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Coexistence on divided habitats: mosses in the family Splachnaceae

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Mosses in the family Splachnaceae grow primarily on dung and have spores that are dispersed to dung by Diptera. Mechanisms of coexistence were examined at local, regional and continental scales in four species of Splachnaceae, two species in the genus *Tetraplodon and two species* in the genus *Splachnum*. On the local scale, few mechanisms appear to promote the coexistence of Splachnaceae on a dropping. Competition between mosses is strong and individual droppings tend to be occupied by a single species. On the regional scale, dispersal may promote habitat separation between the genera while coexistence in *Splachnum* species appears to be influenced by a tradeoff between dispersal and competitive ability. Coexistence in *Tetraplodon* species is facilitated by temporal separation of sporophyte production. Resource fluctuations may also promote the coexistence of Splachnaceae species. The ranges of the species studied overlap extensively and there is no evidence that large scale continental processes such as climate influence the occurrence of these species.

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1. Introduction

The divided nature of the environment can have significant effects on species interactions and coexistence within communities (Elton 1949; Andrewartha & Birch 1954; Huffaker 1958). To examine possible mechanisms of coexistence of potentially competing species on divided resources, the coexistence of four species of mosses in the family Splachnaceae has been examined. These mosses grow on dung and have their spores dispersed to dung by Diptera (flies).

In this study, mechanisms of coexistence in divided habitats are examined at three spatial scales in boreal Splachnaceae communities: 1) the local scale; 2) the regional scale; and 3) the continental scale. The local scale is concerned with the distribution of and interactions between species on individual droppings (< 200 cm^2). Direct interactions, such as intra and interspecific competition for space and mating occur at the local scale. Individuals of the same species on a single dropping will be referred to as populations, in the sense of mating populations. The regional scale covers the distribution of and interactions between species across small geographic areas such as several peatlands and associated areas of dry upland forest (1–2 ha). The area encompassed by the regional scale is approximately the area from which spores from different populations are likely to disperse to the same fresh droppings. This area is a function of the dispersal characteristics of the flies that transport the spores of Splachnaceae. The continental scale is the distribution of species across the North American continent. Large scale climatic and other biogeographic factors influencing the distribution of Splachnaceae occur at the continental scale. Since the choice of scale at which communities are examined can influence interpretations of the processes structuring communities (Wiens et al. 1986; Addicott et al. 1987), I have chosen to examine this system at all three levels.

Coexistence of species that use similar resources can be promoted on a local scale through a variety of mechanisms including dispersal and the influence of habitat and resource heterogeneity. Dispersal can promote coexistence on a local scale through priority effects. An inferior competitor may gain a competitive advantage should its propagules have priority of access to resources (Slatkin 1974). Priority of access to a dropping through more efficient spore dispersal by flies may allow a poor Splachnaceae competitor to gain access to some or all of the dung and to successfully reproduce on that dropping. Differences in the number of propagules dispersed to resources may also allow species using similar resources to coexist. A Splachnaceae species that is inferior competitively may attract fly species that disperse more of its spores to a dropping than those of a competitively superior species, thereby allowing the inferior competitor to have access to some or all of the dung in a dropping.

Differential sensitivity of species to habitat and resource heterogeneity can also promote the coexistence of species on a local scale. The location or type of resource may influence the relative abilities of species to compete for that resource. The location of a dropping in upland forests or in peatlands or the differences between herbivore and carnivore dung, for example, may have an influence on the relative competitive abilities of Splachnaceae species competing for space and resources on that dropping.

Dispersal and resource or habitat partitioning can also influence the coexistence of species using similar resources on a regional scale. Dispersal can promote the coexistence of species on a regional scale if there is a tradeoff between competitive and dispersal ability (Skellam 1951; Hutchinson 1975; Hanski & Ranta 1983). If there is intense competition among Splachnaceae on dung, coexistence could be promoted if the poorer competitors produce more spores and/or attract more or better flies to disperse their spores. If resources are suitable for colonization for only a short period, this further accentuates the importance of dispersal ability. Dispersal such that the propagules of different species are independently aggregated on apparently identical resources is also a mechanism by which dispersal can promote coexistence on a regional scale (Atkinson & Shorrocks 1981, Hanski 1981, Ives this issue).

