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# Interannual variation in bryophyte dispersal: linking bryophyte phenophases and weather conditions

Marion Barbé, Nicole J. Fenton, Richard Caners, and Yves Bergeron

**Abstract:** In the context of global changes that modify the distribution range of species, there is an urgent need to identify climate variables affecting species dispersal. We investigated patterns of aerial propagule release (sexual and asexual) of boreal bryophytes in response to weather. We present the first community-level study that examines the impact of weather on the phenology of bryophytes, and we divided it into phases. Bryophyte propagule rain was trapped in 2013 (summer and fall) and 2014 (spring and fall), and climatic variables were collated from the years 2012 to 2014. The phases of the phenology and the weather variables one season to two years preceding propagule release, which may influence the dispersal of propagules, were identified. Propagule release varies with weather conditions at the time of dispersal (direct effects), but is also associated with weather during the winter and summer one year preceding dispersal (indirect effects), which presumably influences survival, growth, and fertilization of the mother plant as well as propagule and sporophyte development. We suggest that propagule release is related to weather conditions occurring from one to several previous seasons, particularly humidity, temperature, and length (duration) of winter. Dividing the phenology into phases, we present an innovative method that should provide new insights into bryophyte dispersal dynamics in response to climate.

Key words: boreal latitudes, climate, gametophyte, propagule release, phenology.

**Résumé** : Les changements globaux, modifiant les aires de distributions des espèces, rendent opportun d'identifier les variables climatiques jouant sur les patrons de dispersion. Nous étudions les pluies de propagules aériennes (unités sexuelles et asexuelles de dispersion) de bryophytes boréales en réponse au climat. Cette étude est la première effectuée à l'échelle de la communauté et où le cycle phénologique des bryophytes est divisé en phases. Les propagules furent interceptées en 2013 (été et automne) et 2014 (printemps et automne), et les variables climatiques de la région compilées de 2012 à 2014. Les variables climatiques influençant chaque phase du cycle, une saison à deux ans avant la dispersion, furent identifiées pour déterminer quelles phases et quelles variables impactent majoritairement le relargage des propagules. Ce relargage dépendait de variables climatiques contemporaines à la dispersion (directes) et indirectes durant l'hiver et l'été précédent (indirectes). Ces variables joueraient sur la survie/croissance de la plante mère, la fertilisation et le développement des propagules et des sporophytes. Le relargage des propagules semble particulièrement dépendre de l'humidité, de la température et de la longueur de l'hiver des saisons en amont. En divisant leur cycle phénologique en phases nous fournissons ici une méthode novatrice pour comprendre les relations entre la dispersion des bryophytes et le climat.

Mots-clés : écosystèmes boréaux, conditions climatiques, phénologie, phénophases, relargage des propagules.

## Introduction

How species diversity patterns are influenced by the impacts of environmental factors on the organisms' phenology and distribution has been investigated previously (Benson-Evans 1961; Dougherty et al. 1994; Xiao et al. 2013). Phenology is the seasonality of events related to reproduction and growth (Stark 2002; c.f. Laaka-Lindberg 2005), and it includes the dispersal phase, which encompasses the production, transport, and establishment of propagules (seeds, spores, or asexual reproductive units; Bossuyt and Honnay 2006; Johst et al. 2011). Community structure, dynamics, and distribution depend on the phenology of species, which is in turn modulated by climate and season (Glime 2013). Consequently, changes in climate are expected to influence the phenology of species (Hughes 2000; Walther et al. 2002), particularly at northern latitudes where the effects of climate change are

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forecast to be more pronounced (Serreze et al. 2000; Wasley et al. 2006).

Northern ecosystems are dominated by bryophytes, which represent the principal plant biomass, cover, and diversity of the understory of boreal forests, bogs, fens, and tundra, as well as alpine and subpolar fell-fields (Proctor 2011). Bryophytes are poikilohydric and lack specialized mechanisms for regulating water uptake and loss, which explains their close relationship to humidity at the microhabitat scale (Löbel and Rydin 2010). This is also true throughout their phenology, which is composed of the successive phases (phenophases, sensu Stark 2002): vegetative growth, gametangial initiation, fertilization, sporophyte development, and propagule dispersal. Sporophyte, spore, and gemmae development depend on the phenophases that precede them. Indeed, gemmae are directly attached to the mother plant and sporophytes are matrotrophic, and consequently represent a cost for the gametophyte (Ehrlén et al. 2000; Bisang and Ehrlén 2002). Sporophyte maturation time and longevity influence the magnitude of propagule production cost and vary among species (Stark et al. 2000; Hedenäs 2001). Once sporophytes and spores are formed, purely mechanical mechanisms lead to spore release, with no costs for the gametophyte. These mechanisms occur at certain levels of humidity and temperatures and depend on wind velocity. This includes hygroscopic movements of the peristome for mosses and certain liverworts, elater expansion for liverworts, and capsule "explosion" for sphagna (Sundberg 2005; Elbaum and Abraham 2014; Johansson et al. 2015). Propagules are subsequently released into the atmosphere where they stay for indefinite times in aerial propagule clouds and are sporadically washed out by precipitation and wind events.

The phenology of only a few bryophyte species has been investigated (Longton and Greene 1967, 1969; Stark 1997; Laaka-Lindberg 2005), and studies have reported differences in the timing of species dispersal. Indeed, as shown by Sundberg (2002) and Fenton and Bergeron (2006) for sphagna, different species, but also different colonies of a same species, have asynchronous sporulation times. Recently, the links between bryophyte phenology and weather conditions has been of interest, as bryophytes have been reported as bio-indicators of climate change (Gignac 2001; Slack 2011). Various studies have shown that mean summer temperature, number of days above 0 °C, amount of winter or summer precipitation, and humidity are regulators of bryophyte phenology (Sundberg 2002; Johansson et al. 2015). Furthermore, Pohjamo et al. (2006) pointed out the seemingly ambivalent influence of rainy conditions on the liverwort Anastrophyllum hellerianum (Nees ex Lindenb.) R.M. Schust. These conditions enhanced the number of gemmae released but did not affect their dispersal distance patterns. As these studies have all been based on individual

bryophyte species, more general patterns remain anecdotal.

We aim to fill this knowledge gap by investigating changes in bryophyte community phenology in response to weather conditions. We trapped aerial propagule rain during two seasons in two consecutive years in boreal black spruce - feather moss forests of eastern Canada, and described seasonal and annual aerial propagule rain patterns at the scale of the whole bryophyte metacommunity (Objective 1). We investigate the "direct" influence of weather conditions on propagule release, and the "indirect" effects of the weather conditions on propagule release through their actions on phenophases prior to propagule release (Objective 2). The notion of "indirect" refers to the "time lag" between a weather condition one to several phenophases before the release and its influence on the release, and is used instead of "lag" as the antonym of "direct" i.e., a condition at the time of the release. To our knowledge, this study is the first performed at the metacommunity scale trying to link weather variables to each bryophyte phenophase.

