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So close and yet so far away: long-distance dispersal events govern bryophyte metacommunity reassembly

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Summary

1. Metapopulation dynamics have been used to explain bryophyte dispersal patterns and they predict that population abundances vary with the spatial distribution of habitat and with species traits. However, results from stand and landscape studies are contradictory as both distance-dependent and distance-independent patterns have been found. These studies have typically included only a few species, which limits interspecies comparison. It is the time to investigate bryophyte dispersal at the metacommunity scale.

2. We studied bryophyte dispersal patterns in a system made up of burned matrices containing unburned residual forest patches. The importance of short- versus long-distance dispersal was examined by comparing extant and propagule rain communities in residual forest patches of three fire sites using both species and life strategies.

3. Extant and propagule rain communities were distinct. Several propagule rain species, of all life strategies, did not originate from the closest extant community, suggesting that regional dispersal events are important, following the inverse isolation hypothesis.

4. Temporal, spatial and structural characteristics of the environment had a greater influence on dispersal than distance, which only influenced similarity patterns at the regional scale, highlighting the importance of propagule source attributes for the conservation of bryophyte metacommunities.

5. *Synthesis*. Long-distance dispersal may be the rule and not the exception in bryophyte metacommunities. Therefore, bryophyte metacommunity dynamics depend on several dispersal scales, and residual forest patches can contribute both to local and regional diaspore clouds. Species' environmental tolerance during establishment and their ability to produce copious amounts of spores may be more important filters in bryophyte metacommunity dynamics than dispersal distance.

Key-words: bryophyte, geographic distance, inverse isolation hypothesis, life strategies, local dispersal, metapopulation theory, propagule cloud, regional dispersal

Introduction

Dispersal is a key process in regulating population dynamics, along with establishment and persistence (Clobert *et al.* 2012). This is particularly true for species whose habitat is spatially discontinuous, either due to natural or anthropogenic fragmentation (e.g. forest fire or forest harvest) or its inherently patchy nature (e.g. deadwood) (Johst, Brandl & Eber 2002). Local populations of these species are spatially segregated from others in an inhospitable matrix and their persistence through time depends on a positive balance between population colonization and extinction, that is the metapopulation concept (Hanski 1998; Freckleton & Watkinson 2002). Populations are not isolated but exchange migrants with neighbouring populations at a frequency that varies with matrix permeability and mean dispersal distance (Snäll, Ribeiro & Rydin 2003; Löbel, Snäll & Rydin 2006; Johst *et al.* 2011). This concept can be extended to the metacommunity when multiple species are considered (Jacobson & Peres-Neto 2010).

It has long been thought that short-distance dispersal (SDD) dominates most metacommunities following the theory of island biogeography (MacArthur & Wilson 1967), with long-distance dispersal (LDD) occurring only sporadically. However, it has also been recently suggested that the 'inverse isolation hypothesis' is more appropriate for species with fat dispersal tails and that LDD is therefore more frequent than previously expected (Klein, Lavigne & Gouyon 2006; Szövényi, Sundberg & Shaw 2012; Sundberg 2013). This theory suggests that in sites isolated from diaspore sources a

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higher proportion of diaspores originate from a large set of distant sources rather than from the nearest source. This leads to high genetic variation and species richness at these isolated sites (Sundberg 2005; Klein, Lavigne & Gouyon 2006).

Bryophytes are an interesting group for studying dispersal as their habitats are spatially and temporally patchy, they have large distribution ranges (Söderström 1998), their small and light spores (generally < 20 μm) are primarily dispersed by the wind (During & van Tooren 1987), and they have rapid population colonization/extinction rates (Snäll, Ehrlén & Rydin 2005). However, bryophyte dispersal is not yet clearly understood. Two paradigms are suggested: (1) bryophyte dispersal is spatially limited to the local scale (Miles & Longton 1992; Laaka-Lindberg, Korpelainen & Pohjamo 2006) and (2) as small bryophyte spores are produced in great numbers, the few percentage dispersed beyond the local scale represent significant numbers (During & van Tooren 1987). In other studies, distance-independent dispersal has also been found (Sundberg 2013; Lönnell, Jonsson & Hylander 2014) with the suggestion that local habitat characteristics, such as microsite limitation (i.e. number of logs, quality of the substrate, Hylander 2009; Wiklund & Rydin 2004) and physical barriers limiting wind availability (i.e. canopy or stand closure, Fenton & Bergeron 2006; Sundberg 2013), may influence dispersal and colonization. However, studies dealing with LDD remain sparse and typically use proxies, such as the genetic similarity of disjunct populations (Studlar, Eddy & Spencer 2007; Lewis, Rozzi & Goffinet 2014). To our knowledge, this study is the first to examine the relative importance of short- and long-distance dispersal (i.e. SDD versus LDD) at the community level.

An interesting natural system for studying bryophyte metacommunity dynamics is found in boreal forests. Forest fires are the dominant disturbance type in North American boreal forests and they heterogeneously impact the landscape (Perera *et al.* 2009; Carlson, Reich & Frelich 2011) leaving patches of unburnt forest (‘residual patches’) that have partially or entirely escaped fire (Burton *et al.* 2008; Ouarmim *et al.* 2015). They may act as refuges for species during the fire disturbance and as sources of propagules during recolonization after the fire, particularly for species with limited dispersal capacities extirpated from the disturbed matrix. Consequently, dispersal of species from these potential sources to new suitable areas may govern the long-term survival of the metacommunity, particularly in a dynamic landscape. In this study, we examine three large fires each with several residual forest patches nested within them across a 10 000-km^2 region.

The general objective of this study was to determine the relative contribution of the extant bryophyte community to the propagule rain at a given site. To achieve this, three specific objectives are addressed. First, the propagule rain community composition is compared to the extant bryophyte community in both the burned matrix and the residual forest patches. Secondly, we aim to determine whether geographic proximity results in greater compositional similarity between propagule and extant communities. Our third objective is to investigate the relative roles of geographic distance and environmental characteristics of the residual forest patches in driving the dispersal patterns. Finally, in a fourth objective community composition among propagule rains is compared. This comparison eliminates the bias associated with the emergence method used to germinate propagules, which only considers the species able to germinate on an artificial substrate.

We hypothesize that the species found in the propagule rain community reflect the extant community composition in terms of species richness and in proportion of species life forms and life strategies (H1). We expect that the similarity between the propagule rain and the extant community will be negatively correlated with geographic proximity and consequently that SDD occurs more than LDD (H2). We also expect that the similarity between the propagule rain and extant communities will be partially explained by spatial, temporal and structural attributes of the residual forest patches in addition to geographic distance at local scales (H3). Finally, we do not expect a relationship between the similarity of the propagule rain community in two sites and their geographic proximity (H4). Indeed, SDD dominance would produce as many propagule clouds as propagule sources in the landscape and low similarity of propagule clouds regardless of the distance between them.

Materials and methods

STUDY AREA

The study was conducted in the boreal forest in western Québec, Canada, within the black spruce (*Picea mariana* Mill., Briton)–feather-moss (*Pleurozium schreberi* (Brid.) Mitt.) forest bioclimatic domain (Grondin 1996). Average annual temperature and precipitation are, respectively, 1 °C and 927.8 mm (1981 to 2010), recorded at the nearest weather station, Lebel-sur-Quévillon, Québec (55 to 140 km from sites; Environment Canada 2015). Stands are dominated by *P. mariana* with *Pinus banksiana* Lamb., *Populus tremuloides* Michx, *Abies balsamea* (L.) Mill. and *Betula papyrifera* Marshall as secondary species. The understorey is dominated by ericaceous species [e.g. *Rhododendron groenlandicum* (Oeder) Kron & Judd] and bryophyte species (primarily sphagna and feather mosses).