Species can coexist on a regional scale by partitioning similar resources based upon their location in the environment (Whittaker 1972) or on a seasonal basis. Habitat differences in boreal forests such as those between acidic bogs and basic fens, upland aspen and pine forests, hummocks and hollows or areas of open and closed canopy may influence Splachnaceae access to dung or growth on dung. Species may be sensitive to these and other habitat differences and these habitat differences can create 'safe sites' that act as refuges for potentially competing species (Comins & Noble 1985).

Regional resource fluctuations combined with a tradeoff between competitive ability and long-distance dispersal ability may also promote the coexistence of species that use similar resources. Changes in the location and size of large mammal populations will result in changes in the amount of dung available for Splachnaceae colonization. These changes may result in the regional extinction of Splachnaceae populations, thereby allowing species that are better dispersers to recolonize areas of regional extinction. A tradeoff between long-distance dispersal ability and local competitive ability would allow weaker Splachnaceae competitors to persist.

The ranges of many species that use the same resources do not overlap on a continental scale. Such continental segregation may be a function of climate or other biogeographic barriers. Heterogeneity on a continental scale may, therefore, be important in promoting continental diversity of species that use the same resources. The restriction of different Splachnaceae species to largely non-overlapping ranges would suggest that the influence of continental heterogeneity is important in promoting diversity in these moss communities.

In this paper, I will first discuss the natural history of Splachnaceae in central Alberta, then I will examine the mechanisms that may influence Splachnaceae coexistence at the local, regional and continental scales. Experiments examining the influence of the interaction between dispersal and competition on the regional scale will be emphasized.

2. The system

Coexistence has been examined in four species of boreal Splachnaceae: *Tetraplodon angustatus* Hedw. B.S.G., *T. mnioides* Hedw. B.S.G., *Splachnum ampullaceum* Hedw. and *S. luteum* Hedw. These four species coexist at a regional scale at my study site, near Ft. Assiniboine, Alberta, thereby allowing examination of interactions both within and between genera. Sporophyte morphological specializations associated with attracting flies also differ between each of these species suggesting the possibility that the different moss species could attract different fly species and therefore may differ in dispersal ability.

Tetraplodon grow primarily in dry habitats on raised areas within peatlands or on the upland forest

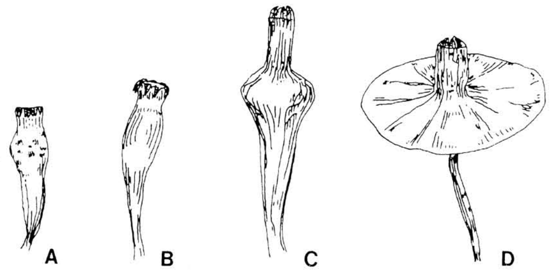

Fig. 1. The apophysis of A) *T. angustatus* (× 7), B) *T. mnioides* (× 8), C) *S. ampullaceum* (× 7) and D) *S. luteum* (× 6).

floor, whereas *Splachnum* grow primarily in moister habitats within peatlands. In each genus two species can be found growing together on a single dropping, and where moist and dry habitats intergrade the two genera can also be found growing together. However, both within and between genera, the coexistence of different Splachnaceae species on the same dropping is generally rare.

Splachnum and *Tetraplodon* often grow on different dung types and this may be related to the different habitats in which they grow. *Splachnum* are most frequently found growing on herbivore dung (primarily summer moose dung) that occurs most frequently in wet habitats. *Tetraplodon* are most frequently found growing on carnivore and omnivore dung (wolf and coyote, and bear, respectively) that occurs most frequently in dry habitats. However, all boreal Splachnaceae grow on all three dung types as long as the dung is in the appropriate dry or wet habitat for *Tetraplodon* and *Splachnum* respectively.

The sporophytes of boreal Splachnaceae are highly modified and are thought to promote spore dispersal to patches of new dung by flies (Vitt 1981). The setae of boreal Splachnaceae range from being short (< 2 cm) in *T. angustatus* to elongate (10 cm) in *S. luteum*. In all species, the upper part of the seta, the apophysis, is variously swollen (Fig. 1) and brightly colored, and the sporophyte of each species has a strong, characteristic odor (Pyysalo et al. 1978, 1983). The capsule, the spore containing structure, is located above the apophysis. The spores are sticky and the walls of the capsule shrink such that the spores are exuded from the capsule and sit above the apophysis in a single sticky clump. Because the spores are dispersed by animals, it is possible to examine and compare spore dispersal in different species of mosses.

