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## Review

# Bryophytes in a changing landscape: The hierarchical effects of habitat fragmentation on ecological and evolutionary processes

Emma J. Pharo<sup>a,\*</sup>, Charles E. Zartman<sup>b</sup>

<sup>a</sup>Geography and Environmental Studies, Private Bag 78, University of Tasmania, Hobart, Tasmania 7005, Australia

<sup>b</sup>Instituto Nacional de Pesquisas da Amazônia (INPA), Departamento de Botânica, Coordenação de Pesquisas em Botânica (CPBO), Avenida André Araújo 2936, Bairro Petrópolis, 69083-000 Manaus, Amazonas, Brazil

## ARTICLE INFO

## Article history:

Received 1 January 2006

Received in revised form

30 May 2006

Accepted 10 October 2006

Available online 18 December 2006

## Keywords:

Bryophyte

Fragmentation

Metapopulation

Dispersal

Forest

Edge

## ABSTRACT

Testing the myriad predictions associated with the community, demographic and genetic impacts of habitat fragmentation remains a high conservation priority. Many bryophyte taxa are ideal model systems for experimentally testing such metapopulation-based and population genetic predictions due to their relatively fast colonisation-extinction rates, high substrate specificity, dominant haploid condition, and diminutive size. Herein, we review the community, demographic and population genetic impacts of habitat fragmentation on bryophytes, highlight the present knowledge gaps, and offer ideas on how experimental studies utilizing bryophytes may be used to address the broader conservation implications associated with fragmented ecosystems. Previous research suggests that dispersal limitation best explains observed patterns of abundance and distribution of bryophytes in some fragmented habitats. However, edge effects influence bryophyte community structure of border habitats especially where abrupt differences in micro-climatic conditions between the matrix and the forest remnant exist, or where the species pool contains members with inherently restricted ecological amplitudes. Existing studies do not agree on the relationship between basic attributes of bryophyte community structure (i.e., species richness and local density), and habitat area and degree of spatial-isolation. Demographic studies are a critical step in structuring conservation strategies, however surprisingly little empirical information exists as to the impacts of habitat fragmentation on plant population dynamics. We propose that bryophytes offer great potential for testing predictions with respect to plant population persistence in spatially-structured landscapes.

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## Contents

- |  |     |
|--|-----|
| 1. Introduction . . . . .  | 316 |
| 2. Community: variable effects on composition, richness, and abundance . . . . . | 316 |

\* Corresponding author: Tel.: +61 3 62262049; fax: +61 3 62262989.

E-mail addresses: [Emma.Pharo@utas.edu.au](mailto:Emma.Pharo@utas.edu.au) (E.J. Pharo), [charles\\_e\\_zartman@hotmail.com](mailto:charles_e_zartman@hotmail.com) (C.E. Zartman).

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doi:10.1016/j.biocon.2006.10.016

2.1. Bryophyte communities and regional factors . . . . .	316
2.2. Bryophyte communities and local factors . . . . .	318
3. Demography: Bryophytes and fragmentation in a metapopulation context . . . . .	318
3.1. Colonisation . . . . .	319
3.2. Extinction . . . . .	319
4. Genetics: integrating evolutionary and ecological processes . . . . .	320
5. Further research . . . . .	321
6. Conclusions . . . . .	322
Acknowledgements . . . . .	322
References . . . . .	322

## 1. Introduction

Bryophytes, represented by the mosses, liverworts and hornworts, entail a grade of nearly 11,000 species which inhabit an astounding diversity of substrates ranging from freshwater sponges in the tropics to caribou dung patches of the arctic tundra. Many bryophytes are ideal for addressing both the ecological and evolutionary impacts of habitat fragmentation due to global ubiquity, fast generation times, substrate specificity, and dominant haploid condition.

Firstly, many bryophyte taxa are characterized by distributions across more than one continent at the generic and familial level: a feature which allows for the unique opportunity of examining habitat fragmentation impacts in disparate geographic areas while minimising the confounding effects of phylogenetic differences among study groups. For example, liverwort taxa documented from far removed regions such as fragmented forests of north-eastern Tasmania (Pharo and Blanks, 2000), and the Brazilian Amazon (Zartman, 2004) exhibit substantial phylogenetic similarities sharing ca. 15% of the same genera.

Secondly, bryophyte tissue is directly exposed to changes in humidity and, does not store or conduct water with anything near the efficiency of vascular plants (Richardson, 1981). This condition, combined with their ability to tolerate long periods of drought, suggests that bryophytes may be utilised to reflect long-term micro climatological changes associated with fragmentation (Hylander, 2005). Understanding long term changes in local climate is a vital pursuit for ecologists given the dual challenges of fragmentation and climate change.