Based on a related study (Barbé et al. 2016), in which we focused on bryophyte propagule cloud patterns, we consider here that several discrete and local propagule clouds intermingle to form a general and persistent regional cloud. These two cloud types sporadically gain and loose propagules, but the local cloud is more affected by punctual and local precipitation and wind events whose impact is diluted in the regional cloud. We therefore expect that the assemblage of germinated bryophyte aerial propagule rain will differ among seasons because the timing of propagule release varies among species (Hock et al. 2004; Ross-Davis and Frego 2004; Hypothesis 1). In addition, slight variations in abundance or presence of the less-frequent species may be found among years, but a similar pool of species is expected, given that the same species make up the extant community (and therefore propagule releasers) (Hypothesis 2). Furthermore, we expect that each phenophase of bryophyte phenology will be influenced by specific weather variables (Hypothesis 3), such as water availability during the fertilization phenophase or wind velocity during the dispersal phenophase (Johansson et al. 2014). We therefore expect to highlight which phenophases govern propagule release and identify the weather variables that have the greatest influence on these phenophases.

#### Materials and methods

#### Study area

The study was conducted within the black spruce (*Picea mariana* Mill., Briton) –feather moss (*Pleurozium schreberi* (Brid.) Mitt.) forest of western Quebec, eastern Canada (Fig. A1). The stands are dominated by *P. mariana* in association with *Pinus banksiana* Lamb., *Populus tremuloides* Michx, *Abies balsamea* (L.) Mill., and *Betula papyrifera* 

Marshall (Saucier et al. 2009). Ericaceous and bryophyte species dominate the forest understory. The dynamics of the forest is driven by wildfires and the average forest age is approximately 140 years (Bergeron et al. 2002). The topography of the region is flat, and altitude varies from 200 to 300 m a.s.l. The climate is subpolar, subhumid continental. The average annual temperature and total annual precipitation are respectively 0.2 °C and 995.8 mm (1981–2010), recorded at the Chapais 2 weather station (100 to 240 km from our sites; Environment Canada 2015*a*). The region is characterized by long winters with 312.9 cm of snowfall annually, and by a short growing season of 140–160 days.

The sampling sites consisted of residual patches of forest and recently burned matrix area located in three wildfires spread across the study area (73 197 km<sup>2</sup>; 50°56'N, 77°53'W; 49°75'N, 76°29'W; 49°91'N, 76°13'W; see Barbé et al. 2016 and Appendix, Fig. A1, as well as the Supplementary data, Table S1<sup>1</sup> for more details on sites and sampling method). Site choice originated from a related study in the same area that focused on the role of post-fire residual forest patches on the dynamics of bryophyte communities (Barbé et al. 2017).

#### Interception of aerial propagule rain

The aerial propagule rain was sampled by the "emergence method" (Rudolph 1970; Ross-Davis and Frego 2004). In each trapping session, 21 groups of six Petri plates (90 mm in diameter) were deposited for six hours in forests and recently burned matrix areas at sampling points spread across the three wildfires (Appendix, Fig. A1). The aerial propagule rain was trapped on the 11th and 16th of August 2013 (summer), on the 4th and 13th of September 2013 (fall), on the 9th and 11th of June 2014 (spring), and on the 14th and 19th of September 2014 (fall). Two days were required for each trapping session, owing to the distances between the sampling points (average of 128 km). A total of 504 Petri plates were exposed over the four sessions [(6 Petri plates × 21 sampling points) × 4 trapping sessions]. In 2013, all six Petri plate traps were filled with Parker Thompson's basal nutrient medium, according to the protocol from Klekowski (1969) [described by C-Fern Project © (1995-2014)]. In 2014, only three plates were filled with nutrient agar whereas the other three plates were filled with pieces of wood collected in the field. The wood pieces were sterilized at 60 °C for 24 h to kill all organisms in the wood without destroying wood structure (A. Koubaa, personal communication). The sterilized wood was subsequently fragmented into smaller pieces (1-3 cm in length) and placed into Petri plates. The wood placed in Petri plates originated from the sampling area in which the plate was subsequently placed. After being exposed for six hours in

the field, the Petri plates were covered and randomly placed in germination chambers for six months, following the protocol described in Barbé et al. (2016). Development of bryophyte gametophytes was assessed twice a week to follow germination patterns and to control potential bacterial or fungal contamination. Six control Petri plates, three with virgin nutrient agar and three with sterilized wood pieces were placed in the germination chambers for the duration of the six-month emergence period to identify potential contaminants. No bryophyte species developed on any of the control plates, indicating that sample plates had not been contaminated during the laboratory growing period.

All of the bryophytes were identified following Faubert (2012–2014). Owing to the artificial growing conditions in the Petri plates, some bryophytes had unusual morphological characteristics, and consequently certain specimens were only identified to genus, particularly sphagna and members of the genera Ditrichum spp., Grimmia spp., Pohlia spp., and Polytrichum spp. Vouchers are stored at the University of Québec in Abitibi-Témiscamingue, Quebec, Canada. Species were classified by growth form (i.e., sphagna, liverworts, and true mosses divided into acrocarps and pleurocarps) and life strategy (i.e., colonist, perennial, shuttle, dominant; During 1992). The dominant life strategy group contained only sphagna species; therefore, the growth form and life strategy groups are confounded. In the Petri plates, one individual refers to a protonema and hence to one propagule. While one protonema can generate several stems making it difficult to distinguish individuals, monthly photographs of the plates were taken to follow individual germination events. While the "emergence method" was designed to trap aerial sexual propagules, asexual propagules may have been present in the plates (i.e., gemmae and vegetative fragments). However, we assumed that their few occurrences (less than five leaf fragments found on 504 Petri plates) did not impact the patterns found.

#### Weather variable choice

Weather data were collated from Environment Canada (2015*a*, 2015*b*) from the two nearest weather stations: Chapais (49°46'N, 74°32'W) and Chapais 2 (49°47'N, 74°51'W; Appendix, Fig. A1). The weather variables that impact the phenology of bryophytes were chosen based on information from the literature: variables that have a direct influence (e.g., precipitation, relative humidity, wind speed) or variables that have an indirect influence (e.g., consecutive days without rain as proxy of drought period) (Hedenäs 2001; Sundberg 2002; Johansson et al. 2015). Of the initial 22 weather variables collated (Supplementary data, Table S2<sup>1</sup>), 11 noncorrelated variables corresponding to monthly values for each year were

<sup>&</sup>lt;sup>1</sup>Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjb-2017-0054.

**Fig. 1.** Phenology cycle (*a*) and weather variables (*b*) used to explain aerial propagule rain patterns trapped in summer 2013 (T1), fall 2013 (T2), spring 2014 (T3), and fall 2014 (T4). Years and seasons (divided into months: F, fall; Sp, spring; Sm, summer; W, winter) are indicated at the exterior of the cycle and bold dotted lines separate the years. Trapping sessions (illustrating propagule release) are represented as dark grey wedges. Phenology is divided into the sporophyte generation containing three phenophases: fertilization during the summer of the year preceding the trapping (1), maturation of sporophytes and dispersal of propagules one season preceding the trapping (2), and the season of the trapping (3); and the gametophyte generation containing five phenophases: winter survival (W), survival and growth of the gametophyte two seasons preceding the trapping (4), one season preceding the trapping (5), and the season of the trapping (3). Weather variables impacting each phenophase are indicated in the table. Each phenophase (from 1 to 5) of 2012 and 2013 impact the trapping sessions of 2013, and each phenophase of 2013 and 2014 impact the trapping sessions of 2014 (see the section on Materials and methods for details). For simplicity, phenophase 3 is combined for both sporophytes and gametophytes.

retained: mean temperature (°C); maximum consecutive days below 0 °C; Julian date before exceeding 0 °C; mean night-day temperature differences (°C); number of days below 0 °C (freezing point of bryophyte cytoplasm is on average 0 °C; Longton 1988); mean relative humidity (%); maximum wind speed (km/h); number of days with maximum wind speed; number of days below -10 °C (estimated temperature of photosynthetic breakdown; Lappalainen et al. 2011); total precipitation (mm); and maximum consecutive days without precipitation. Temperature, relative humidity, and precipitation in the winter were not considered because bryophytes are generally under constant snow cover and therefore not exposed to ambient air temperatures (Longton and Greene 1967). As there is to date no evidence of gametophyte growth or sporophyte maturation under snow cover in boreal latitudes (Longton 1985), we considered that these phenophases were halted during the winter (Glime 2013). The duration of the winter in boreal latitudes delays the phenology compared with species in more temperate latitudes where winters are milder (Longton and Greene 1969; Imura and Iwatsuki 1989). We therefore also included variables characterizing the winters by their duration: maximum number of consecutive days below 0 °C from December to spring and the Julian date in the spring when temperature exceeds 0 °C.

