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To cite this article: Marion Barbé, Émilie E. Chavel, Nicole J. Fenton, Louis Imbeau, Marc J. Mazerolle, Pierre Drapeau & Yves Bergeron (2016) Dispersal of bryophytes and ferns is facilitated by small mammals in the boreal forest, *Écoscience*, 23:3-4, 67-76, DOI: [10.1080/11956860.2016.1235917](https://doi.org/10.1080/11956860.2016.1235917)

To link to this article: <http://dx.doi.org/10.1080/11956860.2016.1235917>



Published online: 03 Nov 2016.



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Dispersal of bryophytes and ferns is facilitated by small mammals in the boreal forest

Marion Barbé^a, Émilie E. Chavel^a, Nicole J. Fenton^a, Louis Imbeau^a, Marc J. Mazerolle^b, Pierre Drapeau^c and Yves Bergeron^{a,c}

^aUniversité du Québec en Abitibi-Témiscamingue, Institut de recherche sur les forêts, 445 Boulevard de l'Université, Rouyn-Noranda, Québec J9X 5E4, Canada; ^bUniversité Laval, Département des sciences du bois et de la forêt, 2405 rue de la Terrasse, Québec, Québec G1V 0A6, Canada; ^cUniversité du Québec à Montréal, Département des sciences biologiques, 405 rue Sainte-Catherine Est, Montréal, Québec H2L 2C4, Canada

ABSTRACT

Bryophytes and pteridophytes are important contributors to ecosystem services in boreal regions. Abiotic agents are considered their main dispersers, but recent studies suggest that biotic agents including invertebrates, birds and large mammals might also be efficient dispersal agents. Dispersal of cryptogams by ground-dwelling small mammals is often assumed to occur, but has yet to be demonstrated. In this study, we present the first evidence of boreal cryptogam species being dispersed by ground-dwelling small mammals. In 2013 and 2014, we recorded bryophyte cover and fern presence in 35 sites in black spruce forest. We also collected diaspores by brushing the fur of 99 ground-dwelling small mammals live-trapped in the same sites. Diaspores were then germinated on nutrient agar for six months. Viable diaspores of five bryophyte species and one fern species were successfully grown. No association was found between the cryptogam community sampled on site and the diaspore community grown on artificial substrate. Unlike abiotic agents that randomly disperse cryptogams, small mammals are more likely to transport diaspores to suitable substrates where microhabitat requirements for germination are met. Our results highlight the need to consider a broad spectrum of dispersal agents when focusing on the community dynamics of cryptogams.

RÉSUMÉ

Les cryptogames (bryophytes et ptéridophytes) représentent une composante fondamentale des régions boréales, et leur dispersion à moyenne et longue distances dépend principalement d'agents abiotiques. Des études récentes suggèrent pourtant l'importance d'agents biotiques tels que les invertébrés, les oiseaux et les grands mammifères comme vecteur de dispersion. La dispersion des cryptogames par les micromammifères est régulièrement admise mais n'a encore jamais été formellement examinée. Dans cette étude, nous présentons la première preuve tangible du transport des cryptogames boréaux par des micromammifères. Au cours des étés 2013 et 2014, nous avons estimé le couvert des bryophytes et la présence des fougères (communauté *in situ*) dans 35 sites en pessière noire à mousses. Nous avons brossé le pelage de 99 micromammifères de cinq espèces différentes capturés vivants dans les mêmes sites. Le matériel végétal collecté a été mis à germer durant six mois sur un gel nutritif d'agar. Nous avons observé la germination de cinq espèces de bryophytes et d'une espèce de fougère. Nous n'avons trouvé aucune association entre la communauté de cryptogames *in situ* présente dans les sites et la communauté germée sur un substrat artificiel. Contrairement à la dispersion aléatoire par des agents abiotiques, la dispersion par les micromammifères est plus susceptible de transporter les diaspores vers des substrats propices à leur germination. Nos résultats soulignent l'importance de considérer une vaste gamme d'agents de dispersion lors de l'étude des dynamiques des communautés de cryptogames.

ARTICLE HISTORY

Received 27 May 2016
Accepted 9 September 2016

KEYWORDS

boreal forest; cryptogams; microhabitat requirements; medium-range dispersal; rodents

MOTS-CLÉS

cryptogames; dispersion à moyenne distance; exigences de microhabitat; forêt boréale; rongeurs

Introduction

Bryophytes (i.e. true mosses, liverworts and sphagna, following Crum [2001]) and ferns play important roles in the functioning of the boreal forest. They provide many organisms with shelter and food (Davidson et al.