Thirdly, the fast colonisation-extinction rates, high substrate specificity, and high turnover rates of habitat patches for many bryophyte taxa (Snäll et al., 2005; Söderström and Herben, 1997) offers the unique opportunity to quantify population parameters, such as patch colonisation and extinction, within experimentally tractable time periods in order to test basic tenets of metapopulation theory in light of habitat fragmentation (e.g., Zartman and Shaw, 2006). No other group of terrestrial plants offers such a combination of life history features that facilitate disentangling the impacts of fragmentation on both local and regional demographic processes. For example, most tropical deforestation in biologically diverse regions, such as the Amazon Basin, has only occurred within the past 30 years (Skole and Tucker, 1993): a time interval barely sufficient to account for even one generation of most forest interior tropical tree species (Wright et al., 2005). The

temporal discrepancy between tropical tree generation times and the short time interval since habitat isolation precludes a comprehensive assessment of forest fragmentation's effects on most tropical plant taxa. However, due to the fast generation times of tropical epiphyllous bryophyte species (Zartman, 2004), these metapopulations have undergone between 20 and 30 generations in three decades, thus removing the confounding effects of the influence of pre-isolation distributions, and allowing for a more precise evaluation of fragmentation effects on both local growth, dispersal and recruitment dynamics.

Finally, advancements in molecular fingerprinting techniques such as AFLPs (Vos et al., 1995) have demonstrably contributed to the development of the field of conservation biology (Haig, 1998). Bryophytes are especially amenable for evaluating genetic relationships utilising neutral molecular markers due to the dominant haploid phase in their life cycle, which means that there are no confounding effects associated with heterozygosity, as is the case with vascular plants. Despite such an advantage, few bryophyte population genetic studies in the context of habitat fragmentation have been conducted (but see Wyatt et al., 1989; Wilson and Provan, 2003, and Zartman et al., 2006 for exceptions). More studies focusing on the evolutionary consequences of fragmentation on bryophyte populations should provide valuable information on the long term impacts of habitat insularity that can be potentially helpful for developing general conservation priorities for all plant groups.

We have organised this review into three hierarchical components: community, demographic and population genetic level impacts of habitat fragmentation on bryophytes. In each section we address the broader conservation implications of bryophyte research conducted to date. Furthermore, we highlight the present gaps in our knowledge of bryophyte conservation in light of fragmentation impacts, and we offer ideas for how bryophyte research may address these concerns in future research. While suggesting adaptations to current conservation strategies is not the primary focus of this review, we do discuss some of the implications of new evidence for land managers.

## 2. Community: variable effects on composition, richness, and abundance

### 2.1. Bryophyte communities and regional factors

There is much discussion in conservation biology on the extent to which organisms are able to disperse within a fragmented

region. By examining bryophytes, we can investigate a range of dispersal abilities, without the complication of species interactions. Bryophytes rely on wind and water to move diaspores, except for a few cases of invertebrate and bird dispersal (Van Zanten and Pocs, 1981; Marino, 1988). Their simplified dispersal system contrasts with the complex system of most mammals and vascular plants. Recent reviews have highlighted the importance of considering species interactions for mammals and vascular plants in order to understand the causal mechanisms which control species richness in habitat fragments (Fox and Fox, 2000; Murphy and Lovett-Doust, 2004). Since much of the empirical evidence has been based on vascular plant and vertebrate data, increased focus on experimental research utilising bryophytes should provide novel insights into how local (i.e., habitat quality) and regional (i.e., spatial) factors influence plant distributions in a fragmented landscape.

Despite evidence of prolific spore production (Longton and Schuster, 1983; Söderström and Jonsson, 1989; Longton, 1997), as well as examples of widely distributed taxa exhibiting low inter-continental genetic structure (McDaniel and Shaw, 2003), many bryophytes are characterised as dispersal limited at local scales (Hedenäs et al., 2003; Snäll et al., 2003). For example, most experimental studies of diaspore dispersal patterns from known sources are strongly leptokurtic with a majority being deposited within centimetres of the parent sporophyte (Wyatt, 1982; Söderström and Jonsson, 1989; Miles and Longton, 1992).

Furthermore, accumulating evidence from establishment experiments (Sillet et al., 2000; Gunnarsson and Söderström, in review), as well as patch-occupancy distributions (Gu et al., 2001; Dettki et al., 2002; Johansson and Ehrlén, 2003; Zartman and Nascimento, 2006) for both bryophytes and lichens repeatedly point to dispersal limitation to explain species absences from fragmented habitats. For example, Zartman and Nascimento (2006) used abundance-occupancy patterns in fragmented and continuous forests to conclude that reduced dispersal capacity, as opposed to the impacts of altered forest edge micro-climates, is the causal demographic mechanism accounting for the abrupt declines in bryophyte diversity in small (<10-ha) tropical forest fragments. Pharo et al. (2004) also found evidence for lower richness and different species composition in younger fragments (<25 years) compared to contiguous habitats, suggesting that some less well-dispersed species may exhibit greater lag times between colonization events. Furthermore, Snäll et al. (2003) found that older aspen trees do support larger colonies of *Orthotrichum*, concluding that age-related availability as a substrate rather than the larger size of older trees was the key, explanatory factor. Studies on lichen taxa as well have demonstrated that dispersal appears to be a limiting factor even when the isolation events occurred decades prior to sampling (Dettki et al., 2002).

