

Bryophytes as potential indicators of forest integrity

Katherine A. Frego*

Department of Biology, University of New Brunswick, 100 Tucker Park Circle, P.O. Box 5050, Saint John, NB E2L 4L5 Canada

Abstract

Forest integrity has been proposed as one conservation endpoint that integrates desirable characteristics such as natural biodiversity, stand structure and continuity. Although its defining criteria are still under discussion, any surrogates must effectively represent or predict their status, and be easier to measure than the criteria themselves. Bryophytes have been proposed as such surrogates, because they are important components of forest integrity, and considerable research indicates that some groups are sensitive to the changes associated with specific forest management regimes. The objectives of this paper are (1) to review the issues in determining indicators of forest integrity, including desirable qualities in such indicators, (2) to review the state of knowledge concerning bryophytes as components of forest integrity (i.e. their responses to forest management practices), and (3) to assess bryophytes as potential indicators of forest integrity, in terms of both qualities desirable in indicators and our understanding of bryophyte response patterns. Although bryophytes possess some characteristics that suggest potential indicator value, many challenges prevent their reliable application. I highlight key areas in which research is required to identify operational bryophyte indicators of forest integrity. Along with a standardized protocol to select and calibrate such indicators, we urgently require strategic research to compile data on undisturbed reference forests on which to base selection of endpoints; species-specific ecological tolerances, with consideration of complex interactions; mechanisms of response to disturbance, with consideration of temporal aspects; population viability thresholds; and recruitment effects on community assembly. Whether we succeed in finding bryophyte indicators of forest integrity, this research would also provide the data to monitor and interpret the integrity of the bryophyte community.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Bryophyte; Community assembly; Disturbance; Diversity; Forest integrity; Indicator

1. Introduction

Maintenance of biodiversity is an integral part of the concept of “sustainable forest management” that is the target of numerous government, scientific, and industrial initiatives, especially in extensively and intensively managed forest systems. Many of these initiatives have adopted the principles of criteria and indicators: identification of specific desired *endpoints* (“focal conservation targets,” Parrish et al., 2003), *criteria* (measurements or assessments of “key ecological attributes” of these target states, Parrish et al., 2003), and *indicators* of the status of these criteria. For this discussion, I use the term indicators *sensu lato* (in the broadest sense) to include surrogate measures, variables or indices that in some way represent and (or) predict the status of stated criteria or key attributes (modified from Brooks et al., 1998), including but not limited to indicator species *sensu stricto* (as described in Caro and O’Doherty, 1998).

The objectives of this paper are:

- (1) to review the issues in determining indicators of forest integrity, including desirable qualities in such indicators;
- (2) to review the state of knowledge concerning bryophytes as components of forest integrity (i.e. their responses to forest management practices); and
- (3) to assess the current status of bryophytes as potential indicators of forest integrity. To what degree do they possess the biological qualities that are required in indicators of changes in forest ecosystem structure and function? What is required to set operational indicators, i.e. to calibrate bryophyte characteristics as measures of stressors, or criteria of the desired endpoint, forest integrity?

2. Forest integrity, criteria and indicators

While the concept of “forest integrity” and the criteria-indicator approach have widespread intuitive appeal to environmental managers and the general public (Niemi and

* Tel.: +1 506 648 5566; fax: +1 506 648 5811.

E-mail address: frego@unbsj.ca.

Table 1
Conceptual comparison of surrogates (i.e. indicators *sensu lato*) and the criteria that they represent or predict