# Relationship between weather conditions and bryophyte phenology

Globally speaking, bryophyte phenology is known for some species (Longton and Greene 1967, 1969; Stark 1997; Laaka-Lindberg 2005) but remains unknown for a substantial number of species. In our study, even though we are considering the assemblage, a representative cycle was used for all species because the cycle of many species are unknown, and all of the species we studied are developing in the same climate. We used the representative phenological cycle described for Polytrichum spp. and Pohlia spp. from the USA and UK (adapted from Stark 2002), which are species found in our study, and which is the phenological cycle geographically closer to our sites. In this 12-month cycle, fertilization occurs in the summer, sporophyte maturation occurs during the following spring/summer, and spore release occurs from the end of the spring to the end of fall of the second year. Gametophyte growth occurs in fall, spring, and summer. Bryophyte phenology was thus divided among the two generations: (1) sporophyte generation, with the phenophases fertilization and maturation-dispersal; and (2) gametophyte generation, with the phenophases winter survival and survival/growth during spring, summer, and fall. Given that sporophyte and spore maturation can take from one to several seasons, we propose that the phenology is spread over two growing years, and therefore sporophyte and gametangial development are influenced by the different phenophases, spread over the four seasons of the preceding year and the four seasons of the year of spore release (Longton and Greene 1969; Bisang and Ehrlén 2002; Sundberg 2002). To simplify our models, all of the species have been assumed to have shortlived sporophytes that only persist and release spores over a single season. Consequently, the weather conditions during the summer and fall of 2012, the four seasons of 2013, and spring and summer of 2014 were tested for correlation with the patterns in aerial propagule rain trapped in 2013 and 2014 (Figs. 1a and 1b). The 2012 and 2013 weather conditions explain the 2013 patterns, and the 2013 and 2014 weather conditions explain 2014 patterns. Weather variables were therefore divided into groups based on the phenophase that they were assumed to impact directly, and by trapping year. For example, the variable "wind speed" was only considered as a direct effect for the phenophase of propagule dispersal, while "mean temperature" may directly influence propagule dispersal, fertilization, sporophyte maturation, and gametophyte growth phenophases.

### Data analyses

Petri plates filled with sterilized woody debris were not analyzed due to fungal and bacterial contamination. Owing to the resulting unbalanced design (i.e., 6 Petri plates per plot in 2013 and 3 Petri plates per plot in 2014) and the correlation between the number of plates and species richness/frequency, analyses were only made at the Petri plate level for the plates filled with nutrient agar (n = 378).The use of mixed models with "sites" and "year" as random effects permits us to take into account the geographic location and a reduction in the effective sample size, and eliminates spatial and temporal pseudoreplication. After identifying the individuals grown in Petri plates, we obtained presence/absence data per Petri



Generation	Phase	Number of seasons preceding the trapping session	Weather variable implied	Number on the phenology cycle
Sporophyte	Fertilization	1 summer	Mean temp. difference (night–day); Relative humidity; Total precipitation; Maximum consecutive days without rain	
	Maturation & Dispersal	1 season	Mean temp. difference (night-day); Number of days below 0°C; Relative humidity; Number of days below -10°C; Maximum wind speed; Number of days with maximum wind speed; Total precipitation; Maximum consecutive days without rain	2
		0 (during trapping session)	The same as for the phenophase ②	3
Gametophyte	Winter survival	1 winter	Maximum consecutive days below 0°C; Julian date before temp. exceeded 0°C	$\otimes$
	Survival &	2 seasons	Mean temp. difference (night–day); Number of days below 0°C; Relative humidity; Number of days below -10°C; Total precipitation; Maximum consecutive days without rain	4
	Growth	1 season	The same as for the phenophase (4)	5
		0 (during trapping session)	The same as for the phenophase $4$	3

plate per trapping session (n = 4; 1 in spring, 1 in summer, 2 in fall) and per year (n = 2; 2013 and 2014). Species richness and species frequency (number of individuals of each species) were studied per Petri plate to obtain mean species richness and mean species frequency per year (comparison of the fall trapping sessions of 2013 and 2014) and season (using the four trapping sessions).

# Aerial propagule rain richness and assemblage among seasons and between years

R software 3.2.1 (R Core Team 2015) was used for statistical analyses with a significance level of  $\alpha$  = 0.05. The assemblage of the aerial propagule rain was compared among trapping sessions [Objective 1, which is to identify differential propagule assemblages among seasons (Hypothesis 1) but not between years (Hypothesis 2)]. Total (all bryophyte groups) mean species richness and total mean species frequency of species per plate grouped by life form and life strategy (During 1992) were compared between years (to be consistent, only fall seasons of each year were used) and among seasons (see Models used below). The overall assemblage was summarized in a principal coordinates analysis (PCoA; Borcard et al. 2011) performed on binary data (i.e., presence/absence data) of all species from all trapping seasons using the R package "vegan" (version 2.3-0). Jaccard's dissimilarity index was used as the distance measure because double-presences (present in the sample in 2013 and in 2014) are not overweighted compared with double-absences (absent from the sample in 2013 and in 2014). Double-absences are frequently not considered informative, but are relevant in this study because they may be due to various factors such as environmental conditions, species dispersal limitation, random local extinction, historical events, or stochastic variation (Legendre and Legendre 2012). The Cailliez correction was performed to correct for the production of several negative eigenvalues by the PCoA, which can affect the representation of objects on the axis (Gower and Legendre 1986). Despite the bias generated, we have chosen to be conservative and to not consider ungerminated propagules or unidentified protonemata, and to remove from the database the specimens that were only identified to genus, and for which other species of the same genus were present. The subsequent ordination matrix contained 41 species and 338 Petri plates (108 Petri plates in summer 2013; 116 in fall 2013; 57 in spring 2014; and, 57 in fall 2014). The remaining 40 Petri plates were empty and were therefore removed from PCoA and MRPP analyses. A distance-based test of multivariate differences among predefined groups (i.e., trapping session groups) from the PCoA was performed using the multi-response permutation procedure (MRPP) on 9999 permutations, also based on species presence/ absence data and Jaccard's dissimilarity.

## Relationships between weather variables and aerial propagule rain richness and assemblage

Eleven weather variables were retained from the initial set of 22 variables (Supplementary data, Table S2) to address our second objective [determine the weather variables impacting each phase of the phenology (Hypothesis 3)]. This limited set of variables (enumerated in the section "weather variable choice" above) was derived by removing variables that were most highly intercorrelated. Some variables that were partly intercorrelated were retained because they were considered highly relevant to explain patterns, but this did not violate any assumptions of PCoA or the multivariate regression tree (MRT, below). The mean seasonal values of the retained variables were then compared among years (2012, 2013, 2014), using linear models or generalized models, depending on their distributions.