Predicting which bryophyte species are likely to be dispersal limited over short distances (i.e., <100 m) is possible only by reviewing the results of detailed autoecological studies of bryophytes. Species that are expected to be better dispersers in a spatially-structured landscape would include those with small, drought-resistant, non-green diaspores (e.g., *Ceratodon purpureus*) that are launched from the sub-

strate above boundary layer (Van Zanten and Pocs, 1981). Epiphytic genera, such as *Orthotrichum*, are likely to disperse further than species released near ground level (Miles and Longton, 1992; Snäll et al., 2003). On the other hand, species that invest heavily in competitive ability (long-lived, large perennials with larger spores) and are abundant in undisturbed forest may run greater risks of extinction in fragmented landscapes compared with more r-selected, mobile taxa. Effect of diaspore type remains unclear, as species that rely on asexual reproduction have been found to be both less effective (Kimmerer, 1991), and more effective dispersers (Hedenäs et al., 2003) compared with sexually reproducing species.

More realistic models of bryophyte dispersal in fragmented landscape are now possible thanks to a recognition of the importance of the matrix surrounding the fragments. Classifying the landscape into a binary network of suitable and unsuitable patches is being replaced with a more sophisticated grading of habitat. The matrix surrounding the fragments can provide stepping-stones, or even long-term habitat (Murphy and Lovett-Doust, 2004), and quality of the matrix has been found to substantially affect the flora of remnants in simulations of fragmented landscapes (Fahrig, 2001). Under certain circumstances, less remnant habitat may be required for population persistence if the quality of the matrix is high (Fahrig, 2001). A low quality matrix, such as the high contrast matrix of a clearcut, could be expected to be inhabited by ubiquitous, drought-adapted species of little conservation interest (Duncan and Dalton, 1982; Harper et al., 2004). However, the matrix may be significantly softened with suitable habitat, such as isolated trees (Vanderpoorten et al., 2004) or logs (Pharo et al., 2004). There are profound implications of this change in view for conservation strategies and for social attitudes towards what is valuable for biodiversity (Fischer et al., 2005).

The direct interaction between the changed spatial configuration of a landscape and dispersal is not easily quantified. Most studies have investigated fragmentation effects indirectly via correlations of diversity with measures of habitat isolation, time since isolation, and remnant area. The majority of studies have sought to correlate measures of bryophyte diversity with area. No clear pattern has yet emerged as some studies report greater moss diversity in larger remnants, with no effect on liverworts (Pharo et al., 2004) while others demonstrate the opposite pattern (Hylander and Hedderson, 2006). Moen and Jonsson (2003) found a weak positive relationship between epixylic (log-inhabiting) liverwort richness and larger islands (4–6 ha), but considerable variation within the group. Such inconsistent results could possibly result from collinearity between area and local factors. For example, larger remnants (>4 ha) present a larger target for dispersing biota, but they also have greater substrate availability (Gignac and Dale, 2005). The confusion may also be due to variability in the ecological amplitudes of the focal species thus resulting in no clear overall community-level response. For example, Zartman (2003) reported a disproportionate number of “rare” bryophyte species inhabiting leaves in the forest understorey in small fragments (<10 ha in size). However, such “rare” understorey species are actually quite common in the outer branches of canopy trees in lowland Amazonian forests



suggesting that the altered micro-environments caused by forest fragmentation (Kapos, 1989) resulted in niche shifts in the epiphytic bryophyte taxa along the vertical structure of the forest architecture. In this case, xerophilic canopy species began inhabiting the increasingly drier environments of the understorey habitats, most likely due to the increased solar radiation caused by high tree mortality rates in the small (<10 ha) forest fragments (Kapos, 1989; Laurance et al., 2001). Indeed, such complex interactions between fragmentation-induced changes on micro-environments and local distribution patterns of bryophytes remain understudied.

## 2.2. Bryophyte communities and local factors

Local factors strongly regulate bryophyte communities because bryophytes are small, poikilohydric, and responsive to their substratum (Söderström and Herben, 1997; Bates, 2000). While results from bryophyte establishment experiments generally emphasise the role of dispersal in structuring communities, there is little doubt that local habitat and microclimate are also strong controls. Snäll et al. (2003) found that while dispersal distance between aspen trees was important in explaining recent colonisations of *Orthotrichum*, it was not quite as important as the sum of the local effects, with shading being particularly influential. Pharo et al. (2004) also concluded that substrate was a stronger predictor of bryophyte diversity than fragment isolation or area.