Surrogate (indicator <i>sensu lato</i>)	e.g.	Criterion represented or predicted			
		Population parameters of one+ species, or community composition	Summary index* for suite of species	Key habitat features	Suite of habitat features, e.g. environmental “health”, habitat classification
(a) Presence or abundance of one species	Bryophyte growth		(Keystone species)	(Indicator species sensu stricto) Soil nutrients (Schaffers and Sýkora, 2000) Humus, CWD, and stand age (Rambo and Muir, 1998) Mineral content of substrate (Shacklette and Erdman, 1982; Shacklette, 1965) Metal deposition (Aboal et al., 2006; Gerdol et al., 2000)	(Umbrella species) Altered microclimate, (Hylander et al., 2005), edge effects (Hylander, 2005)
	Individual bryophyte species Bryophyte mineral content	Locally rare species (Vitt et al., 2003)			Ecotoxicological stress (Pesch and Schroeder, 2006)
Presence or abundance of a suite of species	“Indicator species”	(Focal species) Red List spp. (Gustafsson et al., 2004)		(Indicator species sensu stricto)	(Indicator species sensu stricto) Habitat classification (Gustafsson et al., 2004; Vitt et al., 2003; Nicholson and Gignac, 1995) Altered (drier) microclimate (Moen and Jonsson, 2003) Air pollution, not forest integrity (Glenn et al., 1998)
	Liverwort abundance				
	Total bryo cover				
Summary index for suite of species	Bryophyte richness		See Table 3		Air pollution, not forest integrity (Glenn et al., 1998)
(b) Key habitat feature or suite of features	Spring condition	Bryophyte community persistence and stability (Heino et al., 2005)			
	Forest stand characteristics (e.g. age, CWD, habitat diversity)	Composition of bryophytes, epixylic cryptogams (Jonsson and Jonsell, 1999)	Bryophyte diversity (Rambo, 2001)		

(a) Bryophytes as indicators, (b) indicators for bryophytes. (*) Includes emergent community characteristics such as richness, diversity, evenness. Examples are not exhaustive. **(Bold)** identifies term associated with this specific type of surrogate in the literature (see Caro and O’Doherty, 1998).

McDonald, 2004; Brooks et al., 1998), commentaries on their limitations are abundant (see reviews by e.g. Carignan and Villard, 2002; Lindenmayer et al., 2002; Dale and Beyeler, 2001; Simberloff, 1999, 1998).

The initial identification of one or more desired endpoints has been approached in a variety of ways. Concepts such as ecosystem health are appealing, but inherently flawed, especially in being impossible to define (Simberloff, 1999). The Swedish National Board of Forestry designated woodland key habitats (WKHs) to represent as closely as possible the pristine forest state in structure, biodiversity and by inference, continuity. Some species of concern identified as Red List species show high association with WKHs (e.g. Pykälä, 2004), however Ericsson et al. (2005) assessed cut stumps, high diversity of coarse woody debris (CWD) and species (especially Red List species), and concluded that most of the WKHs surveyed could not be classified as near natural. They recommended more emphasis on determining and restoring pre-industrial forest qualities. In the Acadian Forest Region of eastern Canada, considerable effort has been invested in documenting “pre-European forest” (Forbes et al., 1998) as a potential endpoint. However, the tree species compositions that it defines are more precisely indicators of the full range of species that comprise the forest of that time period, rather than endpoints in themselves. This approach assumes that the entire forest community will reassemble as a result of restoring composition of one component, i.e. that habitat features are the limiting factor in community re-assembly.

Biological integrity, in this case forest integrity, is a more encompassing endpoint: the capacity of an ecosystem to support and maintain a balanced, integrated, adaptive community of organisms having a species composition, diversity and functional organization comparable to that of, and representing the full range of variability in, similar undisturbed ecosystems in the region (modified from Grumbine, 1994; Karr and Dudley, 1981). Forest integrity is an appealing target because it integrates multiple concepts, including forest age, continuity, disturbance regimes (Glenn et al., 1998), and biodiversity.

Defining *criteria* for forest integrity is challenging (Simberloff, 1998; Ferretti, 1997). Some approaches (e.g. Lundquist and Beatty, 1999) assign criteria based on the professional opinion of forest managers, but more objective and repeatable processes for selection of criteria would be based on understanding the defining attributes of that endpoint. In the absence of such understanding, reference standards could be established in “similar undisturbed sites” that provide measures of natural variability against which to compare the same features in disturbed sites. In practice, reference sites may be limited or non-existent in areas of intensive and extensive disturbance, or those with a long history of anthropogenic disturbance (e.g. Swedish boreal forest, Canadian Acadian forest). However, the elements from which the criteria for forest integrity may be selected include:

- species composition, which assumes viability of all populations, and which may be summarized by values such as richness and various measures of diversity;

- ecological organization, e.g. food web;
 - disturbance regime (frequency, intensity, etc.; White and Pickett, 1985);
 - aspects of time, e.g. representation of all age classes and successional stages, temporal continuity; and
 - aspects of space, e.g. variability of all preceding characteristics with spatial scale, and spatial continuity versus its converse, fragmentation,
- all evaluated relative to the reference standard.