Boreal Splachnaceae are fast growing, occupying the entire surface of a dropping within one or two summers, and reproducing within two or three years. No other mosses or vascular plants colonize these habitats as quickly as Splachnaceae, and Splachnaceae have no herbivores. Therefore, interactions between the different Splachnaceae species on a dung patch are direct.

A single moss spore can produce thousands of gametophytes; therefore, few spores are needed to produce enough gametophyte to cover a single dropping. In laboratory experiments examining growth in *S. ampullaceum*, dung placed in 5 petri dishes (63.5 cm^2) and inoculated with ten spores per sample produced enough gametophyte to cover the dung in two months. The growth rate was faster in similar treatments with greater numbers of spores. These observations indicate the great vegetative growth potential in Splachnaceae.

Of the four species of Splachnaceae studied, all except *T. angustatas* produce mature sporophytes throughout the summer. *T. angustatus* produces sporophytes in the early spring, generally just after the trees begin to leaf out. Each population of *T. mnioides*, *S. ampullaceum* and *S. luteum* on the same dropping produces mature sporophytes synchronously. However, at the regional scale, different populations of these species mature at different times throughout the summer.

3. Patterns of spatial distribution

Coexistence in Splachnaceae communities will be considered on a local, regional and continental scale. On a local scale, I shall examine evidence from the field and from herbaria specimens that Splachnaceae often do not coexist on the same dropping. The influence of competition, priority effects and resource or habitat specialization on local coexistence will be assessed. The coexistence of Splachnaceae species on a regional scale will be considered by examining the influence of a tradeoff between dispersal and competitive ability, a temporal separation of sporophyte production in *Tetraplodon* species, resource and habitat specialization and resource fluctuations. The continental distribution of Splachnaceae will be examined to determine if continental heterogeneity influences Splachnaceae distributions and species diversity.

Table 1. The first column gives the Splachnaceae species combinations encountered in herbaria collections. Column two indicates the number of observed combinations and column three gives the percent of specimens of each Splachnaceae species occurring in the given species combination.

Moss species combination	Number	Percent of specimens
S. ampullaceum / S. sphaericum	13	3.24 / 2.35
S. ampullaceum / S. rubrum	2	0.50 / 2.80
S. ampullaceum / S. luteum	5	1.25 / 2.49
S. rubrum / S. luteum	13	18.3 / 6.47
S. sphaericum / S. rubrum	3	0.54 / 4.23
S. sphaericum / S. luteum	127	20.0 / 60.2
T. angustatus / T. mnioides	50	6.75 / 2.25
T. mnioides / S. ampullaceum	1	0.05 / 0.25
T. mnioides / S. sphaericum	5	0.22 / 0.90
T. mnioides / S. luteum	1	0.05 / 0.50
S. ampullaceum / S. rubrum / S. luteum	1	0.25 / 1.41 / 0.54
S. luteum / S. rubrum / S. sphaericum	3	1.49 / 4.23 / 0.54

Table 2. Repeated measures analysis of variance comparing the area occupied by gametophyte in single species dry and wet treatments in a laboratory growth experiment. The upper part of each ANOVA table contains the test for the between-groups (whole-plot) effects. This includes a test for the grand mean and a test of the equality of means between groups. The lower part of each table presents the analysis of the within factor (R) and the interaction of the trial and grouping factors (RG). * = P < 0.001.

Source	Sum of squares	Degrees of freedom	Mean square	*F*
Dry				
Mean	99220.8	1	99220.8	709.7 *
Group	6871.3	3	2290.4	16.4 *
Error	2097.1	15	139.8	
R	44385.4	3	14795.1	231.2 *
RG	5410.2	9	601.1	9.4 *
Error	2880.0	45	64.0	
Wet				
Mean	122786.2	1	122786.2	596.1 *
Group	8034.2	3	2678.1	13.0 *
Error	3295.8	16	206.0	
R	32447.0	3	10815.7	96.3 *
RG	2659.4	9	295.5	2.6
Error	5389.0	48	112.3	

3.1. Local scale

Field observations in central Alberta and a survey of over 5000 herbaria specimens of North American Splachnaceae suggest that individual droppings tend to be dominated by a single species of Splachnaceae. In a survey of the North American distributions of five species of boreal and arctic Splachnum and three species of boreal and arctic Tetraplodon, Marino (1988) found that, with the exception of species combination *S. luteum* and *S. sphaericum*, no species combination occurred frequently in the herbaria collections (Table 1). The fact that the *S. luteum* and *S. sphaericum* mixed species combination occurred relatively frequently in the collections suggests that mixed species specimens were not discriminated against by collectors. The reason for the high frequency of co-occurrence of *S. luteum* and *S. sphaericum* is unclear.