Edge effects play a central role in the biology of fragmented populations (Murcia, 1995; Laurance et al., 2002). The abrupt changes in microclimatic conditions, such as increasing temperatures, increased solar radiation due to tree windfalls and, in many cases, decreased ambient humidity (Kapos et al., 1997; Laurance et al., 2001) associated with exposure to the differing conditions of the surrounding matrix impact local growth of bryophytes (Zartman and Shaw, 2006). For example, Hylander (2005) found significantly less growth of two large mosses (*Hylocomium splendens* and *Hylocomiastrum umbratum*) on the more exposed, south-facing edges of forest compared to the sheltered north edge of boreal forest of northern Sweden, reporting even stronger differences between edge (0–4 m) and interior (45–80 m). Furthermore, differences in bryophyte community between fragment edges and forest interior have been attributed to their drier microclimates which experience greater solar radiation (Gignac and Dale, 2005; Hylander, 2005), increase in coarse woody debris due to windfall (Baldwin and Bradfield, 2005), and fertiliser effects influenced from the burned matrix (Harper et al., 2004).

While many studies do report edge communities as compositionally distinct from interior forest, consistent relationships between diversity and edge processes has not been forthcoming. Contrasting results should be expected given the variability of edges in terms of the type of matrix, season, orientation, and physiognomy (Murcia, 1995). Moen and Jonsson (2003) suggested that the response of bryophytes to edge habitats is strongly species-specific and context-dependent. Landscapes with open, high-insolation forests, such as those dominated by *Eucalyptus*, are less likely to show strong edge effects compared to closed, humid forest (Pharo et al., 2004, 2005). In boreal forest fragments of northern Sweden, Moen

and Jonsson (2003) reported slight increases in species richness of epixylic hepatics in larger (~5-ha) boreal forest fragments, but only marginal overall differences in local abundance relative to both fragment edge and size. In lowland Amazonian rainforests, Zartman and Nascimento (2006) conclude that area-effects explain the differences in species abundance between small ( $\leq 10$  ha) and large ( $\geq 100$  ha) reserves better than proximity to edge.

## 3. Demography: Bryophytes and fragmentation in a metapopulation context

A central challenge of conservation biology research is to link the well-documented community-level changes wrought by fragmentation to the demographic processes driving such alterations. Although the scientific literature is saturated with evidence for community-level impacts of habitat fragmentation (Saunders et al., 1991; Laurance and Bierregaard, 1997; Debinski and Holt, 2000; Harrison and Bruna, 1999; Laurance et al., 2002), few studies have targeted the population dynamic processes driving such changes. Plants are no exception to this trend as their slow response times typically preclude them from being selected for experimental investigations (Honnay et al., 2005). Indeed, comprehensively assessing the demographic consequences of fragmentation in vascular plants may require studies carried out on the order of decades or even centuries (Turner et al., 1995): impractical time scales for most research agendas.

The fast growth, precocious reproductive capacity and transient nature of many bryophytes (Herben, 1994; Longton, 1997; Bradfield and Sadler, 2006) are characteristics which contribute to them being recognized as a model taxon for testing predictions generated by population dynamic theory (Jonsson and Söderström, 1988). Such unique life history features of bryophyte taxa offer a wellspring of opportunities for empirically testing, for example, how changes in the spatial-structure of habitat patches influence demographic structure. In particular, bryophytes are recognized as an ideal plant group for empirically testing hypotheses generated from metapopulation theory (reviewed in Söderström and Herben, 1997), as recently illustrated by the work of Snäll et al. (2005), and Zartman and Shaw (2006).

The theory of island biogeography, which describes the demographic control of species richness in spatially-isolated habitats as an equilibrium between extinction and immigration (MacArthur and Wilson, 1967), is the foundation from which metapopulation theory began exploring the dynamics of population persistence in fragmented habitats (Levins, 1969; Hanski and Gilpin, 1997; Hanski and Ovaskainen, 2000). The metapopulation concept, which defines population persistence as a function of regional processes, has contributed enormously to both the theoretical and empirical understanding of fragmentation effects on biodiversity (Ouborg and Eriksson, 2004). Indeed, the fundamental principals of the theory of island biogeography, which were subsequently adopted by metapopulation theory, have generally remained unaltered in the ensuing three decades. In particular, three central assumptions of the metapopulation concept, with regards to fragmentation ecology, are as follows: (1) patch (re-)colonisation is a distant-dependent process

(i.e., colonisation probability decreases with increasing distance from the nearest potential source; (2) extinction probability and habitat area, considered a proxy for population size, are negatively correlated; and (3) local demographic processes, such as growth, are unimportant. The following sub-sections address these metapopulation-based predictions in light of what is presently known regarding bryophyte biology and habitat fragmentation.