The retained weather variables were projected as linear vectors in the PCoA to visualize their relative positions on the PCoA ordination axes (Borcard et al. 2011). Some variables were duplicated in PCoA (and in the MRT) to relate them to specific phenophases of bryophyte phenology. Finally, the influence of the same set of weather variables on aerial propagule rain assemblage was assessed using MRT (De'ath 2002) performed with the R package "mvpart" (version 1.6-2). Presence/absence data (41 species and 338 Petri plates) was analyzed to determine which weather variables accounted for the largest proportion of the explained variance in the model, and whether the model could discriminate between different years and seasons. Trees are described by their fit (i.e., inverse of relative error, RE), which varies from 1 (0% of the variance explained by the tree) to 0 (100% of the variance explained by the tree); and their predictive accuracy estimated by the cross-validation relative error (CVRE), which varies from 1 (poor predictive power) to 0 (good predictive power; De'ath 2002). Sample sites were included as dummy variables to consider the spatial structure of the dataset, i.e., additional columns represented each of the sampling sites. Subsequently the number of bryophyte species and the weather variables for each leaf (i.e., end group) were calculated. The amounts of variation explained by the tree overall and by each branch were also determined.

#### Models used

As our sampling design was spatially nested, we tested whether the structure of the sampling design (the effect of "site" and "year") influenced the models used to explain species richness and frequency with LogLik tests (Pinheiro and Bates 1995). In cases where the spatial structure was not influential, the model without random spatial effects (lm, glm) was chosen in the spirit of parsimony. When the spatial structure had a significant effect, we used mixed models (lme, glmer). In cases where the assumptions of normality were met, linear models with or without random effects (lm, lme) were per**Fig. 2.** Species richness and frequency by year (fall season only) and season (2013 and 2014) for the aerial propagule rain communities trapped in 2013 and 2014, with statistical significance determined using Kruskall–Wallis tests followed by multiple comparison post-hoc tests. Error bars refers to SD. Levels of significance of the difference in propagule rain assemblages in terms of species life forms and strategies between years and among seasons are indicated by symbols: \*\*, P < 0.01; \*\*\*, P < 0.001; ns, not significant. Bars with different letters are significantly different, as determined from the post-hoc tests.



formed with the R package "nlme" (version 3.1-121). Where the assumption of normality was not met, generalized linear mixed models with or without random effects (glm, glmer) were applied with the R package "lme4" (version 1.1-8), with the associated link function. Models were followed by Tukey HSD post-hoc tests performed with the R package "multcomp" (version 1.4-1). Overdispersion of the generalized models was tested using  $\chi^2$  tests, and was corrected adding the ĉ value obtained as the dispersal parameter to the model summary. The algorithm of nonconverging models was optimized via the bobyqa function of the glmerControl parameter (Powell 2009). Finally, when homoscedasticity assumption was violated, Kruskal–Wallis nonparametric tests equivalent to one-way ANOVA were used, followed by

post-hoc multiple comparison tests performed with the R package "pgirmess" (version 1.6.2).

## Results

## Assemblage of the aerial propagule rain between years and among seasons

To answer our first and second hypotheses, propagule rain assemblages were compared between fall seasons (year to year variation) and among trapping sessions (seasonal variation). A total of 41 taxa were identified during the four trapping sessions: 38 taxa in 2013 (31 in summer, 25 in fall) and 16 in 2014 (14 in spring, 10 in fall; Appendix, Table A1). Twelve taxa were shared between years; 25 taxa were found exclusively in 2013 and three exclusively in 2014. One species was only found in the spring, **Fig. 3.** Principal coordinates analysis (PCoA) plots of (*a*) sites with species for the matrix of 338 Petri plates and 41 species by trapping session, and (*b*) sites with weather variables. The ellipses are the 95% confidence intervals of the mean position of Petri plates groups by trapping sessions in species space. Grey dots represent the sites. Numbers in parentheses following the weather variables refer to different bryophyte phenophases (see Fig. 1. for details). Note (a): In cases where many species were overlapping in the ordination space, the names were replaced by "+" for better interpretability. For complete species names and details about their life strategy see the Appendix, Table A1. Note (b): The term "pool" indicates variables that were superimposed. Pool A includes relative humidity and total precipitation for phenophase 1; and relative humidity, maximum wind speed, number of days without rain for phenophase 2. Pool B includes the maximum consecutive days below 0 °C, maximum consecutive days without rain, and Julian date before 0 °C was exceeded, for phenophase "winter survival - W"; as well as mean difference in night/day temperatures for phenophase 1; and mean difference in night/day temperatures and number of days below 0 °C for phenophase 2.

nine species only in the summer, and nine only in the fall. The number of protonemata grown was 2740 in 2013, and 756 in 2014. The most abundant taxa recorded in the different years and seasons were *Atrichum crispum* (James) Sull., *Ceratodon purpureus* (Hedw.) Brid., *Pohlia spp.*, and *Sphagnum spp*. Three additional taxa, *Aulacomnium palustre* (Hedw.) Schwägr. (30 in 2013; 6 in 2014), *Herzogiella turfacea* (Lindb.) Z. Iwats. (15 in 2013; 2 in 2014), and *Marchantia polymorpha* L. (21 in 2013: 3 in 2014), were mainly found in 2013, whereas *Pleurozium schreberi* (Willd. ex Brid.) Mitt. (1 in 2013: 42 in 2014) was mainly found in 2014.

Mean total species richness and frequency per plate were both significantly higher in fall 2013 than in fall 2014 (both *P* < 0.0001; Figs. 2*a* and 2*b*). Only the mean species richness of perennials differed between year, and was significantly greater in 2013 than in 2014 (P = 0.003; Fig. 2a), whereas the mean frequencies of acrocarps, liverworts, sphagna/dominants, and colonists were significantly higher in 2013 than in 2014 (all *P* < 0.001; Fig. 2b). In contrast, pleurocarps and perennials were significantly more frequent in 2014 than 2013 (both P < 0.001), boosted by the abundance of P. schreberi. In terms of seasons, mean total species richness and total frequency per plate were both significantly higher in summer than in spring or fall (P < 0.001 and P = 0.003, respectively; Figs. 2c and 2d). Propagule rain assemblage did not differ among seasons for any other mean species richness value (Fig. 2c). However, acrocarps, liverworts, and colonists were significantly more frequent in summer than in other seasons (all P < 0.001; Fig. 2d). Pleurocarps were also significantly more frequent in the aerial propagule rain assemblage in spring (P < 0.001) when sphagna were less frequent (*P* < 0.001).

PCoA yielded clear groupings of samples. Aerial propagule rain in each year and season were composed of a specific pool of species with relatively few species shared between years (MRPP, P < 0.001, chance-corrected withingroup agreement A: 0.052). The first axis divided aerial propagule rains seasonally (Axis 1: 43.46%), with little overlap of confidence ellipses between seasons in a given year (Fig. 3*a*). The second axis divided aerial propagule rains annually, with no overlap between years (Axis 2: 40.15%). The assemblage of the aerial propagule rain of 2013 was more homogeneous among sample sites than in 2014. In 2014, some sites were characterized by a distinct aerial propagule rain composed of unique species (e.g., *Dicranella heteromalla* (Hedw.) Schimp., *Pellia neesiana* (Gottsche) Limpr., *P. schreberi*).