Clearly it would be dangerous to focus on any one of these criteria (Simberloff, 1998). For example, maintaining species diversity *per se* does not ensure the maintenance of viable populations of all native species. Similarly, many ecological processes (e.g. nutrient cycling and even productivity) may be equivalent or higher in ecosystems with severely reduced diversity (Simberloff, 1999). Forest integrity therefore requires maintenance of all its component criteria. Therein lies the rationale for indicators *sensu lato*: it would be impractical, if not impossible, to assess all criteria of forest integrity.

The literature offers lively discussions of the indicator approach in general, and proposed surrogates in particular. Numerous types of indicators have been proposed and critiqued (e.g. Caro and O'Doherty, 1998; Table 1). Most are taxon-based (Lindenmayer et al., 2002): presence or abundance (including growth rate) of one taxon or group of taxa, or a summary index for a group of taxa (e.g. richness, diversity). Others consider one or more habitat characteristics, or an index of such characteristics. Indicators have been proposed as surrogates for the presence or abundance of another species, the abundance or summary index of another suite of species, or their required habitat or environmental conditions. Given the range of combinations of indicators and the criteria they are intended to represent, an important first step in identifying reliable indicators should be the resolution of consistent terminology related to indicators [e.g. indicators of response, exposure, habitat, stressor (Ferretti, 1997), health, population and biodiversity, as well as umbrella, flagship and keystone species (Caro and O'Doherty, 1998)], refining the theoretical underpinnings of the indicator approach, and establishing standard methodologies for selecting indicators (Müller and Lenz, 2006).

Ideally, a standardized stepwise process should be developed to select reliable indicators, beginning with one thoroughly documented ecosystem in which patterns of co-variation are determined among a wide variety of taxa, environmental, and other variables. The strongest of these relationships are then tested for nestedness (Saetersdal et al., 2005; Lindenmayer et al., 2002). For example, are species at degraded sites a subset of those at sites with integrity? If nestedness is low, then the predictive power of an individual species for total richness is also low (Jonsson and Jonsell, 1999).

Potential indicators must be evaluated for epistemic (pertaining to their veracity) and practical traits (Table 2). How correctly and consistently do they predict the status of one or more key ecological attribute(s), so that changes in the indicator can reliably be attributed to changes in those attributes? Can they be more easily and/or inexpensively

Table 2

Traits identified as desirable in an indicator organism (compiled from Saetersdal et al., 2003; Carignan and Villard, 2002; Rolstad et al., 2002; Dale and Beyeler, 2001; Lindenmayer et al., 2000, and Ferretti, 1997), and qualitative evaluation for forest bryophytes

Traits desired in an indicator	Trait possessed by forest bryophytes	Important exceptions
(a) Epistemic		
Spatial and temporal distribution	–	
• Fairly well known	(Composition of inherently rare species not readily predictable; no historical data)	
• Nested		
Ecological ranges of tolerance/habitat requirements known	–	At very fine scale, e.g. <i>Sphagnum</i> spp., some species with high substrate affinity
Unambiguously and monotonically sensitive to change from desired endpoint	+	
	(Many species decline with forest disturbance)	
Resilient; less sensitive to factors not directly related to desired endpoint	–	
	(Recovery of many species not ensured with return to environmental endpoint)	
Response calibrated to be independent of sample size	?	
Respond at relevant spatial scale	–	Ubiquitous spp.
	(Respond to changes at very fine scale)	
Standard and low measurement error	??	
(b) Practical		
Perennial	+	Some ruderals
Abundant, widespread	+	Many species inherently rare
Readily sampled/identified	–	Robust ubiquitous generalist species
Cost effective	??	

(+) Trait possessed by most forest bryophytes; (–) trait not/rarely possessed.

monitored than the attributes themselves? The reliability of these indicators should then be tested using data from a similar system, refined, and tested on progressively dissimilar systems to determine under what conditions the value of the indicators holds. Examples of such a process of calibration and validation have been described by MacNally and Fleishman (2004), Lundquist and Beatty (1999), Dufrêne and Legendre (1997), and Stork et al. (1997).