1990; Haines & Renwick 2009), and they contribute to numerous ecosystem services. For instance, bryophytes and ferns contribute to water filtration, nutrient retention and nitrogen fixation (through the association of some bryophytes and aquatic ferns with cyanobacteria),

and they also provide germination substrates for tree seeds (George & Bazzaz 1999; Baker et al. 2003; Clark et al. 2005; DeLuca et al. 2007; Turetsky et al. 2012; Bay et al. 2013). The dispersal capacities of bryophytes and ferns remain a controversial topic, as some studies have reported dispersal distances of only a few metres for bryophytes and ferns (Söderström 1987; Tájek et al. 2011), whereas other studies have demonstrated their ability to travel between 20 and 100 km and beyond (Hylander 2009; De Groot et al. 2012; Sundberg 2013). Both bryophytes and ferns reproduce sexually and asexually, although vegetative reproduction is less common among ferns than bryophytes. Although still debated, it is assumed that the sexual “dust-like spores” of bryophytes are effective dispersal agents contributing to long-distance dispersal. In contrast, vegetative propagation by asexual agents such as gemmae and specialized brood-leaves or by vegetative fragments of leaves and stems mainly supports short-distance dispersal and local population maintenance (cf., Eckert 2002; Muñoz et al. 2004; Pohjamo et al. 2006; Löbel & Rydin 2009; Boch et al. 2013). Fragments of mature individuals can also grow into new individuals (Rocheffort et al. 2003; Benschoter 2006; Mälson & Rydin 2007). Bryophytes and ferns are believed to disperse mainly through abiotic agents, such as water and wind (Muñoz et al. 2004; Johansson et al. 2014). Dispersal by biotic agents also occurs, with evidence of transport by birds (Davison 1976; Lewis et al. 2014; Osorio-Zuñiga 2014), large mammals and bats (Heinken et al. 2001; Parsons et al. 2007; Pauliuk et al. 2011) as well as invertebrates (Kimmerer & Young 1995; Marino et al. 2009; Rudolphi 2009). Such transport may be exozoochorous (i.e. external attachment on animal) or endozoochorous (i.e. internal, passing through the digestive tracts), and consumption of both bryophytes and pteridophytes has been shown (Arosa et al. 2010; Boch et al. 2013). Although one study has indirectly linked bryophyte abundance to the dynamics of small mammal populations (Rydgren et al. 2007), and some authors have speculated that small mammals transport bryophytes (Kimmerer 1994; Carey 2003), to our knowledge external dispersal of bryophytes and ferns by ground-dwelling small mammals (a form of mammiochory) has yet to be demonstrated. Because boreal ground-dwelling small mammals are in continuous contact with the cryptogam layer during their daily activities, we hypothesize that dispersal of cryptogam species by small mammals is likely to occur. We predict that cryptogam diaspores are frequently dispersed by all species of small mammals without any exclusive species-specific associations; that the cryptogam species

found on small mammal fur may reflect the extant cryptogam community found on sites; and that distinct life traits (e.g. formation of large carpets, production of copious quantities of diaspores) may render some cryptogam species more susceptible to be dispersed by small mammals than other cryptogam species.

Materials and methods

Study area and sampling design

The study area covers a total of 8325 km² (79°29'W, 49°00'N–75°39'W, 50°22'N) in the western black spruce (*Picea mariana*)–feather moss (*Pleurozium schreberi*) forest of Québec, eastern Canada (Grondin 1996). This boreal region is characterized by a subpolar continental climate. Average annual temperature and precipitation are respectively 1°C and 927.8 mm (1981–2010), recorded at the nearest weather station, Lebel-sur-Quévillon, Québec (Environment Canada 2015). The main tree species are black spruce (*P. mariana*), jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*), along with occasional broadleaf species such as white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). The understory is primarily composed of ericaceous species (e.g. *Rhododendron groenlandicum*). True mosses form a dense carpet and are slowly replaced by *Sphagnum* species as drainage conditions deteriorate due to paludification with increasing time since fire (Fenton & Bergeron 2006). The region is also characterized by large, recurrent and severe wildfires (8000 ha on average; Bergeron et al. 2004), although fire is increasingly being replaced by forest management practices as the primary agent of disturbance (Imbeau et al. 2015).