The lack of coexistence on single droppings may be a result of processes influencing Splachnaceae distributions on a regional or continental scale. The continental distribution of the four Splachnaceae species studied overlap extensively in North America (Marino 1988). Therefore, it appears that Splachnaceae distributions at the continental scale do not explain the lack of Splachnaceae co-occurrence on droppings. The regional distribution of Splachnaceae species is difficult to quantify since it is impossible to extensively search large areas of forest to determine species abundance. However, field observations in central Alberta suggest that the regional distribution of Splachnaceae is likely to influence the distributions of species on single droppings. Splachnaceae species appear to be distributed in a mosaic pattern such that dry habitats are often dominated by one *Tetraplodon* species and wet habitats by one *Splachnum* species. In areas where several Splachnaceae species are found growing together, individual droppings appear often to be dominated by one species of Splachnaceae.

The relative growth rates of Splachnaceae differ and there is a well defined competitive hierarchy. Relative growth rates and competitive relationships between the species in wet and dry conditions were examined in a laboratory experiment in which moose dung was inoculated with the spores of *T. angustatus*, *T. mnioides*, *S. ampullaceum* and *S. luteum* in single and mixed species treatments (Marino, unpubl.). Experiments examining relative growth rates of the mosses indicate that they differed in both the wet (Table 2a) and dry laboratory treatments (Table 2b).

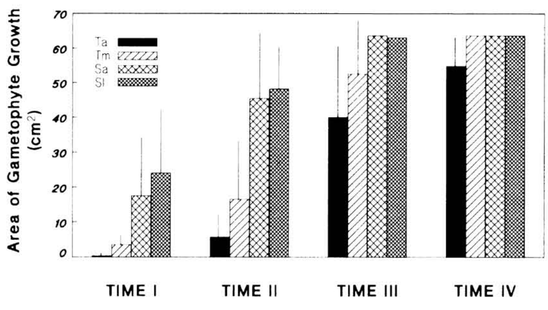

Fig. 2. Area covered by gametophyte growth in the wet treatment of the laboratory growth experiment comparing *T. angustatus* (Ta), *T. mnioides* (Tm), *S. ampullaceum* (Sa) and *S. luteum* (Sl) at four time periods (September, December, February and May). The maximum possible area is 63.5 cm^2. Bars represent standard errors.

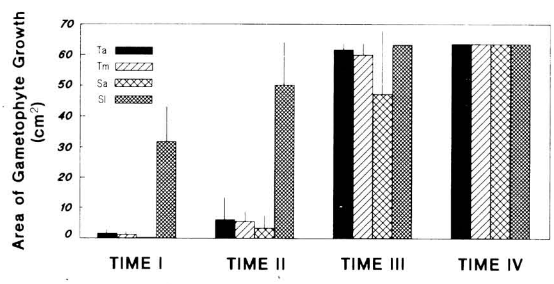

Fig. 3. Area covered by gametophyte growth in the dry treatment of the laboratory growth experiment comparing *T. angustatus* (Ta), *T. mnioides* (Tm), *S. ampullaceum* (Sa) and *S. luteum* (Sl) at four time periods (September, December, February and May). The maximum possible area is 63.5 cm^2. Bars represent standard errors.