Natural fires dominate the disturbance regime, and the average forest age is approximately 140 years (Bergeron *et al.* 2002). Fires burn unevenly and leave residual patches of unburned forests within the burned matrix (Madoui *et al.* 2010). The proportion of residual patches varies with the total area burned, but does not exceed 8% of the burned area, with five 1-ha or smaller residual patches per 100 ha (median), situated from 0 to 700 m from each other (Perron, Bélanger & Vaillancourt 2008).

SITE SELECTION AND SAMPLING OF BRYOPHYTES AND ENVIRONMENTAL VARIABLES

Three fires in natural boreal black spruce forest were chosen in the North of Québec (50°56′N, 77°53′ W; 49°75′N, 76°29′ W; 49°91′N, 76°13′ W). Fires varied in age from 18 to 29 years (i.e. two have occurred in 1997 and one in 1986) and in size from 2 537 to 25 516 ha (SOPFEU 2011). Within each fire, we identified three residual forest patches and three burned matrix areas, for a total of nine residual forest patches and nine areas of burned matrix. Residual forest patches were all dominated by black spruce but varied in size, age, isolation and forest structure (Table 1).

The extant bryophyte community was sampled in 5 × 10 m rectangular plots (50 m^2) in the residual forest patches and in the burned matrix during the summer of 2013. Within each residual forest patch, a north–south linear transect was established, crossing the patch from edge to edge (Fig. 1). In the three residual forest patches smaller than 1 ha, three plots at least 10 m apart were placed along this linear transect, two at the edges of the patch and one in the core of the patch. Two positions were subsequently obtained: edge and core. In the six residual forest patches larger than 1 ha, a second core plot was added for a total of four plots. Three rectangular plots of 50 m^2 were placed in the burned matrix of each fire as far as possible from all residual forest patches (from 200 to 8 500 m). In total, the extant bryophyte community was sampled in 42 rectangular plots spread across three fires (i.e. 33 in the residual patches and 9 in the burned matrix). Sampling of the extant bryophyte community proceeded by a modified form of ‘floristic habitat sampling’ (Newmaster *et al.* 2005), where all the habitats are searched for species with no specific reference to area. Here, it was restricted to the 50-m^2 plots and all microhabitats (e.g. coarse woody debris, tree bases, peat mounds and water holes) within each plot were sampled and the bryophytes present placed in individually marked paper bags. Bryophyte samples were dried and stored until identification.

Propagule rain was sampled by the ‘emergence method’ (Rudolph 1970; Ross-Davis & Frego 2004). Petri plate traps (90 mm in diameter) were filled with 78.5 cm^2 of nutrient agar made in sterile laboratory conditions [Parker Thompson’s basal nutrient medium of Klekowski (1969), described by *C-Fern* Project © (1995–2014)]. All bryophyte propagule types were included (i.e. spores, gemmae and possible vegetative fragments dispersed *via* the air; During & van Tooren 1987). In each residual forest patch, a group of six Petri plates was placed in the centre of one core and one edge 50 m^2 extant community plot. In addition, a group of six Petri plates was also placed in one of the three burned matrix plots per fire. Propagule rain was trapped during four sessions: 11 and 16 August (summer) and 4 and 13 September (autumn) of 2013 as well as 9 and 11 June (spring) and 14 and 19 September (autumn) of 2014. Two days are required in each trapping session due to the distance among the fire sites (average of 128 km). The total number of Petri plates exposed over the four sessions is 504 [(6 × 2 × 9 + 3 × 6) × 4]. Petri plates were deposited in the forest for 6 h from early morning when capsules are moistened by dew to early afternoon when capsules are dried and temperatures are the warmest. During this period, propagule release is

Table 1. Temporal, spatial and structural variables measured in each of the residual forest patch and burned matrix area in the study. Isolation and canopy openness are means ± standard errors, and all other variables are absolute values

			Temporal variables		Spatial variables				Forest structure variables		
Fire	Sites	Position	Time since fire (year)	Estimated age of forest (year)	Area (ha)	Distance from closer continuous forest (m)	Distance to closest residual patch (m)	Isolation (m)	Canopy openness (%)	Trees and snags density (number of stems ha^{-1})	Holdridge complexity indices (C$_{HLC}$)
LQY	RP8	Edge	18	140	3.69	1360	174	86.2 ± 121.3	44.10 ± 5.14	1100	99.99
LQY	RP8	Core	18	140	3.69	1389	157	209.4 ± 108.2	45.14 ± 13.55	1525	210.78
LQY	RP9	Edge	18	240	11.11	557	1943	555.6 ± 136.5	48.96 ± 17.77	950	94.85
LQY	RP9	Core	18	240	11.11	496	2000	765.6 ± 264.8	29.86 ± 4.21	1375	144.04
LQY	RP10	Edge	18	173	2.69	1209	114	73 ± 86.8	15.28 ± 5.24	1000	122.24
LQY	RP10	Core	18	173	2.69	1134	214	245.2 ± 104.9	29.17 ± 6.83	1325	146.69
LQY	B1	Fire	18	18	0.015	984	658	634 ± 210.1	59.72 ± 22.88	314.3	0
LQY	B2	Fire	18	18	0.015	1536	393	275.6 ± 99.6	62.84 ± 17.81	314.3	0
LQY	B3	Fire	18	18	0.015	978	224	323.8 ± 143.4	69.44 ± 11.47	314.3	0
LQO	RP16	Edge	29	82	4.24	829	110	192 ± 248.1	9.72 ± 9.68	650	33.34
LQO	RP16	Core	29	82	4.24	883	165	333.8 ± 208.5	15.63 ± 13.78	2750	587.58
LQO	RP18	Edge	29	80	0.05	555	90	104 ± 52.7	47.92 ± 17.77	1050	62.30
LQO	RP18	Core	29	80	0.05	554	91	114.6 ± 52.7	12.85 ± 6.69	2200	329.82
LQO	RP20	Edge	29	171	2.2	868	535	284.8 ± 139.4	36.46 ± 18.52	1250	183.45
LQO	RP20	Core	29	171	2.2	949	479	376.6 ± 141.6	26.74 ± 6.61	1875	582.19
LQO	B1	Fire	29	29	0.015	1550	717	186.4 ± 35.1	37.85 ± 7.31	212.5	0
LQO	B2	Fire	29	29	0.015	480	474	328.4 ± 140.6	46.18 ± 25.00	212.5	0
LQO	B3	Fire	29	29	0.015	670	546	551.8 ± 226.4	25.35 ± 9.84	212.5	0
MAT	RP27	Edge	18	183	0.17	1591	100	841.8 ± 479.8	52.08 ± 29.70	1400	92.45
MAT	RP27	Core	18	183	0.17	1561	113	879.8 ± 473.2	16.67 ± 8.13	1925	286.98
MAT	RP28	Edge	18	216	1.36	770	230	561.8 ± 774.5	14.93 ± 9.68	800	40.62
MAT	RP28	Core	18	216	1.36	835	198	651.4 ± 775.4	27.08 ± 1.04	1525	294.48
MAT	RP30	Edge	18	79	0.15	1672	93	618.4 ± 415.2	34.72 ± 5.74	500	8.17
MAT	RP30	Core	18	79	0.15	1678	101	645.8 ± 411.3	21.18 ± 6.77	1025	28.00
MAT	B1	Edge	18	18	0.015	313	7195	815.8 ± 137.3	62.85 ± 18.35	240	0
MAT	B2	Fire	18	18	0.015	2290	1101	1128.2 ± 312.2	42.36 ± 7.39	240	0
MAT	B3	Fire	18	18	0.015	1772	1054	1303.2 ± 360.9	55.55 ± 35.62	240	0

B, burned matrix area; RP, residual forest patch.