We selected a total of 35 sites distributed among old undisturbed forest stands (over 100 years old), post-fire remnant patches (3.9 ha; range: 0.4–11.1) left after wildfires that occurred more than 20 years ago, green tree retention patches (0.7 ha; range: 0.1–1.3) left after recent clear-cutting (<10 years) and linear cutblock separators (60–100 m large, connected to old-growth forests) that separate clear-cut areas. Sites were at least 500 m apart, based on the average movement distance of the most mobile species (Larsen & Boutin 1994), to ensure that any two sites were independent. Live-trapping was conducted between 23 July and 15 August 2013 and between 1 June and 21 August 2014, with both Tomahawk live-traps (8.0 cm × 8.0 cm × 41.0 cm; Tomahawk Live Trap llc[®]) and Sherman live-traps (7.5 cm × 9.0 cm × 23.0 cm; H. B. Sherman Traps, Inc.[®]). Tomahawk live-traps were used to trap arboreal mammalian species such as American red squirrels

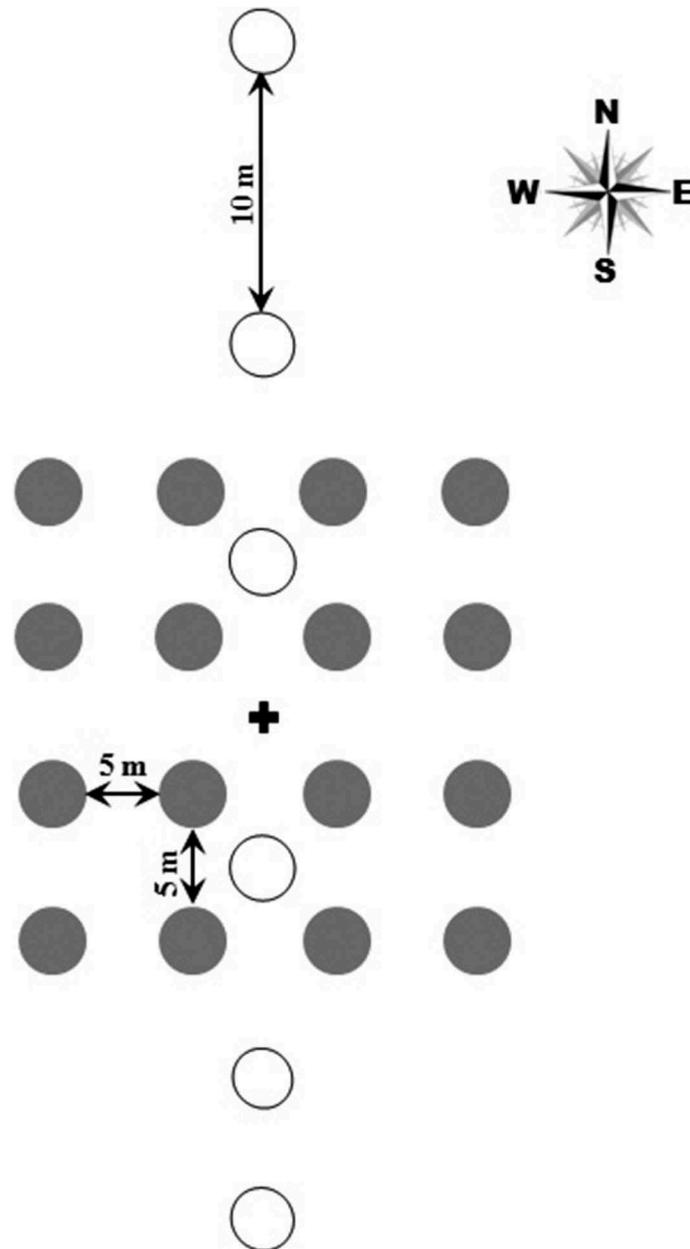


Figure 1. Representation of the trapping station at each site.

Note: Filled cross (+), trapping station centre; empty circles (O), one Tomahawk live-trap; filled circles (●), one Sherman live-trap.

(*Tamiasciurus hudsonicus*) and northern flying squirrels (*Glaucomys sabrinus*). Sherman live-traps enabled us to trap smaller ground-dwelling mammals such as southern red-backed voles (*Myodes gapperi*). All traps were baited with peanut butter and apple pieces, which provide water and food to the trapped individuals. Cotton batting was also added to each trap to provide shelter and insulation in order to ensure better survival. We established one transect of six Tomahawk live-traps per site with a distance of 10 m between traps. Transects were 50 m long in order to accommodate our smallest sites. Then we established a 15 m square trapping grid of 16 Sherman live-traps centred on the

transect line with traps spaced at 5 m intervals (Figure 1). We trapped during 72 consecutive hours, checking the traps twice a day (early morning and late afternoon). Each site was monitored with this trapping regime during one trapping session in 2013 (three nights). In 2014, three trapping sessions were completed (three nights in each of June, July and August). Toothbrushes were used to collect the potential diaspores (i.e. spores, gemmae, vegetative fragments) on the fur of the trapped small mammals. Each small mammal was gently brushed on their back, belly and paws with a new toothbrush for two minutes. We then sealed each toothbrush in a new labelled plastic bag. All

individuals were released after brushing. Diaspores were visible neither on the mammalian fur nor on used toothbrushes. All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the Institutional Animal Care Review Committee at the Université du Québec en Abitibi-Témiscamingue (UQAT, permit no. 2013-04-02). The extant bryophyte and fern community composition of the 35 sites was estimated using three 1-m² (1 m × 1 m) quadrats placed randomly within the Sherman trapping grid. The percentage cover of each bryophyte species present was estimated visually. Species represented by only one individual were noted as trace (i.e. <1% of cover of the 1-m² quadrat). Only the presence/absence of fern species was recorded.