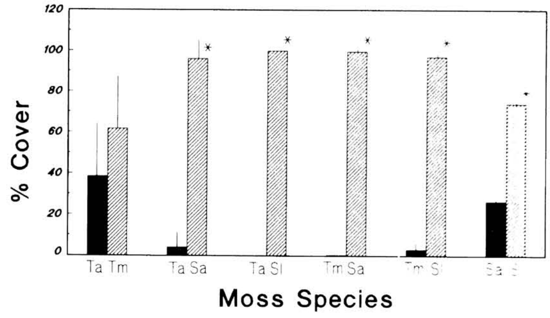

Fig. 4. Percent cover of each species in two species mixtures in the wet treatment of the laboratory growth experiment comparing all two species combinations of *T. angustatus* (Ta), *T. mnioides* (Tm), *S. ampullaceum* (Sa) and *S. luteum* (Sl). Bars represent standard errors. * = indicates a significant difference in the number of gametophytes produced ($P<0.05$).

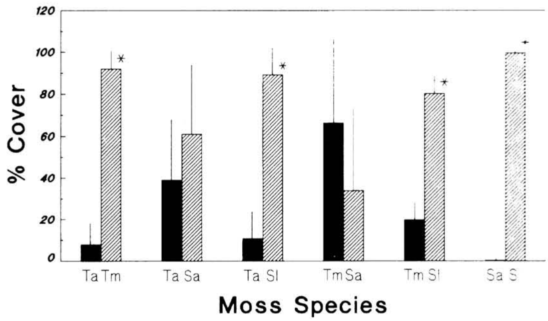

Fig. 5. Percent cover of each species in two species mixtures in the dry treatment of the laboratory growth experiment comparing all two species combinations of *T. angustatus* (Ta), *T. mnioides* (Tm), *S. ampullaceum* (Sa) and *S. luteum* (Sl). Bars represent standard errors. * = indicates a significant difference in the number of gametophytes produced ($P<0.05$).

Both *Splachnum* species grew relatively more quickly than did the two *Tetraplodon* species in the wet treatment (Fig. 2). *S. luteum* grew relatively more quickly than did the other three species in the dry treatment (Fig. 3).

In both the wet and dry treatments of the mixed species competition experiment species differed in relative competitive ability. In the wet treatment, *S. luteum* produced significantly more gametophyte when grown in combination with *S. ampullaceum*, *T. angustatus* and *T. mnioides*. *S. ampullaceum* produced significantly more gametophyte when grown in combination with *T. angustatus* and *T. mnioides*, but the two *Tetraplodon* species did not differ in gametophyte production (Fig. 4). In the dry treatment, *S. luteum* produced significantly more gametophyte when grown in combination with *S. ampullaceum*, *T. angustatus* and *T. mnioides*. *T. mnioides* produced significantly more gametophyte when grown in combination with *T. angustatus*, but there were no significant differences between the number of gametophytes produced between *S. ampullaceum* and *T. angustatus* and *S. ampullaceum* and *T. mnioides* (Fig. 5).

That *Splachnum* grow more quickly than *Tetraplodon* under wet conditions is not surprising considering that *Splachnum* grow on a relatively more ephemeral resource than do *Tetraplodon*. However, the ability of both *Splachnum* species to grow well under dry conditions, and in the case of *S. luteum* to grow more quickly than *Tetraplodon*, is surprising in that *Splachnum* rarely occur in dry habitats. This suggests that both *Splachnum* species are able to survive drying. However, it appears that as habitats become drier the competitive advantage of *Splachnum* species over *Tetraplodon* species decreases.

Although competitive relationships appear to be well defined several factors have not been considered in the laboratory experiment that may influence competitive relationships in the field. The effect of the habitat on the chemical composition of dung and dung type (e.g. carnivore vs omnivore) may also have an influence on competitive interactions, particularly between the genera. Field and laboratory experiments have been conducted to examine the influence of these factors on competitive relationships, and it appears that habitat has a strong influence on the chemical composition of dung but that dung type has little effect on competitive hierarchies (Marino, unpubl.). The influence of priority of access to a dropping has not been examined in this study. However, the period of time in which a dropping attracts most flies is short (1–2 days), and fewer than 1% of flies carrying spores were trapped on dung older than 24 hours. Therefore, the spores of different species are likely to reach a dropping at the same time.