### Weather characteristics of each year and season

Across all of the study sites, monthly mean temperature and precipitation from 2012 to 2014 coincided with 30-year averages recorded for the study area (1981 to 2010; Supplementary data, Fig. S1), although March 2012 and 2013 were 5 °C warmer and March 2014 was 5 °C colder than the 30-year averages. Seasonal weather differed among the years (Table 1). The spring of 2014 was significantly colder and drier than in 2012 and 2013, whereas the spring of 2012 was significantly rainier than in 2013 and 2014. Summer 2012 was significantly windier than summer 2014, whereas the fall of 2012 and 2013 did not differ significantly.

# Relationships between aerial propagule rain community assemblage and weather variables

Linear correlations between weather variables and aerial propagule rain assemblage (Hypothesis 3), as assessed with linear vectors overlaid on the PCoA ordination, varied from 0.31% to 23.85% for Axis 1 and from 1.77% to 23.47% for Axis 2 (data not shown). The variables were clearly divided in two sets: 12 variables mainly correlated with the assemblage of 2013, and a set of seven variables correlated with the assemblage of 2014 (Fig. 3b). Seasonal variation in aerial propagule rain assemblage seemed less clearly correlated with the weather variables. The same set of variables was correlated with the propagule rain trapped during fall and summer of 2013. On the other hand, in 2014, seasonal propagule rain seemed to be correlated with a different set of weather variables, with the fall of 2014 particularly impacted by the number of days without precipitation two sessions before the trapping.

In the MRT, the retained weather variables explained 7.9% of the variability in the aerial propagule rain with the three-split, four-group model (Fig. 4). The first split was generated by three variables of four different phenophases and explained 5.9% of the variability. Petri plates influenced by more humid, rainy, and cold conditions



Dim1

	Seasons									
	Winter		Spring		Summer			Fall		
Weather variables	2012-2013	2013-2014	2012	2013	2014	2012	2013	2014	2012	2013
Mean temp. (°C) Mean temp. difference	–14.92±3.31a 2.48±1.92a	–18.59±1.34a 2.91±0.62a	2.00±7.43a 4.19±0.89a	1.12±7.50a 4.14±1.29a	–2.63±11.93a 4.99±0.94a	16.07±0.66a 4.42±0.76a	14.81±2.08a 5.09±0.92a	15.84±0.39a 4.66±0.63a	3.72±7.16a 2.79±1.05a	3.31±7.58a 3.02±1.30a
(night–day; °C) lax. consecutive days below –10 °C	<u>50.00</u> ±0.00 <u>a</u>	<u>133.00</u> ±0.00 <u>b</u>	NA	NA	NA	NA	NA	NA	NA	NA
ulian date before temp. exceeded 0 °C	<u>63.00</u> ±0.00 <u>a</u>	<u>90.00</u> ±0.00 <u>b</u>	NA	NA	NA	NA	NA	NA	NA	NA
No. of days below 0 °C No. of days below –10 °C	0.00±0.00 <u>55.00</u> ±3.21 <u>a</u>	0.00±0.00 <u>77.00</u> ±2.08 <u>a</u>	35.00±11.50a <u>8.00</u> ±4.61 <u>a</u>	42.00±12.49a <u><b>7.00</b></u> ±2.51 <u>a</u>	48.00±15.00a <u>23.00</u> ±13.28 <u>b</u>	0.00±0.00 0.00±0.00	0.00±0.00 0.00±0.00	0.00±0.00 0.00±0.00	27.00±12.29a <u>7.00</u> ±1.15 <u>a</u>	33.00±12.12a <u>5.00</u> ±2.89 <u>a</u>
Relative humidity (%) Max. wind speed (km/h)	<b>87.45</b> ±3.95 <b>b</b> NA	<b>80.50±</b> 1.37 <b>a</b> NA	66.81±5.03a 26.00±4.04a	73.82±6.10a 22.00±2.88a	69.14±0.08a 19.00±1.73a	75.75±8.30a <b>22.00</b> ±2.51 <b>a</b>	75.18±5.80a <b>19.00</b> ±1.15 <b>ab</b>	73.77±6.59a <b>16.00</b> ±1.00 <b>b</b>	88.49±1.96a <u>19.00</u> ±1.15 <u>a</u>	85.98±4.01a <u>20.00</u> ±0.58 <u>a</u>
No. of days with max. wind speed (km/h)	NA	NA	1.00±1.00ab	<b>2.00</b> ±1.00a	<b>2.00</b> ±0.00 <b>b</b>	1.00±1.73a	2.00±0.58a	2.00±1.53a	3.00±0.58a	2.00±1.00a
Cotal precipitation (mm) Max. consecutive days without precipitation	NA NA	NA NA	<u>60.80</u> ±0.00 <u>c</u> <u>3.00</u> ±0.00 <u>b</u>	<u>42.00</u> ±0.00 <u>b</u> <u>5.00</u> ±0.00 <u>c</u>	<u>25.60</u> ±0.00 <u>a</u> <u>2.00</u> ±0.00 <u>a</u>	317.20±46.96a 4.00±1.15a	277.60±29.23a 4.00±0.58a	319.40±31.25a 6.00±1.00a	347.70±13.25a 4.00±0.50a	334.50±19.5a 7.00±1.50a
wind speed (km/h) Total precipitation (mm) Max. consecutive days without precipitation <b>Note:</b> Linear models were by the same letter are not si in bold font. NA, not availab	NA NA used to compa ignificantly diff ble.	NA NA tre means among ferent (P > 0.05) a	60.80±0.00c 3.00±0.00b gyears except for as indicated by	42.00±0.00b 5.00±0.00c	25.60±0.00 <u>a</u> 2.00±0.00 <u>a</u> te values, for wh t-hoc tests; letter	317.20±46.96a 4.00±1.15a ich generalized n s indicate rankin	277.60±29.23a 4.00±0.58a nodels were used g (i.e., a < b < c).	319.40±31.25a 6.00±1.00a because of their Statistically sign	347.70±13.25a 4.00±0.50a non-normality. V ificant differenc	334.5 7.00± Values f es (P < )

## son, from 2012 to 2014.

	Winter		Spring	Summer		
Weather variables	2012-2013	2013-2014	2012	2013	2014	2012
Mean temp. (°C)	-14.92±3.31a	–18.59±1.34a	2.00±7.43a	1.12±7.50a	-2.63±11.93a	16.07±0.66a
Mean temp. difference (night–day; °C)	2.48±1.92a	2.91±0.62a	4.19±0.89a	4.14±1.29a	4.99±0.94a	4.42±0.76a
Max. consecutive days below –10 °C	<u>50.00</u> ±0.00 <u>a</u>	<u>133.00</u> ±0.00 <u>b</u>	NA	NA	NA	NA
Julian date before temp.	63.00±0.00a	90.00±0.00b	NA	NA	NA	NA

éal on 11/28/17

**Fig. 4.** Multivariate regression tree (MRT) of the aerial propagule rain community. The three-split, four group model was the best model as selected by parsimony and cross-validation relative error (CVRE). Factors generating the splits with their mean values are listed at each split. The amount of variation explained by the entire tree is the inverse of the error, in this case 7.9%. This total is decomposed into the percentage explained by each split. The CV error indicates the potential for the unsuccessful classification of additional samples. Each leaf in the tree has been assigned a group number and shows the number of plots associated with the group. Numbers in parentheses following weather variables refer to different bryophyte phenophases (see Fig. 1. for details). The five dominant species composing each leaf are indicated in dotted boxes, value in parenthesis refers to their frequency in each group.



were found to the right of the split, whereas Petri plates influenced by less humid, rainy, and cold conditions were to the left. The second and third level splits explained respectively 2.3% and 2.1% of the variability observed, and were exclusively generated by weather conditions of the phenophases during the trapping. Several weather variables such as the difference of temperature between night and day, number of days below 0 °C, total precipitation, maximum wind speed, and the number of days with maximum wind speed contributed equally to the splits between groups 1 and 2 and 3 and 4.