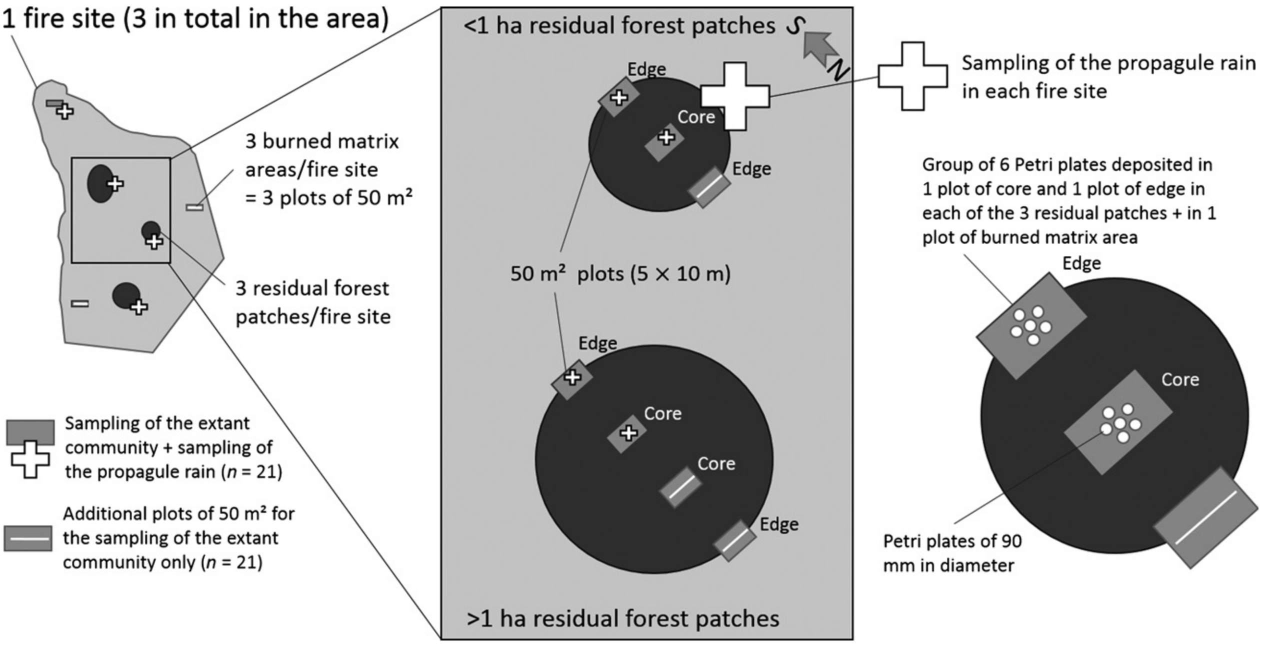

Fig. 1. Sampling design used to sample the extant and propagule rain communities of bryophytes in boreal black spruce–feather-moss forest of western Québec, Canada.

triggered by hydration–dehydration of the capsule and elaters (Vanderpoorten & Goffinet 2009). Petri plates were exposed on days that were both sunny and windy (wind speeds between 3 and 10 km h^{-1}; i.e. optimal conditions for drying and explosion of the capsule for propagule release; Glime 2013). After exposition, the Petri plates were covered and placed in germination chambers for 6 months, under fluorescent light tubes with continuous spectrum Verilux® (Lee Valley Tools Ltd. and Veritas Tools Inc., http://www.leevalley.com) (48″ and 32 Watt) with a 12-h/12-h light/dark regime. Germination chamber temperature was maintained at 22 °C. Petri plates were kept moist by misting with deionized water. When the nutrient agar became too thin, it was transferred onto a new Petri plate. Development of bryophyte gametophytes was assessed twice a week to follow germination patterns and to control potential bacterial or fungal contaminations. Minor contaminations were manually removed from the nutrient agar with forceps. In the case of a major contamination (i.e. all of the Petri plate was infected and survival of the protonemata was compromised), protonemata were removed from the plate, bathed in deionized water and transplanted onto a new Petri plate. Three control Petri plates with virgin nutrient agar were placed in the germination chambers every three months for the duration of the 6-month emergence period to identify potential contaminants (air-borne bryophyte propagules). No bryophyte species developed on any of the control plates, indicating that sample plates had not been contaminated during the laboratory growing period. Bryophyte culture with this method was generally successful; however, the principal bias is that only the species able to germinate in the Petri plates were accounted for.

All bryophytes were identified in the laboratory following Faubert (2012–2014) except for *Sphagnum subtile* (Russ.) Warnst., which follows the nomenclature of the Flora of North America Editorial Committee (2007). Species were classified by taxonomy and growth form (i.e. liverwort, acrocarp, pleurocarp and *Sphagnum*; Meusel 1935) and by life strategy following During (1992) (see Table S1 in Supporting Information). Species' reproductive state in the field was also noted (i.e. sterile or fertile with presence of sporophyte or gemmae, see Table S2). Bryophyte species richness and frequency were calculated per plot for the extant community and per group of six Petri plates for the propagule rain (see Tables S2 and S3). The frequency of each species per plot and per group of six Petri plates was defined as the number of microhabitats where a species was found per plot and as the number of Petri plates of the group where a species was recorded. In the Petri plates, one individual refers to a protonema in one Petri plate. While one protonema can generate several stems making it difficult to distinguish individuals, we took monthly photographs of the plates and used these pictures to identify individuals. Due to the artificial growing conditions in the Petri plates, bryophytes had unusual 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 conserved at the University of Québec in Abitibi-Témiscamingue, Qc, Canada.

The roles of temporal, spatial and forest structure variables in explaining patterns of bryophyte dispersal were evaluated (Table 1). Temporal variables included time since fire (years), determined from the SOPFEU digital map (2011), and the age of the forest in the residual patch. The minimum stand age of the forest in the residual patches (years) was estimated by coring ten dominant trees in the core of the residual forest patches with an increment corer and counting the number of rings. The age of the oldest tree was established as the minimum stand age. Spatial variables were calculated using ArcGis 10.2 (ESRI 2013) and included residual patch area (ha), distance to the closest residual patch (m), shortest distance to continuous forest (m) and isolation (mean of five distances between the point of interest and all forest sources, that is residual forest patch, continuous forest, residual riparian forest; m). Forest structure variables of the residual patches, that is canopy openness (%), tree and snag density (number of stems ha^{-1}) and stand complexity, were measured in the field during the summer of 2013. Canopy openness was measured using a densiometer, a scored concave mirror, at the level of the bryophyte layer (5 to 10 cm above the forest floor). The measure was taken in three randomly chosen positions in each rectangular plot and averaged. Tree/snag density was calculated in 11.28-m-radius (400 m²) circular plots at the core of each residual patch and with the line intersect method at the edge of each residual patch. All trees and snags with d.b.h. > 9 cm were included. Stand complexity was estimated using the modified Holdridge index (C_{HCL}) (Holdridge *et al.* 1971) computed only on trees with d.b.h. > 9 cm (Lugo *et al.* 1978).

DATA ANALYSES

Data analyses of species richness, assemblage and similarity were performed on the extant and propagule rain communities found in the 21 plots where Petri plates had been placed (i.e. core and edge plots in three residual forest patches per fire, and one burned matrix plot per fire) plus two additional burned matrix plots per fire, for a total of 27 plots. The additional burned matrix plots were included for better representation of the extant community in this environment.

R software 3.2.1 (R-Development-Core-Team 2015) was used for statistical analyses with a significance level of $\alpha = 0.05$. Results with *P*-values between 0.1 and 0.05 are also discussed as they suggest trends in the data, which are important to consider in order to identify fine-scale biological responses (Murtaugh 2014; de Valpine 2014).

As we used a nested design (plots of residual forests and burned matrix in fires), we tested whether the spatial structure of the sampling influenced the models in the different analyses with a LogLik test (Pinheiro & Bates 1995). In cases where the spatial structure did not influence the models, the simpler model without random spatial effects (linear model, lm) was chosen in the spirit of parsimony. When the spatial structure had a significant effect, we used linear mixed models (lme), which are equivalent to lm for a structured data set.