Whether selected on the basis of expert opinions, or by “indicator species analysis” (e.g. PC-Ord, McCune and Mefford, 1999) using the predictability of co-occurrence of individual species, a group of samples and, by inference, environmental conditions, the predictive power of an indicator is rarely empirically tested (Rolstad et al., 2002; Caro and O’Doherty, 1998). Selection of indicators, and implementation of other conservation measures, may occur before conclusive data are available (Caro and O’Doherty, 1998), often from a sense of urgency created by potential loss of species and/or habitat (Moser et al., 2002; Rolstad et al., 2002). For example, the Acadian forest of New Brunswick has experienced forest changes related to ship-building and European settlement over 400 years (Forbes et al., 1998); it is currently harvested at the rate of 79,000 ha (~1.5% of the forested land) annually (Canadian Council of Forest Ministers, 1999), primarily by clear-cutting. Concerns that populations and habitats may be near critical thresholds, and funding initiatives that demand

operational indicators as deliverables within short time spans, combine to pressure researchers to select indicators first, and calibrate them later, if funds allow.

3. Bryophytes as indicators of forest integrity in the mixed and boreal forests

Many qualities of bryophytes are intrinsically related to the concept of forest integrity. Bryophytes are important components of forest integrity, with ecological and intrinsic value. They constitute part of the “balanced, integrated, adaptive community of organisms” (Karr and Dudley, 1981), contributing species richness at least as high as that of the vascular plants in many forest types (e.g. Grytnes et al., 2006; Steel et al., 2004; Ingerpuu et al., 2001). They have strong functional relationships to ecosystem processes. Despite their small size, bryophytes comprise major components of the biomass (Rieley et al., 1979) and photosynthetic production (Kolari et al., 2006) in boreal forests. Water and dissolved nutrients are retained in capillary spaces in living bryophyte colonies (Longton, 1984), and cyanobacteria, which colonize bryophyte leaves, contribute to the nitrogen budget of forest systems (Deluca et al., 2002; Billington and Alexander, 1978). Their slow decomposition contributes to the production of humus (Longton, 1984), enhancing soil water and nutrient holding capacity and the proliferation of fine tree roots in the interface between

Table 3

Examples of co-varying patterns between bryophyte community characteristics and forest characteristics, across a range of localities and spatial scales

Scale (sample units)	Bryophyte community characteristic	Variable	Correlation (<i>r</i>)	Reference
16 km ² , <i>n</i> = 87	Species diversity	Cover		Vanderpoorten and Engels (2003)
		Forest canopy	0.71**	
		Sandy loam soils	0.61**	
	Rare species richness	Loamy soils	−0.68**	
		Cover		
		Forest	0.46**	
		Pebbly soils	0.48**	
10,000 m ² , <i>n</i> = 10	Species richness (moss only)	Water surface	0.54*	Jonsson and Jonsell (1999)
		Bryophyte diversity	0.80**	
		Richness		
		Vascular plants	0.62*	
		Lichens	0.47 ns	
2500 m ² , <i>n</i> = 59	Species richness	Wood fungi	−0.52 ns	Saetersdal et al. (2003)
		Wood-living beetles	0.02 ns	
		Richness		
		Vascular plants	0.80***	
		Lichens	0.56***	
		Spiders	−0.54***	
		Carabid beetles	0.37***	
2500 m ² , <i>n</i> = 40	Species richness (moss only)	Gastropods	0.55***	Jonsson and Jonsell (1999)
		Polypore fungi	0.64***	
		Richness		
		Vascular plants	−0.23 ns	
1000 m ² , <i>n</i> = 35	Species richness	Lichens	0.46 ns	Pharo et al. (1999)
		Wood fungi	0.72*	
		Vascular plant cover	0.55**	
		Fern species richness	0.88 ns	
		Overstory	0.63*	
		Topographic position	0.71**	
		Time since fire	0.56**	
		Fire intensity	0.05 ns	
		Time since logging	0.04 ns	
		Logging intensity	0.02 ns	
		Elevation	0.04 ns	
		Aspect	0.04 ns	
314 m ² , <i>n</i> = 38	Species richness	Slope	0.03 ns	Sauberer et al. (2004)
		Richness		
		Vascular plant	0.76***	
		Gastropod	0.78***	
		Spider	0.39 ns	
		Orthopteran	0.56*	
		Carabid beetles	0.27 ns	
		Ants	0.59**	
0.02 m ² , <i>n</i> > 699	Species richness/ha	Birds	0.64***	Humphrey et al. (2002)
		Lichen richness	0.47**	
		Soil moisture deficit	−0.06 ns	
		Vertical cover (%)		
		Field layer	−0.13 ns	
		Upper canopy layer	0.18 ns	
		Cover index	0.10 ns	
		Ht to live crown	−0.14 ns	
		Mean basal area	0.04 ns	
		Leaf area index	0.05 ns	
		Tree species richness	0.26 ns	
		Stand age	0.26 ns	
		Temperature (#day degrees > 5C)	0.05 ns	