The most influential weather variables varied among the groups, with divisions between long and harsh (groups 1 and 2) versus short and mild winters (groups 3 and 4), and between groups with less precipitation and lower relative humidity (groups 1 and 2) versus high precipitation and relative humidity (groups 3 and 4; Table 2). Groups 1 and 2 were particularly characterized by a high number of days below 0 °C and –10 °C during the maturation–dispersal phenophase (phenophase 3); *P. schreberi* was primarily found in these groups (Table 3). Groups 3 and 4 were associated with high relative humidity and had the highest level of species richness and the greatest species frequency, notably a greater frequency of *Sphagnum* spp., *A. palustre, C. purpureus, Pohlia* spp., *Polytrichum* spp., and liverwort species (Table 3).

### Discussion

Aerial propagule rain assemblages differed among seasons and years, and the interseasonal and interannual variations could be linked to differing interannual weather conditions. The division of the bryophyte phenology into phenophases has permitted us to identify that the impacts of weather on gametophyte generation the season before the trapping session and on dispersal are the most susceptible for aerial propagule rain assemblage. These phenophases are especially influenced by relative humidity and cold temperatures. Nevertheless, the chosen weather variables poorly explained interannual variability in the aerial propagule rain assemblage (7.9% of the explained variability). The low percentage of variability explained by our models may reflect the complex mechanisms linking bryophyte dispersal patterns to regional weather and highlight the need for alternative hypotheses to explain it.

### Seasonal aerial propagule rain assemblage is related to winter conditions and differing timing in species phenology

Seasonal variations in the aerial propagule rain assemblage have been reported in the past (Hock et al. 2004; Ross-Davis and Frego 2004), and were explained by differential timing in species phenology (Longton and Greene 1969; Longton 1985). In our study, the phenology

Table 2. Weather variables for the groups determined with a multivariate regression tree (MRT; Fig. 4)

Phenophases	Weather variables	Group 1	Group 2	Group 3	Group 4
Survival after the winter	Max. consecutive days below 0 °C	133	133	50	50
preceding the trapping (W)	Julian date before temp. exceeded 0 °C	90	90	63	63
Fertilization the summer	Mean temp. difference (night–day; °C)	5.09	5.09	4.42	4.42
preceding the trapping (1)	Relative humidity	75.18	75.18	75.75	75.75
	Total precipitation	277.6	277.6	317.2	317.2
	Max. consecutive days without rain	4	4	4	4
Maturation and dispersal one season	Mean temp. difference (night–day; °C)	4.99	4.99	4.14	4.14
preceding the trapping (2)	No. of days below 0 °C	48	48	42	42
	Relative humidity	69.14	69.14	73.82	73.82
	Max. wind speed	19	19	22	22
	No. of days with max. wind speed	1	1	2	2
	Total precipitation	25.6	25.6	42	42
	No. of days below –10 °C	23	23	42	42
	Max. consecutive days without rain	2	2	5	5
Survival and growth and maturation	Mean temp. difference (night–day; °C)	4.83	4.99	5.09	5.57
and dispersal during the season of	No. of days below 0 °C	24	48	0	0
trapping (3)	Relative humidity	71.45	69.14	75.18	71.83
	Max. wind speed	17.5	19	19	19
	No. of days with max. wind speed	1.5	1	2	2
	Total precipitation	172.5	25.6	277.6	151.40
	No. of days below –10 °C	11.5	23	0	0
	Max. consecutive days without rain	4	2	4	4
Survival and growth two seasons	Mean temp. difference (night–day; °C)	4.05	5.09	2.79	2.79
preceding the trapping (4)	No. of days below 0 °C	16.5	0	27	27
	Relative humidity	80.58	75.18	88.49	88.49
	No. of days below –10 °C	2.5	0	2	2
	Total precipitation	250.3	277.6	231.8	231.8
	Max. consecutive days without rain	5.5	4	4	4
Survival and growth one season	Mean temp. difference (night–day; °C)	4	3.02	4.14	4.14
preceding the trapping (5)	No. of days below 0 °C	40.5	33	42	42
	Relative humidity	77.56	85.98	73.82	73.82
	No. of days below –10 °C	14	5	42	42
	Total precipitation	124.3	223	42	42
	Max. consecutive days without rain	4.5	7	5	5

Note: Values are means of each variable classified by phenophase per group (see Fig. 1 for details about values). Group (1), extra-cold; Group (2), cold and dry; Group (3), extra-wet and windy; Group (4), wet and windy.

cycle used is the same for all species, but the timing of propagule release may differ between species, and this may explain the greater number of Sphagnum propagules trapped at the end of summer and fall. Indeed, certain sphagna species are known as "late dispersers," and wait for the wetter conditions of the end of summer and fall for dispersal (Sundberg and Rydin 2002). Similarly, the fact that higher numbers of liverworts were trapped in the hottest and wettest months of summer may be due to their sensitivity to cold and drought (Laaka-Lindberg 2005; Pohjamo 2008). However, seasonal aerial propagule rain patterns of the true mosses (acrocarps and pleurocarps) seemed to be explained primarily by responses to weather conditions, particularly winter length, rather than by species' phenology timing. Low acrocarp richness and frequency in the fall of 2014, compared with the fall of 2013, may be explained by the fact that numerous acrocarps are colonist or shuttle species

that have stress-tolerant propagules or propagules that enter into dormancy (Pohjamo 2008, based on During 1979) that permit them to tolerate episodic stresses such as dry and cold conditions. In contrast, pleurocarps, of which many are perennials (During 1979, 1992), tolerate stress as gametophytes and continue to mature under less suitable conditions (e.g., dry and cold periods; Pohjamo 2008, based on During 1979).

However, we demonstrate that specific weather conditions also explain the seasonality of the aerial propagule rain assemblage. Indeed, the lower species richness of spring propagule rain compared with summer and fall propagule rain may be linked to harsh winter conditions that can delay some bryophyte phenophases (Longton and Greene 1969; Longton 1985). Gregory (1961) and Crum (2001) report that the northernmost latitudes are more "propagule rich" in summer and fall than in midspring and early summer, which may be due to the fact

Table 3	<b>B.</b> Species	assemblage	of the	groups	determined	by	recursive	partitioning	by
weathe	r variables	s in a multiva	riate re	egressior	n tree (MRT).				