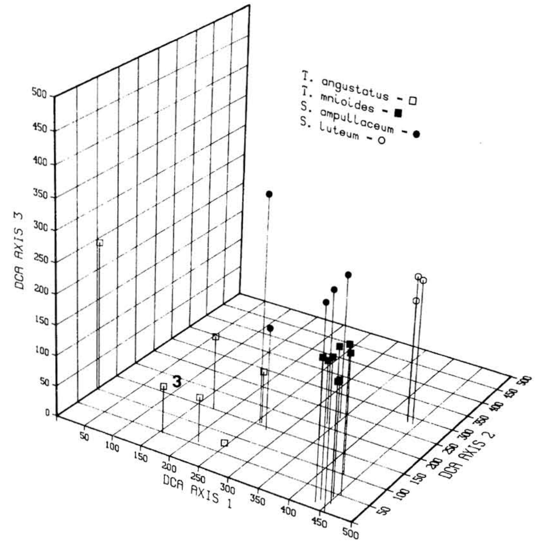

Fig. 6. Detrended correspondence analysis (DECORANA) results comparing the amount of overlap between the fly faunas associated with *T. angustatus*, *T. mnioides*, *S. ampullaceum*, and *S. luteum*. DECORANA is a hierarchical ordination technique that organizes data based on both the presence-absence and relative abundance of variables (Gauch 1982). Trapping dates were used as sample replicates for this analysis. Although trapping dates are not true replicates, trapping intervals were short (3 to 12 days) and therefore there is no important influence of season on the fly faunas.

3.2. Regional scale

The relative spore dispersal abilities of *T. angustatus*, *T. mnioides*, *S. ampullaceum* and *S. luteum* were examined in a trapping experiment by determining: 1) whether the fly faunas attracted to the different moss species were similar or different; 2) which species of flies carried spores; 3) whether spore carrying fly species were equally attracted to dung in dry and wet habitats; 4) how many spores were carried on the different fly species; and 5) which species of spores these flies carried.

In this experiment, flies were trapped on *T. angustatus* in mid May 1986, *T. mnioides* in late June/early July 1986, *S. ampullaceum* in late July 1986 and *S. luteum* in early August 1987. Insects were trapped on two populations of each of the four moss species. Each day of trapping, fresh moose dung was placed in adjacent dry and wet habitats 5–10 m from each moss population. These droppings were left in the field for three days with flies being trapped on the droppings in all three days. Insects were trapped on the mosses with a net and each fly was examined for spores. If spores were found they were rinsed off the flies. The number of spores were then estimated with a bacteria counter and later grown on dung in the laboratory to determine what species of moss they were (Marino, unpubl.). The flies trapped on each of the moss species and associated dung mostly carried spores that grew into the same moss species on which the flies were trapped or with which the dung was associated.

Although the four Splachnaceae species attract some of the same fly species, on the whole the fly faunas that the species attract are relatively distinct (Fig. 6). Splachnaceae may attract distinct fly faunas for several reasons including differences in sporophyte morphologies and odors, differences in the habitats in which the two genera grow and, in the case of *T. angustatus*, differences in the timing of sporophyte production.

There appears to be a tradeoff between dispersal and competitive ability in *S. ampullaceum* and *S. lu-*

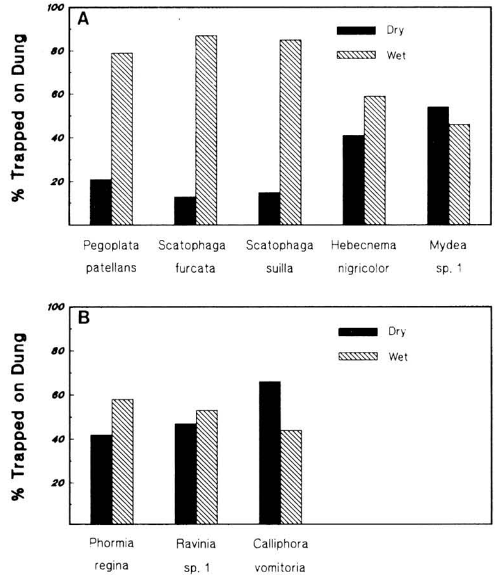

Fig. 7. The percent of individuals of spore carrying fly species that were trapped on associated dung in dry and wet habitats (A, *S. ampullaceum* and B, *S. luteum*). Only fly species in which more than 5 individuals carried spores and more than 20 individuals were trapped on dung are considered.