Comparisons of the composition of extant and propagule rain communities (objective 1) were made using rank abundance curves (Magurran 1988) performed with the package 'BIODIVERSITYR' 2.5-3 (Kindt 2015). The overall composition of the two communities was summarized in a detrended correspondence analysis (DCA; Hill & Gauch 1980; Lepš & Šmilauer 2003) on presence–absence data of species occurring more than five times in the entire data set using the package 'VEGAN' 2.3-0 (Oksanen *et al.* 2015). Specimens identified only to genus and for whom other species of the same genus were present were removed from the DCA analysis as well as from the subsequent analyses of similarity, as the index was calculated from DCA. The subsequent ordination matrix contained 65 species and 48 sites (27 plots of extant community and 21 plots of propagule rain). The significance of the resultant pattern was determined by Multi-Response Permutation Procedure (MRPP) on 2 000 permutations.

In order to address the second objective, to determine the relationship between geographic distance and compositional similarity of the propagule rain and extant communities, Jaccard's index of similarity was used. Jaccard's index was chosen because it compares the number of shared species to the total number of species in the combined assemblage, while Sørensen's index compares the number of shared species to the mean number of species in a single assemblage; Jost, Chao & Chazdon 2011). Jaccard's index of similarity was calculated between each propagule rain groups ($n = 21$) and all the extant community plots where Petri plates were placed ($n = 21$). Similarity between the propagule rain and the extant community was then examined in function of the geographic distance between them. Subsequently, in order to focus on the dispersal into the disturbed matrix, the same analysis was completed considering only the propagule rain of the burned matrix ($n = 3$) but with all the extant community plots ($n = 21$). Geographic distances were classified into spatial scales modified from Ross-Davis & Frego (2004): (i) *In situ*, propagules of the extant community in a given sampling point (50-m^2 plot of group of Petri plates); (ii) Local, propagules from the closest potential source, i.e. the closest residual patch (650–1100 m); (iii) Intrafire, propagules from all residual patches in a given fire (740–8400 m); (iv) Interfire, propagules from communities in all residual patches from the other fires (10–130 km). The intra- and interfire scales together refer to the regional spatial scale. The spatial structure of the sampling design influenced the results of this analysis, as indicated by the LogLik test, and community similarity among spatial scales was therefore compared using linear mixed models (lme) performed with the package 'NLME' 3.1-121 (Pinheiro 2015).

Patterns of individual species in the propagule rain of burned matrices were also examined, to determine from which distance they could have been dispersed. For this comparison, the origin of the species in the propagule rain of the burned matrices ($n = 3$) was determined in function of the extant community in all the plots, that is 42 plots (21 plots where Petri plates were placed plus the 21 additional plots of the linear transect and of the burned matrix; see sampling design for details in Fig. 1). The additional plots increased the sampling of the extant community to better represent potential propagule sources in the surrounding landscape. For each record of each species found in the propagule rain of each fire, we determined in which extant community plots it was also found. The spatial scale (i.e. *in situ*, local, regional) relative to the record in question was noted. If a species of the propagule rain was encountered at two spatial scales in the extant community, each distance was scored in the analysis. This analysis generated a matrix of species × spatial scale, where the presence or absence of each species at each spatial scale is indicated, which indicates the number of species that potentially dispersed from each spatial scale in each fire, for 'total' (all species grouped together, $n = 21$), 'perennial' ($n = 9$) and 'colonist' ($n = 10$) species groups. The three fires were then averaged to have a mean number of species dispersed per spatial scale. In each group (i.e. total, perennial or colonist), the mean number of species was then divided by the number of plots sampled at each spatial scale in the three fires pooled together (n *in situ* $= 3$; n closest RP $= 11$; n intrafire $= 28$; n interfire $= 84$ i.e. $N = 126$) in order to take into account the different number of potential propagule sources analysed at each spatial scale. The value obtained was reported as a percentage of the total number of species present per plot in the four spatial scales. This actual frequency was then compared to a theoretical expected frequency. Expected frequency was calculated by multiplying the sum of the mean number of species present per plot in each spatial scale by the number of plots that could be potential propagule sources in the target spatial scale and dividing by the total number of potential propagule sources available (N). We therefore obtained an expected frequency specific to each spatial scale weighted by the number of plots participating in the propagule rain at this spatial scale. The difference between actual and expected frequencies for total, perennial and colonist species was then calculated and tested for significance with a Fisher test.

In the third objective, we assessed the relative roles of geographic distance and nine environmental variables (divided into temporal, spatial and forest structure classes) in influencing the similarity between extant community where Petri plates were placed ($n = 21$) and propagule rain community of burned matrix ($n = 3$) at different spatial scales. Again, Jaccard's index of similarity represented the similarity between the extant and propagule rain communities. In this analysis, we only considered the propagule rain of burned matrices in order to assess the relative importance of geographic distance compared with environmental variables in bryophyte dispersal after disturbance. We tested the pertinence of including a quadratic relationship between similarity and distance, but the inclusion of this term did not result in a significant increase in explanatory power. In the spirit of parsimony, we therefore retained a linear relationship with geographic distance in our models. A model selection procedure using 18 candidate models plus the null model was performed. The first model tested geographic distance (distance between sites) and the nine following models tested each of the variables of the temporal (two models), the spatial (four models) and the structure (three models) classes individually (see Table S4). The eight other models tested biologically relevant combinations of these variables and interaction terms among several variables in each class. The global model combined together eight of the variables of the four different classes plus an interaction term. Conflict between certain variables prevented the use of all 10 variables in the global model, even after algorithm optimization. Here, we define the global model as the most complex of the model set. The response variable 'similarity', expressed as a proportion follows a normal distribution and was used without transformation in linear mixed models (lme) with random effects, performed with the package 'NLME' 3.1-121 (Pinheiro 2015). The explanatory variable data set was standardized (on columns) to account for the different scales of measurement. Candidate models were ranked based on the Akaike's Information Criterion corrected for small sample size (AICc) (Burnham & Anderson 2002) using the package 'AICCMODAVG' 2.0-3 (Mazerolle 2015). Models with a delta AICc (ΔAICc) > 2.0 were considered to have substantially lower empirical support (Burnham & Anderson 2002). The model with the lowest delta AICc was considered as the most parsimonious and indicated the environmental variables that best explained variations in community similarity. In order to illustrate the effect of each explanatory variable of the most parsimonious model, multimodel inference was used. We obtained 95% confidence intervals and model predictions using the modavgpred function of the 'AICCMODAVG' 2.0-3 package (Mazerolle 2015). Variables with 95% confidence intervals excluding 0 have a significant effect on the explanatory variable (community similarity) and their predicted values were subsequently plotted against values of the explanatory variable. An estimate of model adjustment was indicated by Spearman's Rho. These analyses were carried out first on all dispersal scales combined to identify a general dispersal pattern, and secondly, intra- and interfire scales of dispersal were examined individually.

Finally, the influence of geographic distance on similarity was also examined in only the propagule rain, to eliminate the bias associated with the emergence method (objective 4). The 21 plots where Petri plates were placed were again used in the analysis. We calculated Jaccard's similarity index to determine the relationship between the similarity of the propagule rain in different plots and their geographic distance, which was divided into three categories: < 1.5 km (i.e. propagules rain communities at the *in situ* and local scales), between 1.5 and 10 km (i.e. propagule rain communities at intrafire scale) and > 10 km (i.e. propagule rain communities at interfire scale). The spatial structure of the sampling did not influence this analysis; therefore, the relationship between geographic distance and community similarity was tested by a linear model (lm), followed by Tukey HSD tests using the package 'ADE4' 1.7-2 (Dray, Dufour & Thioulouse 2015).