	Group 1	Group 2	Group 3	Group 4
Species	n = 57	<i>n</i> = 57	<i>n</i> = 116	<i>n</i> = 108
Amblystegium serpens	0	0	0	1
Atrichum angustatum*	0	0	1	0
Atrichum crispum*	29	20	41	24
Aulacomnium palustre	5	1	10	20
Blepharostoma trichophyllum	0	0	0	1
Brachythecium starkii	0	0	0	1
Bryum capillare*	0	3	2	1
Bryum pallescens*	0	4	0	2
Campyliadelphus chrysophyllus	0	3	0	1
Campylium hispidulum	1	0	5	6
Cephalozia bicuspidata	0	0	0	1
Cephaloziella elachista	0	0	0	5
Cephaloziella hampeana	0	0	1	3
Cephaloziella rubella	0	0	4	8
Ceratodon purpureus*	9	18	56	44
Chiloscyphus profundus	0	0	1	0
Dicranum fuscescens*	0	0	2	0
Dicranella heteromalla*	0	1	0	0
Ditrichum spp.*	0	0	2	1
Grimmia spp.*	0	0	2	6
Herzogiella turfacea	1	1	3	13
Hypnum pallescens	0	0	0	1
Hygroamblystegium varium	0	0	0	3
Marchantia polymorpha	0	3	15	6
Pellia neesiana	1	0	0	0
Plagiomnium cuspidatum/drummondii	0	1	0	1
Plagiomnium medium	0	0	0	1
Platydictya subtilis	0	0	1	3
Platygyrium repens	1	1	0	0
Pleurozium schreberi	16	26	0	1
Pohlia spp.*	24	31	87	80
Polytrichum spp.*	0	0	14	44
Pseudobryum cinclidioides	0	0	0	1
Riccardia latifrons	0	0	1	1
Sanionia uncinata	0	0	0	1
Sphagnum spp.	31	24	90	84
Splachnum ampullaceum*	0	0	1	0
Straminergon stramineum	0	0	1	0
Syntrichia ruralis*	0	0	4	11
Tortula cernua*	0	0	1	0
Tetraphis pellucida*	0	0	5	5
Total	118	137	350	381

**Note:** The values are the frequency of each species among all of the Petri plates per group. Bold font indicates liverwort species; \*, acrocarp species; *n*, number of plots associated with the group.

that propagules released in the summer and fall benefitted from two or three maturation seasons (previous fall and spring, and previous fall, spring, and summer, respectively) whereas propagules released in the spring have only benefited from the previous fall, before halting sporophyte maturation during the winter (Glime 2013), and the early spring, when winter is not too long. This was especially true in 2014, when winter persisted until the end of April, with several weeks below –10 °C (where the compensation point of photosynthesis is reached, Lappalainen et al. 2011). These conditions could have led to the inhibition of growth/maturation of gametophytes/sporophytes, and might explain the poor pool of species trapped in 2014. However, our conclusions about seasonality in the aerial propagule rain are biased by the trapping design: spring trapping only occurred in 2014 when winter was harsher and longer than in 2012–2013. Consequently, our first hypothesis, which proposed seasonal differences in propagule rain composition, is not entirely supported. Indeed, both species' phenology and weather conditions explained seasonal bryophyte propagule rain patterns.

# The interannual difference in aerial propagule rain assemblage

Our second hypothesis was based on the existence of several local propagule clouds that intermingle to form a general and persistent cloud at the regional scale. The local and regional clouds can gain and lose propagules, but local clouds may be more affected by local precipitation and wind events, whose impacts are diluted in the regional cloud. However, in addition to a significant decrease in species richness and abundance in 2014 (in spring as well as in fall), we observed a marked change in community propagule rain assemblage. This point led to the rejection of our second hypothesis: expectation of the same propagule rain composition from one year to the next, owing to the same pool of species acting as releasers in the community between years. This may in part be explained by the importance of maternal investment in reproduction and the subsequent cost for the female gametophyte. Individuals that have invested in the formation and release of propagules one year may have a reduced sporophyte development and propagule release the next year, as they are energetically limited compared with other individuals (Bisang and Ehrlén 2002).

In this paper we have, however, focused on a second possibility, suggested by Callaghan et al. (1997) and Slack (2011), that bryophyte development may be impacted by interannual climatic variations because of gametophyte exposure to environmental factors.

As suggested by our third hypothesis, critical weather conditions seem to influence propagule release both directly and indirectly, by acting, respectively, on dispersal phenophase and on phenophases prior to dispersal, i.e., growth and maturation of the gametophyte and maturation of the sporophytes before dispersal. However, considering the poor predictive power of our models, the set of weather variables retained in our study was only weakly correlated with propagule rain assemblage values. In this way, we cannot validate our third hypothesis, and we suggest, but do not demonstrate a phenophase– weather relationship.

### The importance of summer conditions

For bryophytes, gametangial development and antherozoid movement are entirely dependent on water availability (Reynolds 1980). We found that precipitation and humidity levels during the fertilization as well as the growth and maturation of the gametophyte were consistent with changes in the pool of trappable propagules one year later. In accordance with Sundberg (2002) and Proctor (2011), we found that high humidity during the summer correlated with a richer trappable species pool the next year. Consequently, propagule release in the summer and fall could depend on moisture levels during the previous summer and fall, whereas spring propagules could depend in part on the conditions of the previous summer. The suitable moisture conditions of 2012 can therefore explain the propagule richness and abundance in 2013.

In addition, weather conditions during dispersal presumably also influenced the trapped species pool. The difference in temperature between night and day seemed positively associated with species richness and assemblage, which may be explained by associated changes in humidity that induce spore release (Johansson et al. 2015). Dew formation is higher when there is a greater difference in night and day temperatures, and the evaporation of dew in the morning allows spore ejection via drought-rehydration of the capsule peristome and hygroscopic movements of the elaters (Ingold 1959). Furthermore, heating of the air near the soil in the morning after a cold night causes turbulence as the sunrises. This, along with strong gusts of wind, could drive long distance dispersal of propagules after their ascension into the air column.

The existence of a winter chilling process in bryophytes?

An interesting point raised by our study is the positive impact of low temperatures on aerial propagule rain species richness and frequency. Indeed, one month of cumulative days below –10 °C the season before the propagule release seems correlated with more species trapped. Bryophyte response to low temperatures depends on the season (Rütten and Santarius 1992), and cold periods in the fall may act as signals of winter's arrival and may prompt species to allocate energy to gametophyte survival rather than to the formation of dispersal units.

Compared with the fall, cold periods during the spring may act as signals of a delayed summer. In 2014, the long winter that lasted until April may have delayed photosynthesis and invoked a "winter chilling process", already described for trees, which prevents budburst at the "wrong period" after warming events in the middle of the winter (Harrington et al. 2010). Applied to bryophytes, we can imagine that the energy allocated to sporophyte and spore production may have been more limited in 2014, resulting in sporophyte abortion (Stark 2002) and may explain the low diversity of propagules trapped. The need for stimuli to initiate the development of sexual organs has been reported by Glime (2013), who also underlines the paucity of knowledge about initiation signals in bryophytes, but more focused studies are required to confirm whether a "winter chilling process" exists for bryophytes.

#### Limitations of the study

As stressed in Barbé et al. (2016), both the timing of Petri exposure (morning to early afternoon) and the emergence method used to germinate propagules introduced some biases to the study, i.e., over-representation of local propagules compared with the more distant ones that are deposited later in the afternoon (Johansson et al. 2015), and nondifferentiation between real absence and nongermination of a species ex situ (Ross-Davis and Frego 2004). These biases were accounted for in this study, as they were constant among trapping and germinating sessions. The fact that our design was unbalanced between years may also have affected our results, but we believe that it would not lead to different conclusions, given the evident annual difference in propagule rain assemblage. In contrast, the major limitation of this study comes from the use of a single representative phenological cycle for all bryophyte species. However, this limitation was imposed by the lack of phenological descriptions of numerous species and our objective of working at the community level. Similarly, the longevity of sporophytes, spores, gemmae, and the sexual investment of the species were not considered. In parallel, mechanisms responsible from the gain and loss of propagules from clouds and the residence time of the propagules in the atmosphere were not considered. Indeed, the addition and loss of propagules from clouds depends on propagule features and on precipitation and wind events during release but also days preceding the release (Gregory 1961). These points that were not addressed in this study introduce biases because the cloud assemblages were not equal to the pool of propagules released at a "time t". While critical, these simplifications were inevitable because there is a general lack of knowledge about the phenology of each species and aerial propagule patterns. Furthermore, the objective was to consider the community as a whole. Finally, this study is a "snapshot" of propagule rain patterns; using weather variables and trapping data from only two years increases our chances of finding spurious patterns as compared with longer-term studies.

