahlberg, N., Löndahl, J., Pettersson, L. B., Andersson, G. K. S., Boke Olén, N., & Clough, Y. (2022). Airborne environmental DNA metabarcoding for the monitoring of terrestrial insects—A proof of concept from the field. *Environmental DNA*, 4, 1–18. <https://doi.org/10.1002/edn3.290>
- Rojo, J., Picornell, A., Oteros, J., Werchan, M., Werchan, B., Bergmann, K.-C., Smith, M., Weichenmeier, I., Schmidt-Weber, C. B., & Buters, J. (2021). Consequences of climate change on airborne pollen in Bavaria, Central Europe. *Regional Environmental Change*, 21(1), 9. <https://doi.org/10.1007/s10113-020-01729-z>
- Roos, R. E., Asplund, J., Birkemoe, T., Halbritter, A. H., Olsen, S. L., Vassvik, L., van Zuijlen, K., & Klanderud, K. (2023). Three decades of environmental change studies at alpine Finse, Norway: Climate trends and responses across ecological scales. *Arctic Science*, 9(2), 430–450. <https://doi.org/10.1139/as-2020-0051>
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T. L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., & Imeson, A. (2008). Attributing physical and biological impacts to anthropogenic climate change. *Nature*, 453(7193), 353–357. <https://doi.org/10.1038/nature06937>
- Roslin, T., Antão, L., Hällfors, M., Meyke, E., Lo, C., Tikhonov, G., Delgado, M. M., Gurarie, E., Abadonova, M., Abduraimov, O., Adrianova, O., Akimova, T., Akkiev, M., Ananin, A., Andreeva, E., Andriychuk, N., Antipin, M., Arzamascev, K., Babina, S., ... Ovaskainen, O. (2021). Phenological shifts of abiotic events, producers and consumers across a continent. *Nature Climate Change*, 11, 241–248. <https://doi.org/10.1038/s41558-020-00967-7>
- Rousk, K., Jones, D. L., & DeLuca, T. H. (2013). Moss-cyanobacteria associations as biogenic sources of nitrogen in boreal forest ecosystems. *Frontiers in Microbiology*, 4, 150. <https://doi.org/10.3389/fmicb.2013.00150>
- SMHI. (2024). PTHBV—en areellt högupplöst klimatdatabas för hydrologiska modellberäkningar. <https://www.smhi.se/kunskapsbanken/hydrologi/pthbv-en-areellt-hogupplost-klimatdatabas-for-hydrologiska-modellberakningar-1.190268>
- Söderström, C., Ban, S., Jansson, P., Lindh, K., & Tooloutalaie, N. (2007). Radionuclides in ground level air in Sweden Year 2006. <https://www.foi.se/en/foi/reports/report-summary.html?reportNo=FOI-R-2260--SE>
- Song, Z., Du, Y., Primack, R. B., Miller-Rushing, A. J., Ye, W., & Huang, Z. (2021). Surprising roles of climate in regulating flowering phenology in a subtropical ecosystem. *Ecography*, 44(9), 1379–1390. <https://doi.org/10.1111/ecog.05629>
- Stark, L. R. (2002). Phenology and its repercussions on the reproductive ecology of mosses. *Bryologist*, 105, 204–218.
- Sullivan, A. R., Karlsson, E., Svensson, D., Bindefall, B., Villegas, J. A., Mikko, A., Bellieny, D., Siddique, A. B., Johansson, A.-M., Grahn, H., Sundell, D., Norman, A., Esseene, P.-A., Sjödin, A., Singh, N. J., Brodin, T., Forsman, M., & Stenberg, P. (2023). Airborne eDNA captures three decades of ecosystem biodiversity. *bioRxiv* preprint this version posted December 11, 2023. <https://doi.org/10.1101/2023.12.06.569882>
- Sundberg, S. (2002). Sporophyte production and spore dispersal phenology in *Sphagnum*: The importance of summer moisture and patch