Results

COMPOSITIONAL SIMILARITY BETWEEN THE EXTANT COMMUNITY AND THE PROPAGULE RAIN

Of the 123 taxa found, 23 were present in both the extant community and the propagule rain. Nineteen species were exclusively found in the propagule rain, and of these, 32% were colonist, 37% were perennial and 26% were shuttle (see Tables S2 and S3). In the extant community, 67% of the species sampled were seen fertile at least once and 28% of these fertile species were encountered in the propagule rain (see Table S2). In terms of species richness, the extant community was dominated by pleurocarps, whereas acrocarps dominated the propagule rain (21 acrocarps: 25 pleurocarps and 20 acrocarps: 12 pleurocarps, respectively). In contrast, extant and propagule rain communities were equally divided between perennial and colonist species (40 perennial: 45 colonist and 18 perennial: 18 colonist, respectively, see Tables S2 and S3). Five shuttle species were present in each of the communities. Rank abundance curves indicated that the 10 most abundant species differed between the extant community and the propagule rain (Fig. 2a, b). Half of the species were pleurocarps and liverworts in the extant community whereas in the propagule rain most species were acrocarps. Of the 10 most abundant species in the extant community, half were perennials and one species was colonist, while in the propagule rain community, half were colonists and four were perennials (Fig. 2a,b).

The DCA indicated that the extant community and the propagule rain differed in overall community composition (MRPP, $P = 0.0004$). The first axis divided the extant community and the propagule rain community, with no overlap in the plots (eigenvalue = 0.57, gradient length = 3.40 SD unit; Fig. 3). Each community was composed of a specific pool of species and a few common species were shared. The second DCA axis (eigenvalue = 0.17, gradient length = 2.12 SD units) separated the different positions in the residual forest patches (core, edge and burned matrix). This gradient is less

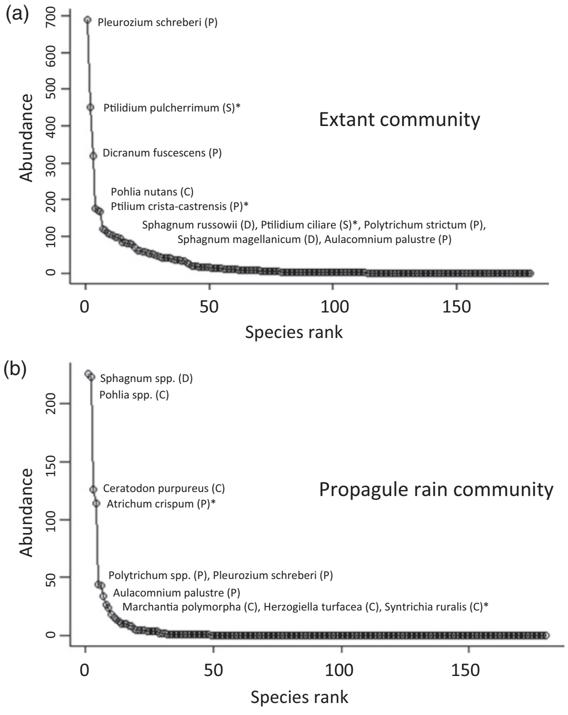

Fig. 2. Rank abundance curves of the extant (a) and propagule rain communities (b). Only the 10 most abundant species are indicated. Letters in brackets behind species names indicate species life strategy: C, colonist; P, perennial; S, shuttle; D, dominant. For more details on species life strategies, see Table S1. *, species exclusive to the community considered.

obvious in the propagule rain. Even though it was not significant, a trend towards distinct community assemblage among positions within the forest patches is visible (including both extant and propagule rain communities) (MRPP, $P = 0.099$; Fig. 3).

RELATIONSHIP BETWEEN GEOGRAPHIC DISTANCE AND COMMUNITY SIMILARITY: RELATIVE IMPORTANCE OF SDD VERSUS LDD

Similarity between the propagule rain and the extant community (considering all plots) and considering only the burned matrix propagule rain (objective 2) was low and varied from 0% to 4% and from 0% to 10.2%, respectively (Jaccard's index; data not shown). The degree of similarity between extant and propagule rain communities was not explained by geographic distance (no significant spatial scale was detected; data not shown).

When the potential sources of individual species were examined for the propagule rain of the burned matrix plots ($n = 3$), the frequency of occurrence of species was independent of the spatial scale of dispersal for both total ($P = 0.612$) and colonist species ($P = 0.868$), while a dependence was detected for perennial species ($P = 0.048$) (Fig. 4). Geographic distance does not influence bryophyte dispersal and potential sources of propagule situated from 0 to 30 km have an equal chance to contribute to the propagule rain. The interfire scale was slightly less represented for perennial species and slightly more for colonist species, and *vice versa* for the intrafire scale.

Of the 46 taxa trapped (i.e. 42 species plus 4 taxa only identified to genera and for which species of the same genera have been recorded in the extant community), 19 were not present in the extant community.

INFLUENCE OF GEOGRAPHIC DISTANCE AND RESIDUAL PATCH CHARACTERISTICS ON COMMUNITY SIMILARITY

The influence of geographic distance and nine environmental variables on the similarity of the extant community and the propagule rain of the three plots of burned matrix was tested at different spatial scales. When all four spatial scales are pooled together, the model including only temporal predictive variables (forest age and time since fire) was the most parsimonious (i.e. with the lowest ΔAICc value; Tables 2 and S4). Multimodel inference indicated that community similarity decreased with increasing forest age (confidence interval: −0.022, −0.0067) and time since fire (confidence interval: −5.6383, −1.9653; Fig. 5a,b).

When we only considered the intrafire scale, the model containing only the predictive spatial variable 'patch area' had the lowest AICc (confidence interval: −0.0262, −0.0131; Tables 2 and S4). Multimodel inference indicated that community similarity decreased with increasing patch size (Fig. 5c).

At the interfire scale, the global model was the most parsimonious and multimodel inference indicated that the variables 'patch area' and 'forest age' had a significant negative effect on the similarity between the communities (confidence intervals: −0.0203, −0.0052 and −0.0278, −0.0089, respectively, data not shown). In contrast, the variables 'canopy understorey' and 'distance between sites' had a significant positive effect on the similarity between the communities (confidence intervals: 0.0017, 0.0165 and 0.0233, 0.0389, respectively; Fig 5d,e).

Overall, environmental characteristics of the residual forest patches and of the landscape (i.e. temporal, physical and structural attributes) had a greater influence on the similarity between communities than geographic distance.

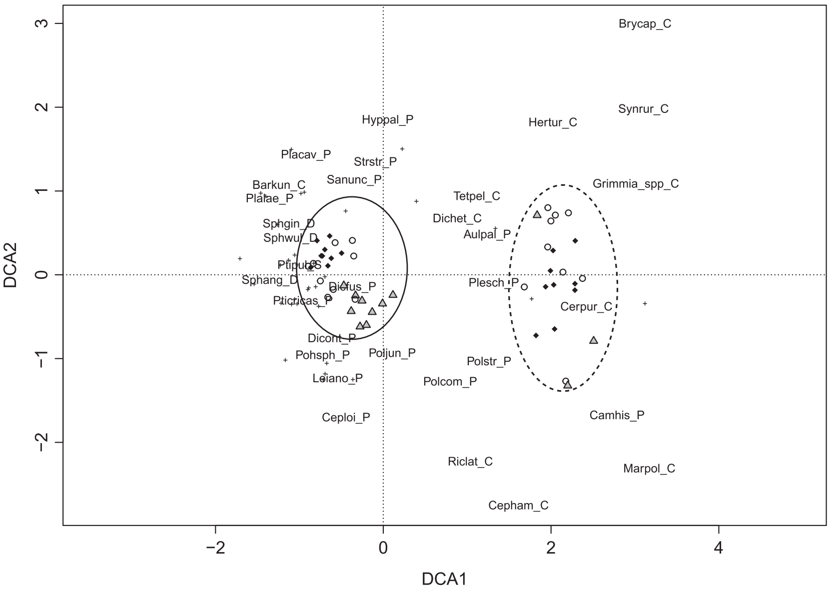

Fig. 3. Species and site plot of the detrended correspondence analysis of the total matrix of 48 plots including the extant and propagule rain communities. Only the 34 most frequent species are indicated, and positions of less frequent species are indicated by +. For complete names, see Table S2. The ellipses indicate community types, the extant community as a solid line and the propagule rain community as a hatched line. Symbols indicate habitat type: core, black diamond; edge, white circle; and fire, grey triangle. Letters behind species names indicate species life strategy: C, colonist; P, perennial; S, shuttle; D, dominant. For more details on the species life strategies, see Table S1.