We germinated the collected diaspores on an agar substrate following the “emergence method” used by Ross-Davis and Frego (2004). In the laboratory, we washed each toothbrush with deionized water over a Petri plate 90 mm in diameter to extract potential diaspores. Each Petri plate contained 78.5 cm² of nutrient agar prepared in sterile laboratory conditions (Parker Thompson’s basal nutrient medium of Klekowski [1969], described by *C-Fern* Project © [1995–2014]). After the extraction, the Petri plates were covered and placed randomly in germination chambers for six months (from September 2013 to March 2014 after the 2013 trapping session and from September 2014 to March 2015 after the 2014 trapping session) under continuous-spectrum Verilux® (48” and 32 Watt) fluorescent light tubes with a 12 hour/12 hour light/dark regime. Petri plates were misted with deionized water as needed to prevent them from drying out. The germination chamber temperature was maintained at 22°C. When the nutrient agar became too thin, the entire content of the Petri plate was transferred to a new Petri plate with fresh nutrient medium. When the growing bryophytes and ferns were too tall for the Petri plates to contain, they were placed in individual transparent plastic pots. Development of bryophyte gametophytes was assessed twice a week following germination. Minor contamination by fungus or algae was manually removed from the nutrient agar with forceps. In the case of a major contamination, where the Petri plate was entirely covered by fungus or algae and survival of the protonemata was compromised, protonema were removed from the plate, bathed in deionized water and transplanted into 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 six-month emergence period to identify potential contaminants

(air-borne diaspores). No species developed on any of the control plates, indicating that sample plates had not been contaminated during the laboratory growing period. Cryptogam culture with this method was generally successful, even though it introduces a bias towards cryptogam species able to germinate in artificial conditions.

All individuals were identified in the laboratory following Faubert (2013, 2014) for bryophytes. Ferns were identified following Martineau (2014). Because of the artificial growing conditions in Petri plates, bryophytes lacked some critical features for species identification, which is why some specimens were only identified to genus, in particular sphagna and members of the genera *Pohlia* and *Polytrichum*.

Statistical analyses

Data from 2013 and 2014 were pooled for analyses. Furthermore, we made no distinction among the types of sites where small mammals were trapped due to the low sample size in each site type (old-growth forests, post-fire remnant patches, green-tree retention patches and linear cut-block separators). We consequently pooled data for all small mammals. We conducted analyses according to cryptogam species taxonomic groups and life forms: liverworts, sphagna and true mosses, divided into acrocarpous and pleurocarpous groups. No distinction was made between individuals germinated from spores or gemmae because we could not distinguish among these two forms of diaspores on the Petri plates. Vegetative fragments (i.e. stem and leaf fragments) deposited on the Petri plates were also considered. To avoid overestimating the number of dispersed diaspores, cryptogam individuals were counted using the number of individual protonema and vegetative fragments instead of the number of stems produced, given that a single protonema can generate several stems in one Petri plate. Because it is difficult to distinguish protonema once the plant is fully developed, monthly photographs of the plates were used to identify individual protonema. We counted the number of protonema germinated from spores/gemmae as well as the number of vegetative fragments in each Petri plate. Species abundance was calculated as the number of individuals for each species per Petri plate. The extant community present on each site was described using the mean percentage cover of each bryophyte species recorded in three 1-m² quadrats. Ferns were considered present if observed in at least one of the three 1-m² quadrats per site.

We compared the composition of the extant community and the diaspore community grown in Petri

plates using Kendall rank correlations (Legendre & Legendre 2012). The individuals identified to genus in the Petri plates were compared with the species from the same genus in the extant community (e.g. *Polytrichum* sp. from Petri plates were compared with *Polytrichum commune* sampled on site). Because there was no linear pattern between the two variables and because some variables included outliers, the Kendall rank correlation was more appropriate than the Pearson product-moment correlation to quantify the association between the abundance of species grown in Petri plates and the percentage cover of species in the extant community. Similarly, to assess whether the abundance of species grown in Petri plates was linked to their presence on site, we used a second Kendall rank correlation on the abundance of the cryptogam species grown in Petri plates and their cover in small mammal trapping grids. We obtained the p value for each Kendall rank correlation coefficient by randomization after 1000 iterations. This approach consisted of permuting the original data for each variable to break the pairwise structure of the data in agreement with the null hypothesis of no correlation and computing the test statistic at each iteration. All analyses were conducted in R 3.0.1 statistical software (R Core Team 2015).