### 3.1. Colonisation

Bryophyte colonisation into fragmented habitats may change as a result of two features: (1) reductions in dispersal potential; or (2) alterations to substrate quality. Whereas variation in dispersal potential is primarily controlled by spatial processes (e.g., distance from nearest potential diaspore source), changes in substrate quality are typically the result of physical changes wrought by the processes of fragmentation. Clearly, these two phenomena are not mutually exclusive and many biological factors, typically imposed by phylogenetic constraints such as spore size and fecundity, contribute greatly to the inter-specific variation in the importance of these two controls on colonization.

Nonetheless, studies of both bryophyte and lichen taxa alike typically invoke dispersal limitation as the causal demographic mechanism for reduced population densities in isolated habitats (Sillet et al., 2000; Gu et al., 2001; Dettki et al., 2002; Johansson and Ehrlén, 2003; Snäll et al., 2003; Öckinger et al., 2005; Zartman and Nascimento, 2006). In such cases, patch-occupancy patterns are typically used to infer distant-dependent colonisation processes (Gu et al., 2001; Snäll et al., 2003; Zartman and Nascimento, 2006); however, caution must be taken as such patterns, especially if only gathered at one point in time, are potentially explained by a number of alternative demographic processes. For example, Clinchy et al. (2002) demonstrated that patch-occupancy patterns of pika populations in the American West are as likely to be explained by metapopulation-based processes (i.e., distant-dependent colonisation) as by non-metapopulation processes, such as spatially-correlated extinction events. Confirmation of this mounting indirect evidence for dispersal limitation in bryophytes is desperately needed, and research agendas which directly quantify, for example, patch colonisation-extinction rates will help to identify which demographic parameters are most sensitive to the effects of habitat fragmentation.

For many bryophyte species, changes in immigration and (re-)colonisation in the context of habitat fragmentation may be relatively easily tested through transplant experiments or by altering resident population densities within a given study site (e.g., Krebs, 2001). For example, Zartman and Shaw (2006) provide supporting evidence for dispersal limitation by using transplant experiments of two epiphyll species demonstrating that patch colonization rates decline as the intensity of fragmentation increases. Nonetheless, substrate availability is likely to play a more important role than dispersal limitation in influencing populations of longer-lived substrates (e.g., rock faces) when compared to more ephemeral ones such as those occupied by epiphyllous, epiphytic, and corticolous species. For example, long term demographic

studies on spatially-isolated rock faces, report repeated, long (>1 km) distance dispersal and effective establishment (Bremer and Ott, 1990; Cronberg, 2002; Miller and McDaniel, 2004).

Theoretical exercises have offered various predictions as to how the stability of metapopulations may be affected by habitat fragmentation (Hanski, 1994; Earn et al., 2001; Johst et al., 2002); however some of the inherent assumptions in such models await empirical confirmation. In our view, two of the more immediate questions needing attention relate to the spatio-temporal scale at which bryophyte metapopulations operate: (1) At what spatial scale do reductions in bryophyte patch-occupancy density detectably reduce patch colonisation rates? and (2) Does the relative importance of substrate availability and dispersal limitation to metapopulation persistence change as substrates (e.g., patches) become more ephemeral? To our knowledge, neither of these questions have been empirically addressed with regard to plants and both could be implemented with relative ease through manipulative studies of bryophyte populations in mesoscale (<1 km<sup>2</sup>) experiments.

### 3.2. Extinction

Extinction is a notoriously difficult demographic parameter to estimate in experimentally tractable time periods due, in part, to the typically long generation times of most plant taxa (Turner et al., 1995; Fischer and Stocklin, 1997; Honnay et al., 2005). Furthermore, complications arise in the accuracy of estimating extinction in natural populations when the probability of (re-)detecting the focal species in a given patch is less than 1 (MacKenzie et al., 2003). Such logistical challenges have led most population biologists interested in the demographic consequences of habitat fragmentation to conduct experiments in the laboratory (Burkey, 1997), or in artificially manipulated mesocosms (Gonzalez et al., 1998; Kneitel and Miller, 2003; Rantalainen et al., 2004) utilising invertebrates, protozoa or bacteria as the focal species. However, bryophytes, due to their small size, high colonisation-extinction rates, and habitat specificity are an ideal plant group for quantifying extinction in spatially-structured habitats.