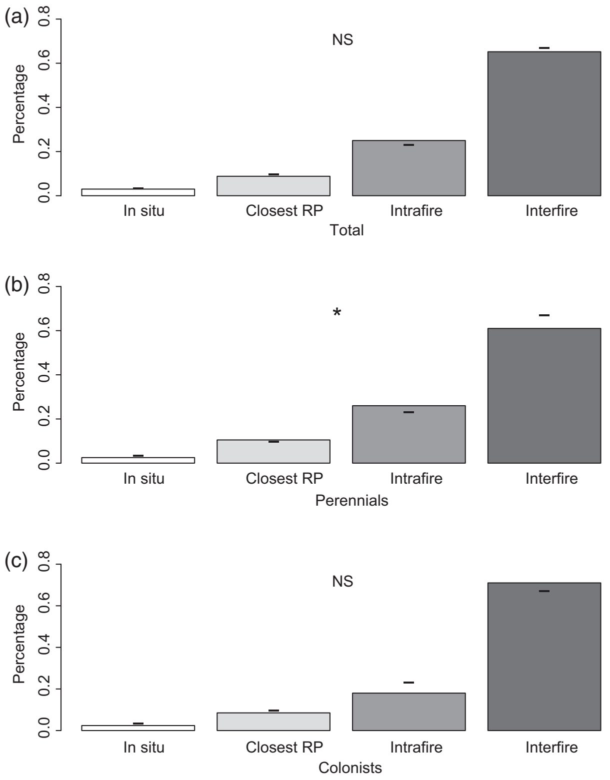

Fig. 4. Species-level comparisons between the propagule rain of burned matrices and the extant community of residual forest patches and burned matrices. Species were grouped in (a) total ($n = 21$), (b) perennial ($n = 9$) and (c) colonist ($n = 10$). Bars represent percentages of occurrence of species per plot and per spatial scale calculated as the mean number of species occurring at one spatial scale divided by the number of plots sampled at this spatial scale in the three fire pooled together (n *in situ* = 3; n closest RP = 11; n intrafire = 28; n interfire = 84 i.e. $N = 126$). This actual frequency was compared, with Fisher tests, to a theoretical expected frequency calculated by multiplying the sum of the mean number of species present per plot in each spatial scale by the total number of plots that could be potential propagule sources in the target spatial scale and dividing by the total number of potential propagule sources available (N). Expected frequencies at each spatial scale are indicated by dashed lines. *In situ*, 1–50 m; Closest RP: closest residual patch, 650–1100 m; Intrafire: 640–8400 m; Interfire, 12 800 m – 30 km. Significance of the Fisher tests is indicated by the symbols: *, $P < 0.05$; NS, non-significant.

Table 2. Ranking of the models used to assess the role of spatial, temporal and structural variables on similarity between communities based on the ΔAICc*i* value. The response variable, Jaccard's similarity (SimJaccard), compared the propagule rain in each of the 50-m^2 plot of the burned matrix ($n = 3$) to each of the 50-m^2 plot of the extant community ($n = 21$). *In situ* and local/closest residual patch scales were not analysed because of the small number of replicates. Only the models with a ΔAICc < 2 and the first models with a ΔAICc > 2 are indicated. K_i, number of parameters including the intercept; w_i, Akaike weight; and ρ, model adjustment, are only indicated for the best model. See Table S3 for complete model list

Model	K_i	AICc$_i$	ΔAICc$_i$	w_i	ρ
All four dispersal scales pooled					
Mod15 (SimJaccard ~ TSF + AGE)	5	−349.03	0.00	0.82	0.78
Global (SimJaccard ~ DIST + TSF + AGE + ISOL + AREA*ISOL + CANOP + DENS + HOLD)	12	−345.80	3.24	0.16	
Intrafire scale					
Mod2 (SimJaccard ~ AREA)	4	−81.13	0.00	0.93	0.93
Mod14 (SimJaccard ~ AREA*ISOL)	6	−73.85	7.29	0.02	
Interfire scale					
Global (SimJaccard ~ DIST + TSF + AGE + ISOL + AREA*ISOL + CANOP + DENS + HOLD)	11	−235.13	0.00	0.86	0.78
Mod15 (SimJaccard ~ TSF + AGE)	5	−231.48	3.65	0.14	

AGE, estimated age of forest in residual patch (year); AREA, area (ha); CANOP, canopy openness (%); DENS, trees and snags density (number of stems ha^{-1}); DIST, distance among sites (m); DIST CF, distance from closer continuous forest (m); DIST CRP, distance to closest residual patch (m); HOLD, complexity index; ISOL, isolation (m); TSF, time since fire (year).

~, in function of; +, additive effect; *, interactive effect.

THE UNIMODAL RELATIONSHIP BETWEEN GEOGRAPHIC DISTANCE AND PROPAGULE RAIN COMMUNITY SIMILARITY

Similarity among propagule rain communities varied from 25% to 77% for distances from 10 m to 130 km (data not shown). Propagule rain community composition similarity varied significantly with distance ($P = 0.007$) and differed significantly at distances between 1.5 and 10 km ($P = 0.028$; Fig. 6a) but did not differ significantly at distances < 1.5 km and > 10 km (Fig. 6a).

Discussion

The dispersal patterns observed in this study suggest that long-distance dispersal is more common than had hitherto been assumed (Jacobson & Peres-Neto 2010), and this for all bryophyte life strategy groups. Some species found in the propagule rain were not encountered in the extant community, and the similarity between the communities was positively correlated with geographic distance between the communities. Furthermore, maximal similarity among propagule rain communities was observed at moderate distances (i.e. between 1.5 and 10 km) suggesting a unimodal relationship between community similarity and distance. More than a purely local provider of propagules, the scope of the residual forest patches seems to extend several hundred kilometres, regardless of the life strategy considered.

EXTANT AND PROPAGULE RAIN COMMUNITIES HAVE DISTINCT COMPOSITIONS

As predicted by previous studies (Ross-Davis & Frego 2004; Caners, Macdonald & Belland 2009; Kövendi-Jakó *et al.* 2016), there was little similarity between the extant and propagule rain communities. Colonist and acrocarp species occurred