Results

A total of 99 small mammals were trapped and brushed, including southern red-backed voles (*M. gapperi*), American red squirrels (*T. hudsonicus*), deer mice (*Peromyscus maniculatus*), northern flying squirrels (*G. sabrinus*) and common heather voles (*Phenacomys ungava*) (Table 1). Approximately half of the trapped individuals carried viable bryophyte

Table 1. Number of Petri plates incubated with material brushed from five small mammal species trapped in the boreal forest.

Mammal species	Total Petri plates incubated (n)	Petri plates with germination (n)	Petri plates with germination (%)
<i>Glaucomys sabrinus</i> (northern flying squirrel)	11	6	54.5
<i>Tamiasciurus hudsonicus</i> (American red squirrel)	28	14	50.0
<i>Myodes gapperi</i> (red-backed vole)	40	20	50.0
<i>Peromyscus maniculatus</i> (deer mouse)	18	8	44.4
<i>Phenacomys ungava</i> (common heather vole)	2	2	100.0
Total	99	50	50.5

Note: A separate Petri plate was used for each small mammal individual and represents the number of small mammals carrying viable diaspores.

and pteridophyte diaspores that germinated within six months (i.e. 50.5%; Table 1). We counted a total of 172 individuals on the Petri plates, germinated from spores/gemmae or identified as vegetative fragments such as leaf or stem pieces. Six bryophyte species (*Ceratodon purpureus*, *Platygyrium repens*, *P. schreberi*, *Pohlia* sp., *Polytrichum* sp. and *Sphagnum* sp.) and one pteridophyte species (*Dryopteris* cf. *carthusiana*) were recorded, along with 11 unidentifiable protonema (Figure 2 and Table 2). *Sphagna* represented 68.6% of the identified bryophyte protonemata. Three acrocarpous and two pleurocarpous species were encountered consisting of 22.1% and 9.3% of the identified protonemata, respectively. No liverworts developed on the Petri plates.

The number of mammalian species transporting a given bryophyte or fern species ranged from one to all five small mammal species (Table 2). Mammalian species transported from 8 to 64 diaspores from two to five different bryophyte or fern species. We found no association between bryophyte species and mammalian species. However, the one fern species was exclusively found on the fur of American red squirrels.

In the extant community, we found 16 bryophyte taxa: 5 pleurocarpous, 7 acrocarpous, 3 liverworts and *Sphagnum* sp. (Figure 3). This value represents the minimum species richness of the sites; true species richness was probably much higher. Two bryophyte species found in Petri plates were not encountered in the extant community: *C. purpureus* and *P. repens*. *Sphagna* were present in all sites. Various ferns were present as isolated individuals. *Sphagna* dominated both the pool of diaspores collected and the species cover on site. However, there was no association between the species composition of bryophytes and ferns on site and the species composition grown in Petri plates (Kendall tau = 0.05, $p = 0.752$; Figure 3). Similarly, we found no association between the abundance of bryophyte and fern species grown in Petri plates and their cover on site (Kendall tau = 0.69, $p = 0.078$).

Discussion

Southern red-backed voles, American red squirrels and deer mice were the most abundant mammal species in our study sites. We found that these three species along with northern flying squirrels and common heather voles were dispersal agents for true mosses, sphagna and ferns. We also found that small mammals can transport several species of bryophytes, and in some cases a copious amount of viable diaspores of individual bryophyte species. Our results