- characteristics. *Canadian Journal of Botany*, 80, 543–556. <https://doi.org/10.1139/B02-060>
- Sundberg, S. (2010). The *Sphagnum* air-gun mechanism resurrected. *New Phytologist*, 185, 886–889. <https://doi.org/10.1111/j.1469-8137.2009.03086.x>
- Sundberg, S., Hansson, J., & Rydin, H. (2006). Colonization of *Sphagnum* on land uplift islands in the Baltic Sea: Time, area, distance and life history. *Journal of Biogeography (J. Biogeogr.)*, 33, 1479–1491. <https://doi.org/10.1111/j.1365-2699.2006.01520.x>
- Taulavouri, K. (2013). Vegetation at northern high latitudes under global warming. In I. Dincer, C. O. Colpan, & F. Kadioglu (Eds.), *Causes, impacts and solutions to global warming* (pp. 3–16). Springer. <https://doi.org/10.1007/978-1-4614-7588-0>
- van Zanten, B. O., & Gradstein, S. R. (1988). Experimental dispersal geography of neotropical liverworts. *Nova Hedwigia*, 90, 41–94.
- van Zuijlen, K., Kassel, M., Dorrepaal, E., & Lett, S. (2024). Frost damage measured by electrolyte leakage in subarctic bryophytes increases with climate warming. *Journal of Ecology*, 112, 220–232. <https://doi.org/10.1111/1365-2745.14236>
- Virtanen, R., Parviainen, J., & Henttonen, H. (2002). Winter grazing by the Norwegian lemming (*Lemmus lemmus*) at Kilpisjärvi (NW Finnish Lapland) during a moderate population peak. *Annales Zoologici Fennici*, 39, 335–341.
- Wiklund, K., & Rydin, H. (2004). Ecophysiological constraints on spore establishment in bryophytes. *Functional Ecology*, 18, 907–913. <https://doi.org/10.1111/j.0269-8463.2004.00906.x>
- Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*, 6(12), e325. <https://doi.org/10.1371/journal.pbio.0060325>
- Wood, D. E., Lu, J., & Langmead, B. (2019). Improved metagenomic analysis with Kraken 2. *Genome Biology*, 20, 1–13.
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 73, 3–36.
- Xiao, B., & Bowker, M. A. (2020). Moss-biocrusts strongly decrease soil surface albedo, altering land-surface energy balance in a dryland ecosystem. *Science of the Total Environment*, 741, 140425. <https://doi.org/10.1016/j.scitotenv.2020.140425>
- Yu, Z. (2012). Northern peatland carbon stocks and dynamics: A review. *Biogeosciences*, 9(10), 4071–4085. <https://doi.org/10.5194/bg-9-4071-2012>
- Zanatta, F., Vanderpoorten, A., Hedenäs, L., Johansson, V., Patiño, L., Lönnell, N., & Hylander, K. (2018). Under which humidity conditions are moss spores released? A comparison between species with perfect and specialized peristomes. *Ecology and Evolution*, 8, 11484–11491. <https://doi.org/10.1002/ece3.4579>

SUPPORTING INFORMATION

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

Figure S1. DNA fragment length for bryophytes is stable over time. The lengths of pair-end reads assigned to each bryophyte genus were summed, and the average combined length plotted by year.

Figure S2. Yearly annual weather data from the closest Kiruna weather station for all years between 1974 and 2008. Plots show (a) mean temperature and fitted line (linear regression) and (b) summed annual precipitation and fitted line (linear regression).

Figure S3. (a) eDNA reads used to describe bryophyte phenology and phenological changes over time in genera *Andreaea*, *Bartramia*, *Bryum* and *Ceratodon*. Left panel: heatmaps based on pivot coordinates

showing the relative abundance (scaled to vary between 0 and 1, using $(x - \min(x))/(\max(x) - \min(x))$) of classified reads for each week during each sampling year across the Kiruna time-series. Right panel: Plotted smoothed regressions describing the weekly relative abundance, using generalized additive models (GAMs). (b) eDNA reads used to describe bryophyte phenology and phenological changes over time in genera *Dicranum*, *Funaria*, *Pleurozium* and *Pogonatum*. Left panel: heatmaps based on pivot coordinates showing the relative abundance (scaled to vary between 0 and 1, using $(x - \min(x))/(\max(x) - \min(x))$) of classified reads for each week during each sampling year across the Kiruna time-series. Right panel: Plotted smoothed regressions describing the weekly relative abundance, using generalized additive models (GAMs). (c) eDNA reads used to describe bryophyte phenology and phenological changes over time in genera *Pohlia*, *Polytrichum*, *Sanionia* and *Sphagnum*. Left panel: heatmaps based on pivot coordinates showing the relative abundance (scaled to vary between 0 and 1, using $(x - \min(x))/(\max(x) - \min(x))$) of classified reads for each week during each sampling year across the Kiruna time-series. Right panel: Plotted smoothed regressions describing the weekly relative abundance, using generalized additive models (GAMs). (d) eDNA reads used to describe bryophyte phenology and phenological changes over time in genera *Tetraplodon*, *Marchantia*, *Ptilidium* and *Tritomaria*. Left panel: heatmaps based on pivot coordinates showing the relative abundance (scaled to vary between 0 and 1, using $(x - \min(x))/(\max(x) - \min(x))$) of classified reads for each week during each sampling year across the Kiruna time-series. Right panel: Plotted smoothed regressions describing the weekly relative abundance, using generalized additive models (GAMs).

Table S1. Correlations between mean annual temperature, mean temperature of the autumn of the previous year (3rd and 4th quarters) and phenological variables for the start of season, that is, the week number that the 10th, and 20th percentiles (SS_{10} , SS_{20} , respectively) of relative abundance were reached every year. Rows containing taxa for which the phenological change was not significant in our models are shown in grey. *p*-values above 0.1 are shown in red.

Table S2. Duration of different stages in the reproductive cycles based on Lackner (1939) of taxa shared between our study and Lackner (1939). The numbers denote the month numbers marking the initiation and completion of each stage within the reproductive cycle for each taxon. The letter “W” indicates that the taxon overwinters at the end of that particular stage, in parenthesis means it is not always the case. By “Contributing species” we mean that the species listed under “Species” is one of the species that should be the origin of the eDNA signal in our study.

How to cite this article: Bengtsson, F., Cronberg, N., Lozano Villegas, J. A., Siddique, A. B., Stenberg, P., & Ekroos, J. (2025). Rapid shifts in bryophyte phenology revealed by airborne eDNA. *Journal of Ecology*, 113, 3564–3578. <https://doi.org/10.1111/1365-2745.70180>