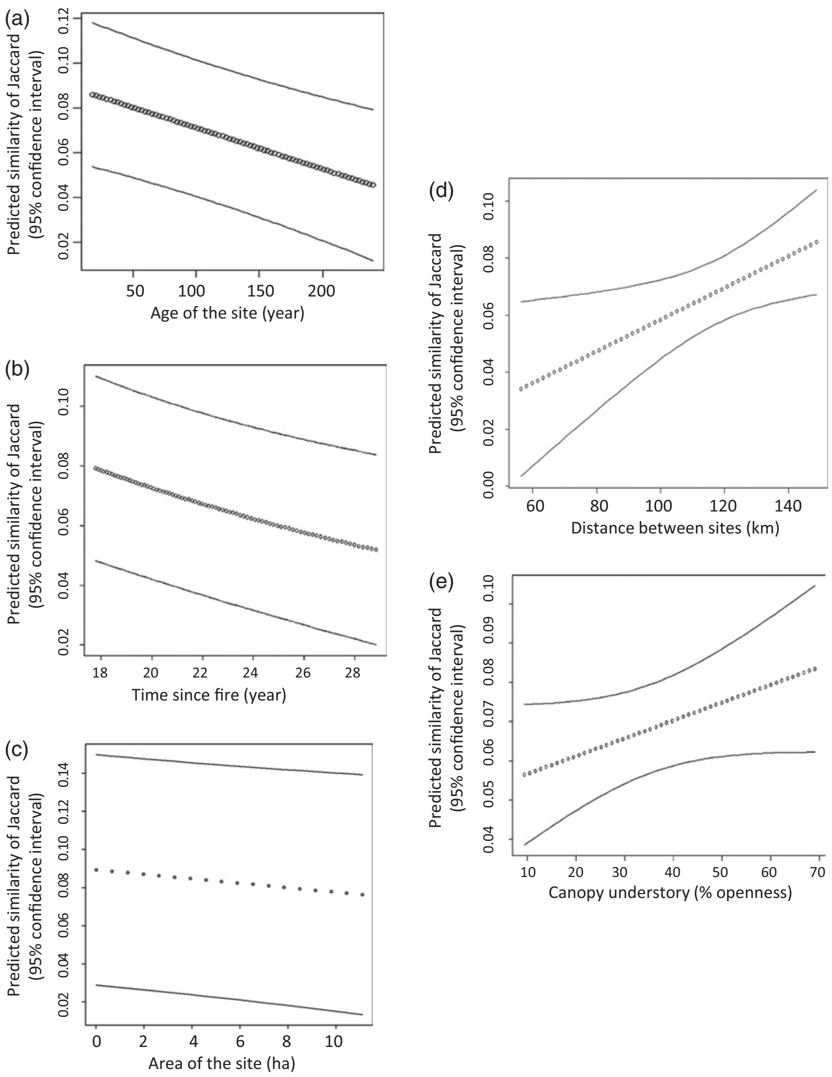

Fig. 5. Prediction graphs of Jaccard similarity indices between extant and propagule rain communities after multimodel inference of the environmental variables that best explained dispersal patterns observed. (a) and (b) at the global scale (i.e. pool of the four dispersal patterns of bryophyte), (c) at the intrafire scale, (d) and (e) at the interfire scale. Dispersal patterns are indicated by dotted lines, and 95% confidence interval is represented by solid lines.

more in the propagule rain, while the extant community was dominated by perennial and pleurocarp species. Shuttle species richness did not differ between communities. This pattern could be explained by species' life strategies (During 1992); however, a number of species, including many perennials, were observed in a fertile state and were not found in the propagule rain. The absence of these species in our propagule rain can be explained by the fact that the propagules of these species may not enter the propagule rain (particularly in the case of gemmae), they may be released at temporally distinct moments not covered by our four capture sessions, or they may not germinate in the Petri plates. Alternatively, they may be present in the rain at sufficiently low density that they were not captured by our random sample, or may be exclusively dispersed at a hyperlocal scale (i.e. surrounding the source colony). Our first hypothesis is therefore rejected as the closest extant community contributes little to the propagule rain. Furthermore, several perennial, colonist and shuttle species found in the propagule rain were not present in the closest extant community or in any of the sampled communities. The question of the origin of these propagules remains unanswered.

NONLINEAR RELATIONSHIP BETWEEN COMMUNITY SIMILARITY AND GEOGRAPHIC DISTANCE: LDD DOMINATES SDD

The spatial limitation of bryophyte dispersal indicated by numerous studies (Miles & Longton 1992; Laaka-Lindberg, Korpelainen & Pohjamo 2006) suggests that community similarity should decrease with increasing distance. Our study indicates that propagule rain composition is unrelated to distance from a putative propagule source. When we compare the distances travelled by the propagules at the regional scales (both intra- and interfire scales; average 21 400 m) with the distances travelled at the *in situ* scale (average 25 m), it becomes evident that regional dispersal is common despite a significant handicap. This is true regardless of the species life strategy, although slightly more for colonist than perennial species, which may be justified by their life strategies. Indeed, colonist species are characterized by a high reproductive effort and the production of numerous and light spores (During 1992). In contrast, perennial species have an overall low sexual reproductive effort (Longton & Schuster 1983; During

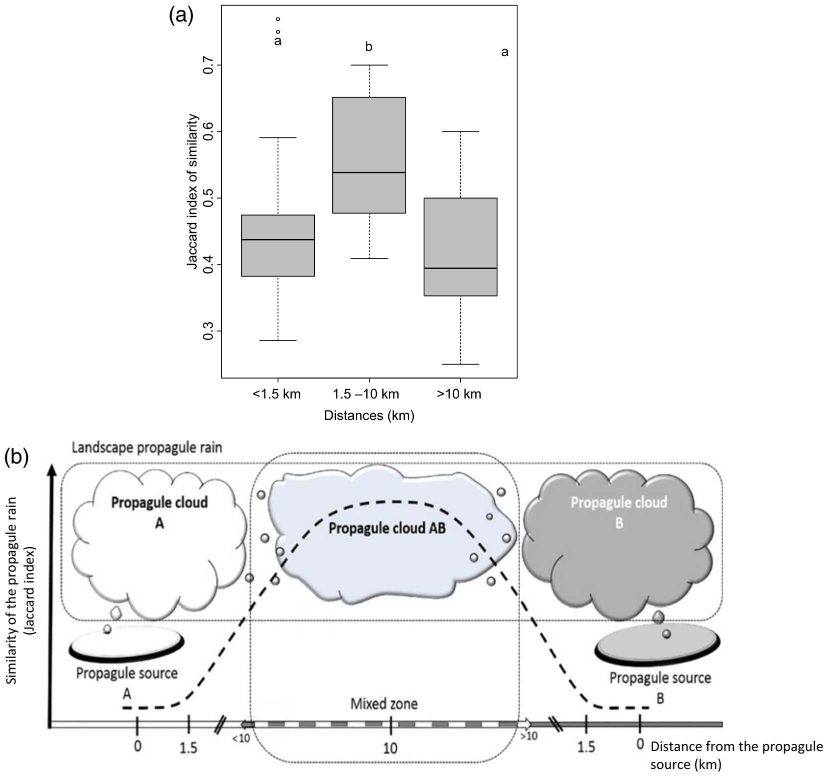

Fig. 6. Jaccard similarity index among propagule rain communities by distance: < 1.5 km, *in situ* and local/closest residual patch scales; 1.5–10 km, intrafire scale; > 10 km, interfire scale. (a) Results of the linear model (lm) tests, boxplots topped by the same letters are not significantly different as indicated by a Tukey HSD for a given distance. The horizontal line of the boxplot indicates the median, while the bottom and the top of the box indicate the 25th and the 75th percentiles. The whiskers indicate 2 SD. Points above or below 2 SD are indicated by dots. (b) Schematization of the bryophyte propagule clouds given the distance to the propagule source. Up to 1.5 km radius, the propagule rain was regulated by the propagule cloud of each potential source, generating heterogeneous propagule rain patterns. From 1.5 to 10 km, propagule clouds from each potential propagule source were mixed generating homogenous propagule rain patterns at the regional scale. Beyond 10 km, the propagule rain becomes heterogeneous due to differences in propagule clouds at distant sites. The dashed curve represents the similarity of the propagule rain in the landscape, which reaches a maximum at the intrafire scale (i.e. between 1.5 and 10 km).

1992), and while many of them are commonly fertile, there are few sporophytes per colony (Rydgren & Økland 2001; Cronberg 2002). Despite this, Longton & Schuster (1983) have shown that *Hylocomium splendens* may produce large quantities of spores (around 100 000 per capsule) whose relatively small size (14–17 μm in diameter; Hill *et al.* 2007) favours wind dispersal. The tall sporophytes of these species enhance the probability of spore uptake by the wind, and in this way, one fertile colony with a few capsules may release large numbers of spores to air layers several kilometres high. Thus, these spores can travel long distances due to stochastic wind events (Lönnell, Jonsson & Hylander 2014). Coupled with the large colonies of perennial and dominant species (i.e. sphagna), this may explain the high number of their spores in the propagule rain.