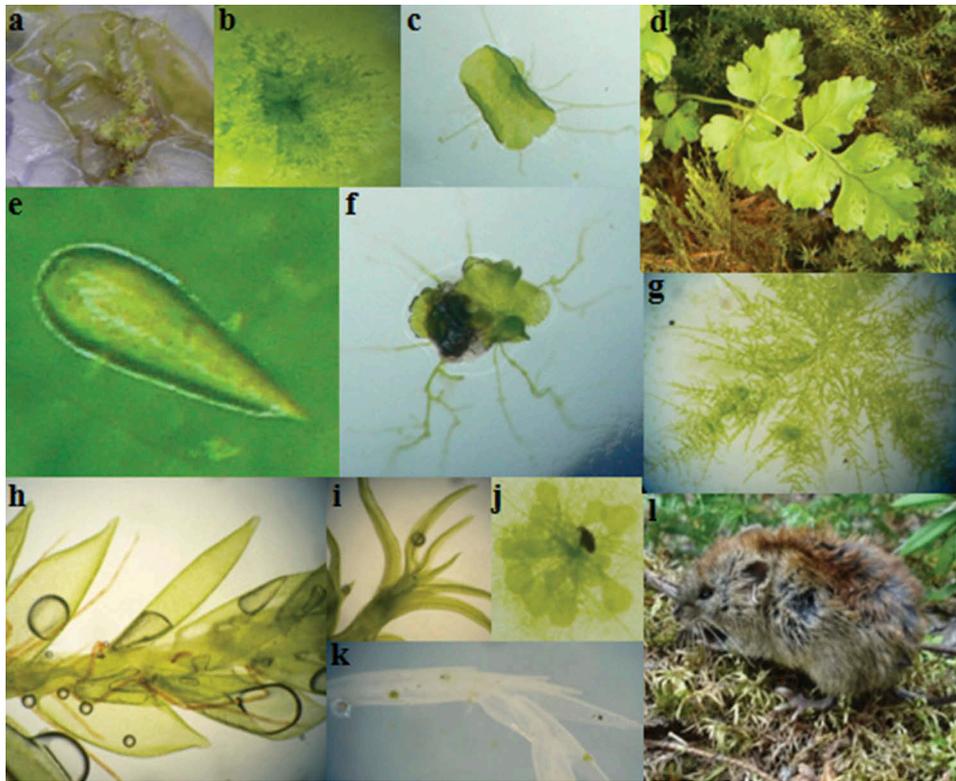


Figure 2. Photography of cryptogam species grown *ex situ* (a–k) and of one southern red-backed vole found *in situ* in *Pleurozium schreberi* (l). Protonemata (a–c, f–g and j); juvenile *Dryopteris cf. carthusiana* (d); leaf and branch of *Sphagnum* sp. (e and k); stem of *P. schreberi* (h); stem of *Polytrichum* sp. (i); southern red-backed vole (*Myodes gapperi*) (l).

Photograph credits: M. Barbé (a–k); D. Fauteux (l).

Table 2. List of bryophyte and fern species brushed from five small mammal species trapped in boreal forests ($n = 99$ individuals trapped).

Bryophyte species	<i>Glaucomys sabrinus</i> (northern flying squirrel)	<i>Tamiasciurus hudsonicus</i> (American red squirrel)	<i>Myodes gapperi</i> (southern red-backed vole)	<i>Peromyscus maniculatus</i> (deer mouse)	<i>Phenacomys ungava</i> (common heather vole)	Sum of diaspores	Number of species as dispersal agents
<i>Ceratodon purpureus</i> ^a	0	1 (1)	0	3 (1)	0	4	2
<i>Platygyrium repens</i> ^b	2 (1)	0	0	0	0	2	1
<i>Pleurozium schreberi</i> ^b	0	10 (2)	1 (1)	0	0	11	2
<i>Pohlia</i> spp. ^a	0	0	11 (1)	8 (2)	0	19	2
<i>Polytrichum</i> spp. ^a	1 (1)	1 (1)	3 (2)	1 (1)	2 (1)	8	5
<i>Sphagnum</i> spp.	6 (5)	19 (10)	18 (11)	47 (4)	6 (1)	96	5
Protonemata unidentified	2 (4)	3 (1)	5 (4)	1 (1)	0	11	4
<i>Dryopteris cf. carthusiana</i> ^c	0	2 (2)	0	0	0	2	1
<i>Sphagnum</i> sp. leaves ^d	2 (2)	4 (1)	6 (5)	4 (2)	0	16	4
Stems/leaves unidentified ^d	0	1 (1)	2 (1)	0	0	3	2
Sum of individuals germinated from spores/gemmae + vegetative fragments	11 + 2	36 + 5	38 + 8	60 + 4	8		
Cryptogam species richness per small mammal species	3	5	4	4	2		

Note: Values refer to the number of bryophyte individuals grown in Petri plates counted as number of protonemata germinated from spores/gemmae or as number of vegetative fragment. Because one Petri plate may contain several protonemata, values in parentheses represent the number of Petri plates in which the cryptogam species were found. In species richness of bryophytes and ferns, protonemata of *Sphagnum* sp. and *Sphagnum* leaves were grouped together and unidentified protonemata and unidentified stems/leaves were omitted because we could not determine whether they were new species or not.

^aacrocarpous. ^bpleurocarpous. ^cFern. ^dreferring to vegetative fragments.

demonstrate that ground-dwelling small mammals are not occasional dispersal agents but instead represent important dispersers of bryophytes and ferns.