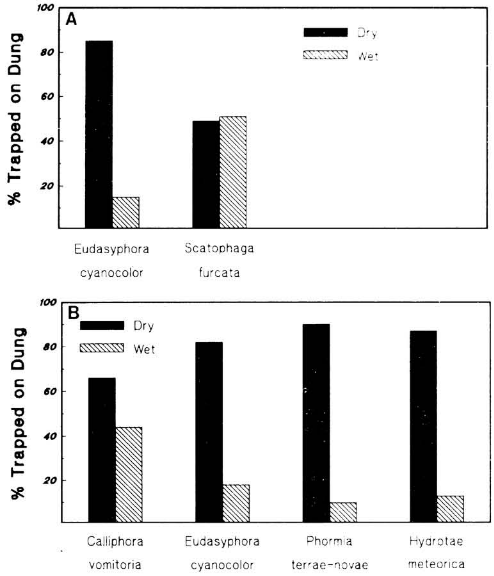

Fig. 8. The percent of individuals of spore carrying fly species that were trapped on associated dung in dry and wet habitats (A, *T. angustatus* and B, *T. mnioides*). Only fly species in which more than 5 individuals carried spores and more than 20 individuals were trapped on dung are considered.

teum. More *S. ampullaceum* spores were carried by flies per hour than were spores of *S. luteum* (80 625/hour and 50 694/hour respectively). Also, of those fly species in which five or more individuals carried spores and more than 20 individuals were also trapped on dung, a greater percentage of individuals carrying *S. ampullaceum* spores were associated with dung in wet habitats than were of flies carrying *S. luteum* spores (Fig 7a and 7b). Therefore, it appears that more spores of *S. ampullaceum*, the weaker competitor, are dispersed to dung in wet habitats than are spores of *S. luteum*.

There appears to be no tradeoff between dispersal and competitive ability in *T. angustatus* and *T. mnioides*. For both *Tetraplodon* species the average number of spores carried on flies per hour are similar (51 118/hour for *T. angustatus* and 53 423/hour for *T. mnioides*). Also for both *Tetraplodon* species, of those fly species in which five or more individuals carried spores and more than 20 individuals were trapped on dung, most fly individuals carrying spores were associated with dung in dry habitats (Fig 8a and 8b). Therefore, there is no evidence that the weaker competitor, *T. angustatus*, has a dispersal advantage over the superior competitor, *T. mnioides*.

The difference in the timing of spore production between *T. angustatus* and *T. mnioides* may be important in promoting the coexistence of these two species. This would be true if flies that visit each of these moss species visit mainly fresh dung. This was found to be the case: fewer than 1% of flies carrying spores were trapped on dung older than 24 hours. In an experiment at a site where both *T. angustatus* and *T. mnioides* are equally abundant, dung placed into the field in May, when *T. angustatus* matured, was only occupied by *T. angustatus,* and dung placed into the field in June, when *T. mnioides* matured, was mainly occupied by *T. mnioides* (Marino, unpubl.). Both the May and June droppings were left in the field throughout the summer.

Dispersal of *Tetraplodon* spores mainly within dry habitats may help to promote the habitat differences that exist between the two genera. This hypothesis however makes the yet untested assumption that the relative densities of spores of different species at droppings influence the outcome of interspecific competition.

Within regional areas, the hypothesis that different Splachnaceae species may occupy 'safe sites' from which they colonize marginal habitats is not a likely mechanism promoting coexistence within genera. Splachnaceae grow in a wide variety of microhabitats; all *Splachnum* species, for example, can be found growing in habitats ranging from bogs to rich fens, habitats in which the bryophytic flora otherwise changes completely. *T. angustatus* and *T. mnioides* are found growing at the same sites in upland habitats as diverse as northern Appalachian montane forests and the dry *Pinus banksiana* forests of central Canada.

It is unclear whether 'safe sites' influence coexistence between Splachnaceae genera. Under field conditions, *Tetraplodon* and *Splachnum* tend to grow in different habitats. However, both laboratory and field experiments have shown that *Tetraplodon* species are capable of growing under wet conditions and *Splachnum* are capable of growing under dry conditions (Marino, unpubl.). It is more likely that the observed habitat differences between the two genera reflect the influence of a combination of factors including: 1) dispersal; 2) resource specialization on dung type (Marino, unpubl.); 3) resource specialization based on chemical differences between dung in dry vs. wet habitats as caused by differential leaching (Marino, unpubl.); and 4) differences between the genera in tolerance to desication.