A basic tenet of metapopulation theory, that extinction probability is inversely proportional to population size, has, until recently, never been tested in bryophyte populations. Zartman and Shaw (2006) reported that mean per-generational patch (e.g., leaf) extinction rates for two epiphyllous bryophyte species in tropical forest fragments are unchanged among small ( $\leq 10$  ha), and large ( $\geq 100$  ha) reserves despite the nearly 10-fold difference in local epiphyll population sizes between the reserve classes (Zartman, 2003). In this particular case, no relationship between habitat area, local population density, and bryophyte extinction rates was detected; however, future experimental tests investigating extinction dynamics in the context of habitat fragmentation should be implemented over relatively longer (e.g., >3 year) time-scales.

Metapopulation models have historically followed Levins (1969) assumption that extinction is not distance-dependent (Hanski, 1994). However, others have argued that if the rates of colonisation, and subsequently immigration, are distance-dependent and immigration rescues populations from extinction (Brown and Kodric-Brown, 1977) then populations

of more isolated patches will exhibit higher extinction rates than less isolated ones (Moilanen et al., 1998). The rescue effect hypothesis assumes that patch extinction rates increase linearly until a threshold patch-occupancy density is reached in which the overriding presence of immigrants begin offsetting extinction events (Gotelli, 1991). Experimental studies utilising bryophytes for investigating how extinction rates vary in relation to patch-occupancy density would offer important empirical insights into interactions between extinction dynamics and patch-occupancy patterns: information which could be directly applied to plant conservation strategies in the context of habitat fragmentation.

In comparison to temperate species, bryophytes of tropical regions exhibit relatively fast population dynamics (Monge-Najera, 1989; Coley et al., 1993; Zartman, 2004) making them a particularly suitable group for conducting experimental population studies. With recent advancements in the Neotropical taxonomy and floristics of bryophytes (e.g., Gradstein et al., 2001; Gradstein and da Costa, 2003), the tools for identification of potential focal species in demographic studies are available for any population biologist who has acquired a working knowledge of bryophyte morphology. Moreover, the high rates of habitat loss accompanied by the mounting number of plant extinctions presently occurring in the tropics (Pittman and Jorgenson, 2002), is yet another justification for prioritizing demographic studies focusing on the remnant native habitats of this region in particular.

#### 4. Genetics: integrating evolutionary and ecological processes

The rapid, widespread transformation of the world's remaining forests into a network of habitat patches (Skole and Tucker, 1993) highlights the urgent need to better understand how forest fragmentation alters both the ecological stability and evolutionary potential of the surviving flora and fauna. Molecular markers provide a fast and convenient means to assess the condition of populations of a wide variety of species (Spielman et al., 2004). However, the degree of correspondence between genetic measures based on neutral markers and demographic survey data is relatively unexplored (Lavery et al., 1996; Lande, 1988; Young and Clarke, 2000).

In theory, subdividing habitats constricts the genetic neighbourhood of surviving species by reducing population size, and increasing average inter-population distances (Templeton et al., 1990). Such regional-scale changes wrought by habitat fragmentation are expected to erode local genetic variability, and augment genetic differentiation among populations by increasing the likelihood of breeding among related individuals (Frankham et al., 2002; Arnaud et al., 2003). Evidence from plant studies indicates that decreased genetic variation, resulting from inbreeding and genetic drift, may lower fitness and increase extinction risk in isolated populations (Charlesworth and Charlesworth, 1987; Menges, 1991; Ellstrand and Elam, 1993; Newman and Pilson, 1997).

Due to their sessile nature, plants are predicted to be especially sensitive to the population genetic consequences of increased insularity resulting from habitat fragmentation (Young et al., 1996). The few bryophyte studies which have addressed habitat fragmentation impacts on population genetic

structure generally provide evidence contrary to that reported for angiosperm taxa (but see Thinggaard, 2001 for an exception). For example, bryophyte populations of both fragmented peat bogs (Wilson and Provan, 2003), and deciduous forests (Wyatt et al., 1989) harbour less genetic variability, and exhibit increased inter-population genetic differentiation relative to those of continuous habitat. Reduced genetic diversity in bryophytes may result from the random loss of alleles due to drift acting on these isolated populations (Wyatt et al., 1989). However, both of these studies focused on temperate species occurring in landscapes which have endured upwards of six centuries of large-scale, anthropogenic disturbance (Wilson and Provan, 2003). To the contrary, the tropics have only relatively recently experienced modifications to bryophyte-rich habitats (Gradstein, 1992), and few comparative population genetic studies have yet been conducted in this region (Zartman et al., 2006).

Since demographic processes demonstrably influence population genetic structure (Slatkin, 1987; Wade and McCauley, 1988; Goodell et al., 1997; Richards et al., 2003), the evolutionary consequences of habitat fragmentation can only be accurately assessed in light of its specific impacts on demography as well. For example, genetic divergence among local populations depends on interactions between the frequency of extinction and (re-)colonisation events relative to migration (Wade and McCauley, 1988), the genetic background of the colonising groups (Whitlock, 1992a), and the degree to which such demographic parameters may vary with time (Whitlock, 1992b). Owing to the mounting empirical evidence that fragmentation increases the demographic instability in many species (Laurance, 2002), it is imperative that the genetic effects of fragmentation be evaluated in light of its impacts on population processes.