Furthermore, ground-dwelling small mammals are in direct contact with the cryptogam layer and this may enhance the dispersal of cryptogams that rarely

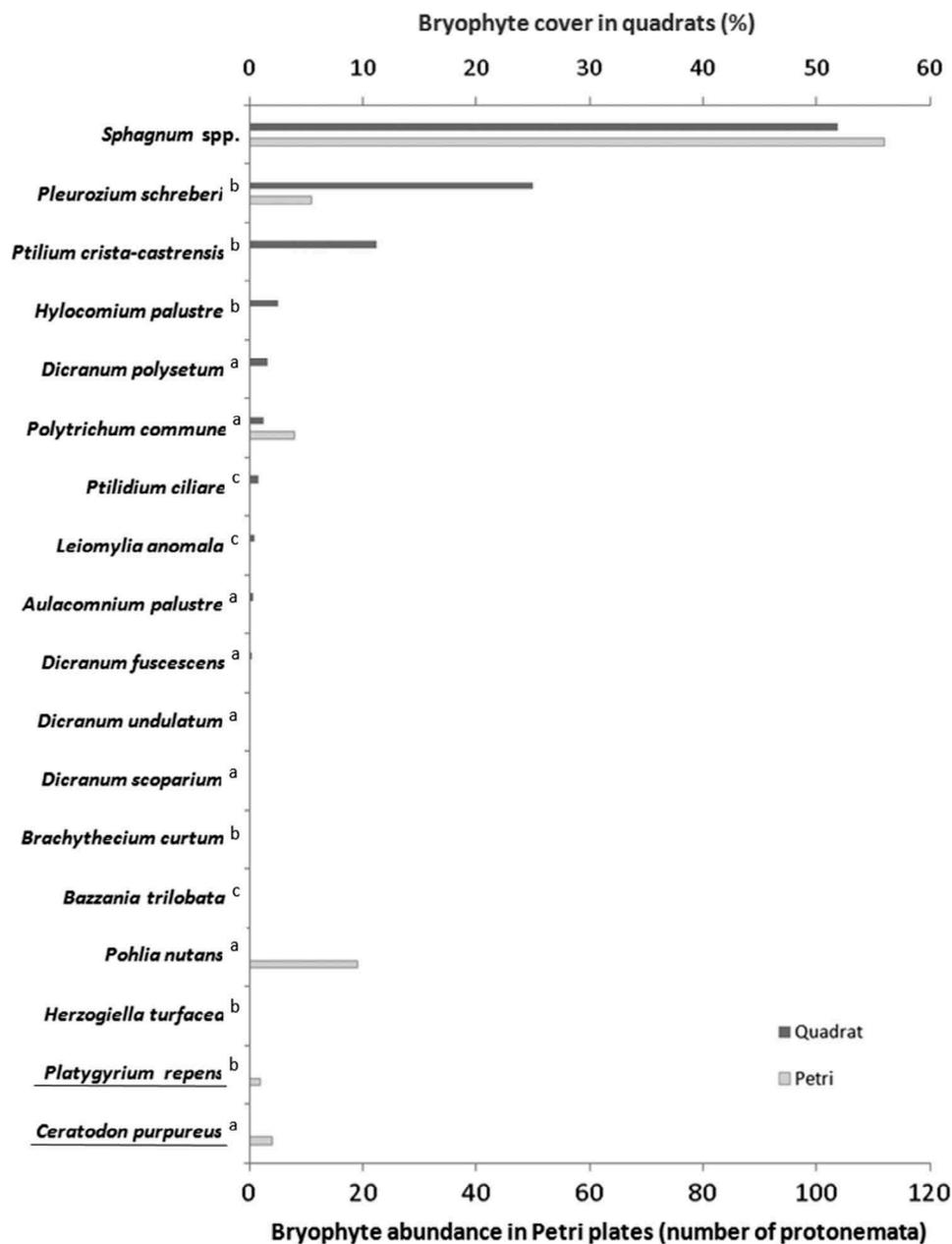


Figure 3. Comparison of bryophyte cover sampled on site and bryophyte abundance in Petri plates.

Note: Dark grey, mean bryophyte cover (%) per 1-m² quadrats; light grey, bryophyte abundance in Petri plates (number of protonemata from spores/gemmae + number of vegetative fragments in the case of *Sphagnum* sp.). Species are ranked by percentage cover on site; species reported on site but with no apparent bars on the graph were present as less than 1% of cover and are noted as trace, except for the underlined species that were not recorded on site. a, acrocarpous; b, pleurocarpous; c, liverwort. The fern *Dryopteris* cf. *carthusiana* is not displayed on the graph because only the presence/absence of fern was recorded on site without consideration of the percentage cover.

produce spores or that are poorly dispersed by the wind.

Mammalian species transported a fraction of species from the pool of bryophyte genera available on sites. Keeping in mind that some of the taxa which germinated were not identified to species due to germinating constraints, the pool of species found in the Petri plates only represented 20% of the species encountered on site. This represents less than half of what was found by

Pauliuk et al. (2011) who collected 40% of the bryophytes species found in European dry grassland ecosystems on large mammals. One factor explaining the low percentage transported may be that none of the species collected are known to have developed features on their diaspores to actively rely on zoochory for dispersal (e.g. spore ornamentation, colourful spores and sticky or odorous secretion to attract animal species; Demidova & Filin 1994; Ignatov & Ignatova 2001;

Rudolphi 2009). Alternatively, if the main agent transported was spores, species phenology may have impacted our results, because not all cryptogam species produced dispersal agents during our trapping sessions. For instance, the over-abundance of sphagna diaspores may be explained by the coincidence of diaspore release and our experiment (Sundberg & Rydin 2002).