We cannot turn a blind eye to the low power of our models. Indeed, while 7.9% of explained variance is suggestive, it is also far from sufficient to state definitively that specific weather variables impact directly on dispersal and propagule rain assemblages among seasons and years. These results suggest that additional variables and processes, not considered in this paper, govern propagule rain assemblage more than weather variables. We can suggest that these may include the possible effects of recent disturbance, distance from propagule sources, germination timing, or even of propagule residence time in the atmosphere. Furthermore, we cannot exclude neutral stochasticity and founder effects that imply that the assemblage of one community depends on the identity of species composing it at the beginning (Vellend et al. 2014) and on the order of the arrival of species in the community (Herben 1995). These alternative hypotheses may be at the root of the limited power of our models and attest of the complexity of bryophyte dispersal mechanisms.

### Conclusions

Impacts of climate change on biodiversity are manifest (Walther et al. 2002; Root et al. 2003) and can alter the phenology of species, their dispersal patterns, and their distributional ranges. The understanding of bryophyte phenology in response to weather conditions is crucial, especially in the contemporary context of climate change and in the use of bryophyte species as bioindicators. This study is the first to attempt to disentangle the influence of weather variables on the phenologies (divided into phenophases) of bryophyte metacommunities. We report that propagule release may not only depend on the weather conditions during dispersal, but also on those that affect the survival and growth of the mother gametophyte (in the preceding winter) and on the fertilization phenophase. Consequently, propagule release seems to be linked with indirect and direct conditions of humidity and temperature, from one to several preceding seasons. Further studies, involving longterm trapping and weather variables and including stochastic effects, will offer clearer and stronger answers about bryophyte dispersal patterns in response to regional climate.

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### Appendix A

Appendix Table A1 and Figure A1 appear on the following pages.

Table A1. Number of bryophyte individuals found in propagule rain by trapping session (i.e., summer and fall 2013 and spring
and fall 2014) in boreal black spruce – feather moss forest after natural fire in western Quebec.

		2013		2014		
	Life	Summer	Fall (n = 126)	Spring $(n = 63)$	Fall $(n = 63)$	
Taxon	strategy	(n = 126)				Species code
Acrocarp						
Acrocarp spp.	_	0	1†	0	0	_
Atrichum angustatum	Р	0	1†	0	0	Atrang
Atrichum crispum	Р	23	42	20	29	Atrcri
Aulacomnium palustre	Р	16	14	1	5	Aulpal
Brvum capillare	С	1	2	3	0	Brvcap
Bryum pallescens	P	2	0	4	0	Brypal
Ceratodon purpureus	C	49	51	18	9	Cerpur
Dicranella heteromalla	Ċ	0	0	1†	0	Dichet
Dicranum fuscescens	P	0	1†	0	0	Dicfus
Ditrichum spp	C	1‡	2‡	0 0	0	Ditrichum spp
Grimmia spp.	C	<b>7</b> ‡	- 1‡	ů 0	0	Grimmia spp
Placiomnium cusnidatum/drummondii*	S	1	0	1	0	Placus/dru
Plagiomnium medium	S	1†	ů 0	0	0	Plamed
Pohlia spp		80	87	31	24	
Polytrichum spp.	_	43‡	15‡	0	0	
Pseudohrvum cinclidioides	S	1†	0	0	0	Psecin
Snlachnum ammillaceum	C	0	1†	0	0	Splamp
Syntrichia ruralis	C	10±	5±	0	0	Synrur
Tetranhis nellucida	C	2±	7±	0	0	Tetpel
Tortula cornua	S	0	7 · 1†	0	0	Torcer
Deurocarp	3	0	1'	0	0	Torcer
Amhlustagium samans	D	1†	0	0	0	Ambear
Anolystegium scrpens	D	1†	0	0	0	Practa
Commulia dalmhus ahmuomhullua	r D	1	0	0	0	Comehr
Campyliadelphus Chrysophylias	r D		0	3	0	Cambia
Campylium nispluulum	r C	J 14	4	0	1	Ugitter
Herzogiella lurjacea	C	14	2	1	1	Hertur
Hygroamblystegium varium	C	31	0	0	0	Hygvar
Hypnum pauescens	P	1'	0	0	0	нурраг
Pleurocarp spp.		1	1	1	0	 D1 1
Platyaictya subtilis	P	3+	1+	0	0	Plasub
Platygyrium repens	P	0	0	1+	1+	Plarep
Pleurozium schreberi	P	1	0	26	16	Plesch
Sanionia uncinata	P	0	[' 1*	0	0	Sanunc
Straminergon stramineum	Р	0	1'	0	0	Strastr
Sphagnum	P			2.4	24	
Sphagnum spp.	D	83	91	24	31	
Liverwort	0	<b>.</b>	0	0	0	D1 / 1
Blepharostoma trichophyllum	C	1'	0	0	0	Bletri
Cephalozia bicuspidata	С	1 <sup>r</sup>	0	0	0	Cepbic
Cephaloziella elachista	С	5*	0	0	0	Cepela
Cephaloziella hampeana	С	3‡	1‡	0	0	Cepham
Cephaloziella rubella	С	11 <sup>‡</sup>	1#	0	0	Ceprub
Cephaloziella spp.		5 <sup>‡</sup>	2‡	0	0	
Chiloscyphus profundus	C	0	1†	0	0	Chipro
Marchantia polymorpha	С	6	15	3	0	Marpol
Pellia neesiana	S	0	0	0	1†	Pelnee
Riccardia latifrons	С	1 <sup>‡</sup>	1‡	0	0	Riclat
Unidentified prothallus		4	3	6	9	

**Note:** Only the frequency of species in Petri plates filled with nutrient agar are given. The number (*n*) of Petri plates per trapping session is indicated. Nomenclature follows Faubert (2012–2014). Species are presented by growth form and life strategy (adapted from During 1992). The six-letter codes used to name species in the analyses are presented. *C*, colonist; D, dominant; P, perennial; S, shuttle.

\*Impossible to distinguish between the two species given the lack (i.e., fertile phase) or modification of diagnostic characters because of their growth in laboratory conditions.

<sup>†</sup>Only found in the year and in the season.

<sup>‡</sup>Only found in the year.

**Fig. A1.** Location of the study area and studied wildfires, as well as an illustration of the sampling design used for trapping of aerial propagule rain. (*a*) Location of the study area in Quebec, Canada. Black dots and numbers represent wildfires; stars represent weather stations. (*b*) Detail of the three wildfires studied. Small dots represent residual forest patches (three per fire); triangles represent burned matrix areas (one per fire). (*c*) Detail of one residual forest patch (light grey shape) surrounded by the burned matrix (dark grey shape). Squares represent 50 m<sup>2</sup> plots of edge and core used to trap the aerial propagule rain; white crosses represent groups of six Petri plates.



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