Similarity between propagule rain and extant community was positively correlated with increasing distance, leading to the rejection of our second hypothesis and validating the occurrence of LDD in bryophyte metacommunities. The occurrence of the LDD suggests that dispersal ability alone does not regulate bryophyte colonization of new areas. At least two non-mutually exclusive filters could also apply to select species: sexual reproductive ability (i.e. quantity and viability of spores) and environmental conditions at the establishment sites (Lönnell, Jonsson & Hylander 2014; Mota de Oliveira & ter Steege 2015). Furthermore, the apparent dominance of regional dispersal events suggests that dispersal mode is not affiliated to the life strategy group but rather depends on species traits. In the context of our second objective, LDD did not appear to be the prerogative of colonist species. The 'inverse isolation hypothesis' already advanced by several authors (Szövényi, Sundberg & Shaw 2012; Sundberg 2013) seems to explain the patterns observed here and bryophyte metacommunity dynamics depends on several dispersal scales, and propagule sources therefore contribute both to local and regional diaspore clouds (Sundberg 2005).

ENVIRONMENTAL CHARACTERISTICS OF THE LANDSCAPE AS MAIN GOVERNORS OF BRYOPHYTE METACOMMUNITY REASSEMBLY

As suggested in our third hypothesis, environmental characteristics of the local habitat also explained the similarity patterns observed between extant and propagule rain communities. Similarity increased with canopy openness, probably due to increased wind speeds and therefore more efficient dispersal in more open stands (Fenton & Bergeron 2006; Sundberg 2013). The pattern of decreasing similarity with increasing time since fire, age and area of the residual forest patches reflects that the oldest and largest patches may better mimic 'continuous/undisturbed' forests. They may shelter species with specific microhabitat requirements (i.e. deadwood, canopy enclosure) typical of more advanced stages of succession, increasing the dissimilarity with the propagule rain assemblage composed of species of earliest successional stages. Cronberg (2002) has also suggested that the maintenance of perennial species depends on the age of the patch as sexual reproduction is less common in young patches compared with older patches, which therefore contribute more to propagule clouds. Similarly, Löbel, Snäll & Rydin (2006) demonstrated that many obligate epiphyte bryophytes are affected by patch conditions that are linked to forest stand age. Maintaining old and large sources is therefore critical for the persistence of late seral species that take decades to reappear in a landscape without these refugia (Caners, Macdonald & Belland 2009).

BRYOPHYTE PROPAGULE RAIN OVER THE LANDSCAPE IS HOMOGENIZED BY LDD EVENTS

Our results suggest a nonlinear relationship between propagule rain community similarity and distance. The propagule rain at the landscape scale was, as suggested by the fourth hypothesis, composed of various propagule clouds and dispersal within 1.5 km of a focal point (SDD), resulted in little similarity between propagule rain communities (Fig. 6b). Sundberg (2005) found similar results for sphagna. However, beyond this distance up to 10 km from the focal point (> 1.5 km and < 10 km), similarity among propagule rain communities was at its maximum as the effects of SDD were diluted in a 'regional cloud' of LDD contributing to the homogenization of the propagule rain across the landscape. As suggested by Hylander (2009) and Sundberg (2013), the roles of microsite limitation and/or rapid decline of local availability are masked by a higher regional propagule rain (LDD), which corroborates our species-level propagule results that indicated limited local dispersal. Beyond 10 km, the similarity decreased due to the dominance of other propagules clouds from more distant sources. Appropriate meteorological conditions coupled with the absence of physical barriers to the wind in the landscape matrix have been advanced to facilitate the LDD (Sundberg 2013).

Based on the spatial scales used in this study (both in the comparison between extant and propagule rain communities and among propagule rain communities), a working definition of SDD and LDD can be formulated. We might conclude that LDD refers to propagules dispersed from regional sources, that is from 1.5 to over than 100 km, whereas propagules dispersed from more local sources, under 1.5 km, are included in SDD. However, definitions of LDD and SDD are system and taxon dependent and this definition should only be applied to bryophytes of boreal black spruce–feather-moss forests of eastern Canada.

LIMITATIONS OF THE STUDY

Results of this study should be interpreted with some degree of caution as propagule traps cannot discriminate between the absence of a species and its non-detection due to unsuitability of *ex situ* growing conditions (Ross-Davis & Frego 2004). Also, the nutrient medium used to fill Petri plates does not seem suitable for epixylic species such as various liverworts (Caners, Macdonald & Belland 2009). Sterilized and moistened pieces of wood were tried to trap epixylic species (Kimmerer 1991), but they were rapidly contaminated by fungal hyphae.

One other limitation of the emergence method is linked to the timing of 6-h exposure of the Petri plates from the morning to early afternoon. Indeed, propagules are generally released in the morning (Johansson *et al.* 2015) and spores that are released at distant sites may thus be primarily deposited later in the afternoon and the evening because of the extended transportation times. This timing could lead to a bias with an excessive sampling of the propagules from local to very local scales (SDD) compared with propagules from farther distances (LDD). This may have affected our results, but would not lead to a different conclusion, given the evident importance of LDD. The exposure time may have affected the species trapped, and our study may even have minimized the proportion of propagules from distant origins. Indeed, 6 h of exposure may lead to less propagules from the regional dispersal scale compared with an entire day of exposure (24 h).

Finally, the propagule rain varies among seasons and years (Ross-Davis & Frego 2004). Similarly, sporophyte production and diaspore release varies among species (Longton & Greene 1969; Damsholt 2002) and among years with climatic conditions, such as precipitation and air humidity (Rydgren, Cronberg & Økland 2006; Johansson *et al.* 2015). This can affect the pool of propagules potentially available to be trapped. However, our study is based on two trapping sessions in two seasons of 2 years, capturing spring, summer and fall species. In addition, the climatic conditions of the 2 years were substantially different (e.g. in temperature, humidity, precipitation) and the compositions of the propagule communities were significantly distinct in 2013 and 2014 (data not shown). Consequently, we suggest that a significant part of the natural variability in the propagule rain that is due to seasonality and climate are included in this study. Moreover, considering the extensive sampling design used (i.e. over 10 000-km^2 region in the boreal forest) and the number of taxa recorded (i.e. 123), we estimate that we present a realistic spatial pattern of the propagule rain and extant community.

IMPLICATIONS, CONSERVATION AND FUTURE RESEARCH

The occurrence of LDD in bryophyte metacommunities explains the Holarctic distribution of several bryophyte species (Vanderpoorten & Goffinet 2009). Furthermore, the preponderance of LDD in all life strategies suggests that the traits used to generate these groups, and especially the size of the spores, do not adequately describe dispersal potential. Timing of propagule release, capsule morphology and climatic events such as wind turbulence and air humidity seem more limiting to bryophyte dispersal than spore size (Johansson *et al.* 2014, 2015). Long-distance dispersal capacities associated with species life strategy is therefore put in doubt.

Results of this study compel us to no longer consider bryophyte dispersal patterns as a purely local mechanism but rather as a regional one. More than the specific location of propagule sources, the distribution of sources across the landscape determines bryophyte propagule dispersal and *a fortiori* bryophyte conservation. Moreover, several filters (e.g. sexual organ production, environmental requirements, microhabitat availability) may be more limiting than dispersal capacity for bryophyte metacommunity assemblages. Future studies should be performed to assess how germination requirements and habitat availability interact with dispersal patterns. Finally, while our results are consistent with those for sphagna, studies in other biomes could inform the generality of these findings.

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Data accessibility

All data used are included in the paper and Supporting Information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Classification of bryophyte species based on life strategy (adapted from During 1992).

Table S2. Total number of bryophyte taxa found in extant community propagule rain by position in boreal black spruce feather-moss forest after natural fire in western Québec.

Table S3. Species richness, species frequency and number of plots with the presence of the different bryophyte taxonomic groups and life strategies sampled in boreal black spruce feather-moss forest after natural fire in western Québec.

Table S4. Candidate models used to assess the role of distance between sites and environmental variables on the similarity among communities.