In contrast, two species germinated in the Petri plates that were not found in the extant community, namely *C. purpureus* and *P. repens*. These species may have become attached to the fur of the small mammals when they dig in the moss layer and mineral soil searching for food such as seeds and insects (Merritt 1981). This activity may result in some spores present in the soil propagule bank becoming attached to their fur.

The only species of fern transported by a small mammal, *D. cf. carthusiana*, is common in the boreal forest and produces large amounts of spores easily dispersed by wind (Rünk et al. 2012). However, ferns also reproduce by vegetative fragments and alternative diaspores (cf., Boch et al. 2013), which may be brushed off by passing animals. In the present study, American red squirrels are the largest species trapped on our study sites and the only one that carried fern spores. Despite this, we found no apparent exclusive association between cryptogams and small mammals, which can possibly be explained by the low number of individuals trapped for some mammalian species.

Small mammal transport offers two main advantages over wind transport. First, because small mammals and bryophytes share the same types of microhabitats (Mills & Macdonald 2004; Löhmus et al. 2007; Fauteux et al. 2012), small mammals offer oriented dispersal of the diaspores over the landscape. In contrast, during wind dispersal all diaspores are randomly deposited in microhabitats up to several kilometres away during wind dispersal (van Zanten & Gradstein 1988; Lönnell 2011). Secondly, ground-dwelling small mammals can transport species that are not efficient at wind dispersal, due to either low sporophyte production or sporophyte morphology. Ground-dwelling small mammals can transport cryptogam diaspores within their home range (from several metres for deer mice, up to 3.5 km for red squirrels; Wells-Gosling & Heaney 1984; Larsen & Boutin 1994, 1995; Bowman et al. 2002). Cryptogams could also be transported beyond small mammal home ranges during mammalian species dispersal and establishment of new home ranges. As a possible example, we brushed one individual that was carrying *C. purpureus* 80 m away from the closest *C. purpureus* colony found in a concurrent study performed on the same study sites (Barbé et al. 2016).

We showed that ground-dwelling small mammals disperse bryophytes and ferns. However, additional species could be identified. Indeed, some species do not germinate on the agar substrate and others may have germinated after six months. Yet a concomitant study performed with the same protocol yielded the germination of 46 bryophyte species (Barbé et al. 2016), so we argue that the reduced pool of species from this study is not due to the germination protocol. The composition of the bryophyte aerial propagule rain will differ among seasons with species phenology (Stark 2002; Hock et al. 2004; Ross-Davis & Frego 2004). Moreover, weather conditions such as relative humidity, night temperature and rainfall might also have influenced cryptogam phenology via spore release (Glime 2014; Johansson et al. 2015), small mammal activity (Wróbel & Bogdziewicz 2015) and diaspore adherence to fur. In addition, other constraints associated with the sampling methods could have affected the results, such as the use of cotton balls for the small mammal trapping in which diaspores might have been deposited during the many hours spent by the animals in the traps. In the future, we recommend also collecting the cotton balls provided in the traps. Finally, it may be important to consider the effectiveness of toothbrushes at removing diaspores that are electrostatically charged. Alternative collection methods on the fur might yield different species, and this topic could be explored in future studies.

To our knowledge, we provide the first direct evidence of epizoochory involving bryophytes and ferns and ground-dwelling small mammals in boreal forest ecosystems. The daily interaction between small mammals and the cryptogam layer could contribute to the directed transport of bryophyte and fern diaspores over medium distances and towards suitable substrates. Persistence of bryophyte and fern metapopulations depends on dispersal across the forest matrix and small mammals are identified as “mobile link organisms” (*sensu* Couvreur et al. 2004) that may participate in connecting fragmented bryophyte and fern populations. Our results open the door for a timely revision of bryophyte and fern dispersal mechanisms, extending the notion of epizoochory by ground-dwelling small mammals to other cryptogams such as horsetail, lichen or liverwort species.

Acknowledgements

The authors thank Pierre Martineau for confirming fern identifications, and Dominique Fauteux for lending photographs of small mammals. The authors thank all of the field

and laboratory assistants who provided logistical support, and helped in collecting the samples and growing the bryophytes.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The work was supported by Fonds de Recherche du Québec–Nature et Technologies (FRQNT) [grant 2013-FM-170582]; Natural Sciences and Engineering Research Council of Canada (NSERC) [NSERC CRD 428686-11 Bergeron].

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