Their combination of fast generation times of many bryophytes, and dominant haploid condition make them an ideal taxon for studies which integrate the ecological and evolutionary consequences of fragmentation. Especially in biologically rich regions, such as the tropics, in which a majority of the deforestation has only occurred in the past half century (Whitmore, 1997); it is of utmost importance that the evolutionary consequences of fragmentation be evaluated utilising species with inherently shorter generation times. For example, despite dramatic reductions in both local population sizes (Zartman, 2003), and colonisation rates (Zartman and Shaw, 2006) of the epiphyllous bryophyte *Radula flaccida* in small ( $\leq 10$  ha) Amazonian forest fragments, both the levels of genetic diversity and degree of differentiation were nearly identical to those populations inhabiting larger reserves ( $\geq 100$  ha) (Zartman et al., 2006). In this case, interpreting the population genetic results in light of information of both community and population level changes wrought by fragmentation led to the conclusion that either: (1) an equilibrium between migration and drift has yet to be reached since isolation of the forest fragments nearly three decades ago; or (2) the demonstrably reduced colonisation rates of *R. flaccida* does not sufficiently impact inter-fragment gene flow to offset genetic drift.

Nonetheless, evaluating the evolutionary impacts of fragmentation in the absence of complementary data on demographic processes presents many difficulties. Although not a case specifically involving habitat fragmentation, Cronberg



(2002) investigated spatially-structured populations of the bryophyte *Hylocomium splendens* on a series of oceanic island of the Baltic uplift region. Cronberg (2002) reported that both clonal diversity and genetic variation increase significantly with *H. splendens* population age suggesting repeated recruitment of the species on the islands since becoming inhabitable. Interestingly, he detected no isolation by distance suggesting that, over the spatial scale of the study area, gene flow is essentially random. Such results are apparently in contrast with ecological experiments (Dettki et al., 2002; Sillet et al., 2000; Gunnarson and Söderström, in press) which repeatedly infer dispersal limitation to explain the restricted distributions of many cryptogamic taxa. However, ecological and evolutionary processes clearly operate at different time scales (Lande, 1988), and, as demonstrated by Zartman et al. (2006), the impacts of habitat fragmentation on demographic processes may result in significant ecological repercussions (e.g., local extinctions) but have little to no effect on the genetic structure of the species. Indeed, population genetic theory predicts that even limited gene flow (ca. 1 recruiting seed or diaspore per generation) may sufficiently reduce genetic differentiation caused by counteracting effects of drift (Wright, 1951; Slatkin, 1987).

## 5. Further research

Most fragmentation studies to date represent single 'snapshots' of community structure, resulting in interpretations which may be biased by the single time interval sampled. While some bryophytes may readjust relatively quickly to fragmentation effects, others may experience a slower relaxation effect. These species persisting in altered conditions may experience insufficient reproduction, recruitment or local growth to ensure long term persistence. The possibility of rapid bryophyte species turnover has not been considered enough in the community ecology literature. Its importance was recently highlighted by Ross-Davis and Frego (2004), who found diaspore rain composition was highly seasonal, with a high turnover in forest floor bryophyte composition between plots. Unpublished work cited by Scott (1971) showed that bryophyte composition in grassland changed markedly, and sometimes completely, from season to season. In contrast with longer lived organisms, re-sampling bryophytes is expected to generate valuable data over the three years of a typical granting period.

Further studies are needed to extract information from bryophyte community datasets to determine species-level responses. Some of the conflicting or unclear results are no doubt due to the variety of life history strategies among bryophytes. A potentially effective approach is classifying bryophytes into functional groups or guilds (e.g., Fenton and Frego, 2005). The morphometric information needed for classification is available at least at a coarse-scale, even for taxa in countries where the local biodiversity is largely unknown, due to the wide distribution of most bryophyte genera. A species-level understanding of bryophyte community response would help identify targets for population-level and experimental work. This research sequence has played out in Fennoscandia, a region with a long history of cryptogamic research, which has resulted in a rich catalogue of species

distributions and detailed autoecological information (ECCB, 1995). Their detailed level of understanding of lichens such as *Lobaria pulmonaria* has provided vital new information in the understanding of ecological processes determining cryptogam distribution and consequences of human activity (e.g., Scheidegger, 1995; Öckinger et al., 2005).