In central Alberta, regional areas are often dominated by one species of Tetraplodon in dry habitats and one species of *Splachnum* in wet habitats. This apparent checkerboard pattern of Splachnaceae distribution may be a result of regional extinction and recolonization events. Fluctuations in resource levels (dung) may result in the regional extinction of Splachnaceae populations. Two years without fresh droppings would be sufficient to drive regional populations of *Splachnum* to extinction, while a longer period of time would be necessary to cause the extinction of local populations of the less ephemeral *Tetraplodon* species.

The regional abundance of Splachnaceae has been extensively surveyed at the Ft. Assiniboine study site. Within a 20 km radius are areas of upland forest in which only *T. angustatus* is found growing and other areas of upland forest where both *T. angustatus* and *T. mnioides* are equally abundant. Within the same study area are peatlands where *S. ampullaceum* accounts for over 95% of the *Splachnum* and other areas where *S. ampullaceum* and *S. luteum* are equally abundant.

There is also evidence of resource fluctuations. In 1983, at the Alberta study site, more than 300 populations of *Splachnum* were found. In 1985, a slightly larger area at the same site was searched with greater effort and fewer than 20 populations of *Splachnum* were found. This fluctuation in the number of local populations of *Splachnum* within a regional population is a direct result of resource fluctuation since all summer moose dung was colonized by Splachnaceae at the study site. Large fluctuations in the numbers of large mammals, such as moose, are not necessary to cause large fluctuations in the supply of dung. A single moose produces more than five droppings a day; therefore, minor changes in moose abundance in regional areas will have a dramatic influence on the amount of dung available for Splachnaceae colonization.

Although the long distance dispersal of spores between different regions has not been examined, the fact that the different moss species attract different fly species suggests that the moss species may differ in their long-distance dispersal abilities.The combination of resource fluctuations and a possible tradeoff in long-distance dispersal ability and competitive abilities may, therefore, promote Splachnaceae coexistence on a regional scale.

3.3. Continental scale

The four species of Splachnaceae examined all have widespread North American distributions from the east to the west coast of the continent with considerable overlap in their ranges (Marino 1988). Therefore, there is no evidence that dung is partitioned between Splachnaceae species because of large scale continental factors such as climate or other biogeographic barriers. The central Alberta location of this study is well within the distributional ranges of these species. Central Alberta, therefore, is not a marginal area for any of the species studied and all species are likely to be equally well adapted to environmental conditions found in this area.

4. Summary

Species interactions in communities can be examined at several spatial scales (Wiens et al. 1986; Addicott et al. 1987). In Splachnaceae communities, processes influencing the coexistence of species growing on divided habitats have been examined at local, regional and continental scales.

The ability of Splachnaceae species to coexist on a dropping may be influenced by competition, priority effects and resource or habitat specialization. Evidence from the field and from herbaria specimens suggest that single droppings tend to be occupied by a single Splachnaceae species. This may partly be a result of strong competition between species for space on a dropping. Priority effects do not appear to play an important role in promoting coexistence on a dropping since few flies are attracted to dung older than 24 hours and therefore few spores are likely to be dispersed to dung older than 24 hours. The location of a dropping in the environment may influence competitive interactions.

The ability of Splachnaceae species to coexist regionally may be influenced by a tradeoff between dispersal and competitive ability, a temporal separation of sporophyte production, resource and habitat specializations and resource fluctuations. A tradeoff between dispersal and competitive ability exists between *Splachnum* species but not between *Tetraplodon* species. A temporal separation of sporophyte production appears to be important in promoting the coexistence of *T. angustatus* and *T. mnioides*. Between genera, limited dispersal between habitats may help to promote habitat differences. Within genera, dung does not appear to be partitioned by Splachnaceae species based upon its location in the environment. In central Alberta fluctuations in the regional abundance of droppings combined with a tradeoff in Splachnaceae long-distance dispersal and competitive abilities may also promote the regional coexistence of Splachnaceae species. The combination of resource fluctuations resulting in regional population extinctions and random recolonization events may also help to explain the apparent mosaic distribution of Splachnaceae in central Alberta.

Splachnaceae do not appear to partition resources on a continental scale. The ranges of the Splachnaceae species studied overlap extensively. Therefore, there is no evidence that dung is partitioned between Splachnaceae species because of heterogeneity at the continental scale.

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