More experimental work is also needed to disentangle the roles that both dispersal limitation and local factors play in governing bryophyte community structure in fragmented habitats as most results to date have only implied process from studies of pattern. While documenting pattern is clearly important, with bryophyte diversity and ecology in many parts of the world largely undocumented, a better balance between experimental and descriptive work is needed.

An important extension on this research would be to determine the relative importance of dispersal versus establishment limitation. Propagules may be available, but changes in microclimate and substrate quality caused by fragmentation may render edge habitats and small fragments generally unsuitable for establishment. Experimental studies to track propagule arrival and establishment are relatively simple and quick for bryophytes compared to most seed plants and vertebrates. For example, a successful method used in Canada involved catching spore rain for 4–6 hours over a period of months (Wright, 1951). Growing up both the spore rain and the soil spore bank yielded insights into the role of various factors in shaping the extant community.

Studies linking community changes to demographic processes are also needed. For example, observed patterns of patch-occupancy can be produced by very different demographic processes (Clinchy et al., 2002). Bryophytes, due to their substrate specificity and fast generation times, are an effective plant group to be utilised for empirical confirmation of population processes inferred through site occupancy data with direct information on population parameters. Such research will require relatively long-term demographic studies that include removal and establishment experiments.

Furthermore, there exists a plethora of theoretical research on the dynamics of species persistence in fragmented habitats that has yet to be empirically tested. For example, Johst et al. (2002) incorporate both local growth and regional dynamics in modelling species persistence in a fragmented system. They concluded that species exhibiting low growth and low dispersal are unlikely to survive in dynamic landscapes. However, parameterising these theoretical results with real plant data remains problematic due to the incompatibility of life history characteristics, such as generation time, with the logistics of field experimentation (Honnay et al., 2005). However, bryophyte population processes, especially those of ephemeral substrates, are highly dynamic (Hansson et al., 1992), and are a model system with which to test the growing cadre of metapopulation models in the context of fragmentation ecology.

Field studies testing the basic tenets of metapopulation theory are desperately needed in plant ecology research. There is an ongoing debate as to whether plants of fragmented habitats are governed by metapopulation dynamics (Husband and Barrett, 1996; Ouborg and Eriksson, 2004). For example, the extended generation times, and presence of

seed banks in plants may compromise the accuracy in the measuring demographic parameters such as rates of patch colonisation and extinction (Eriksson, 1996). Furthermore, distinguishing what represents the habitat patch from the surrounding matrix has also led to doubts as to the efficacy of utilising the metapopulation concept for plants (Murphy and Lovett-Doust, 2004). Investigating the relationship between a species' patch-occupancy density and colonisation and extinction rates through manipulative field experiments utilising bryophytes will offer novel information regarding the regional dynamics of plant populations. For longer lived organisms, the spatial and temporal scale of the study has been shown to have a significant effect on the likelihood of detecting a fragmentation effect (Stephens et al., 2003). However, bryophyte populations can be identified and monitored with relative ease, with habitat patches readily identified within a given study area.

## 6. Conclusions

Our knowledge of bryophyte response to fragmentation of landscapes is progressing rapidly, particularly in the understanding of population-level processes. However, we still need clear experimental and observational data among a variety of bryophyte species to flesh out existing evidence. Below are key areas for future research in this exciting area. (1) Which bryophyte species or life history strategies appear to be limited by their inability to disperse in fragmented habitats? (2) For which species is substrate quality best explaining observed patterns of abundance and distribution of fragmented habitats? (3) How do edge environments interact with the type of remnant and type of matrix to affect bryophyte diversity? What changes could be made to the quality of the matrix surrounding the fragments to encourage species to inhabit this inferior quality habitat? (4) Why is there inconsistency in the literature on the relationship between the basic attributes of bryophyte community structure (i.e., species richness and local density) and the spatially-explicit measures such as habitat area and degree of isolation? Are these relationships highly time and space dependent? What role does variation in life history characteristics play in understanding response to habitat area and isolation? (5) What roles do habitat insularity and the time since the isolation event play in changing the population genetic structure of bryophytes in fragmented habitats?

Conclusions from studies in landscapes as different as tropical Amazonia and central Finland suggest that many bryophytes are probably not routinely dispersing further than a few tens of metres. The implications of these findings for conservation are that the spatial configuration of fragments of native vegetation and the quality of the matrix play a vital role in bryophyte community structure and population dynamics. An understanding of the underlying causes of rarity is important both for managing species known to be rare (e.g., European red-listed species) and for preventing more species being identified as at risk of continued population decline and possible extinction. Bryophyte ecology is a dynamic field with much to offer our understanding of the importance of local and landscape level processes in controlling biodiversity.

## Acknowledgements

Thanks to L. Richard Little and the two anonymous reviewers for improving the manuscript, and R.D. Seppelt for locating literature. This is article #465 in the Biological Dynamics of Forest Fragments Project (BDFFP) technical series.

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