Values are correlation (*r*), significant at **P* < 0.05, ***P* < 0.001, ****P* < 0.00002, ns: not significant.

decomposing moss and the humus layer (Weetman, 1968). However, none of these features guarantees that bryophytes are robust indicators of forest integrity.

3.1. Bryophyte sensitivity to criteria of forest integrity

One feature that meets the criteria of effective indicators of forest integrity (Table 2) is the sensitivity of many bryophytes to disturbance associated with forest management activities. Studies worldwide provide evidence that bryophyte species diversity, and populations of certain species, decline in association with a range of forest management scenarios (e.g. Ericsson et al., 2005; Fenton and Frego, 2005; Hylander, 2005; Uotila and Kouki, 2005; Vanderpoorten et al., 2004; Fenton et al., 2003; Newmaster et al., 2003; Newmaster and Bell, 2002; Ross-Davis and Frego, 2002; Jalonen and Vanha-Majamaa, 2001; Vellak and Paal, 1999). Liverworts may be particularly susceptible to indirect, as well as direct, disturbance impacts (e.g. Åström et al., 2005; Fenton et al., 2003; Ross-Davis and Frego, 2002).

A central assumption of an indicator approach is that the criteria of forest integrity, including species and habitat features, co-vary. Significant *correlations* have been reported between bryophyte summary indices (diversity, richness) and a wide range of other variables (Table 3); however, it is worthy of note that even the significant correlations tend to have low explanatory power, and vary with spatial scale. For example, at the landscape scale, bryophyte diversity may be significantly correlated with forest cover and soil type (e.g. Vanderpoorten and Engels, 2003). Over a range of scales from 2500 to 314 m², there have been significant correlations between bryophyte richness and a variety of biotic and environmental variables, the strongest of which appear to be bird richness (Sauberer et al., 2004), vascular plant richness [(Saetersdal et al., 2003; Jonsson and Jonsell, 1999), especially fern richness (Pharo et al., 1999)], and lichen richness (Saetersdal et al., 2003, however see Jonsson and Jonsell, 1999). At a finer scale (<1 m²), bryophyte diversity is correlated with lichen richness (Humphrey et al., 2002) and substrate diversity (e.g. Mills and MacDonald, 2004; Newmaster et al., 2003; Zechmeister and Moser, 2001; Vellak and Paal, 1999), especially decay state of wood (Turner and Pharo, 2005; Ross-Davis and Frego, 2002; Crites and Dale, 1998).

Bryophytes have been explicitly proposed as various types of indicators for a wide range of criteria (Table 1). In some cases, selection of bryophyte indicators was based on direct measurements rather than correlational relationships. For example, mineral accumulation was assessed by comparative elemental analysis (e.g. Shacklette, 1965), and extent and severity of microclimatic change associated with forest canopy removal was assessed using growth rates of individual species (e.g. Hylander, 2005). Interestingly, Glenn et al. (1998) noted that air pollution reduced the predictive power of bryophytes as indicators of microclimatic alteration at forest edges, reinforcing the probability of complex interactions and the need to consider relative impacts of multiple stressors. However, few studies have explicitly delimited the applicability of bryophyte

indicators: are the reported patterns of co-variation nested, and at what spatial scales?

3.2. Issues of spatial and temporal scale

Effective indicators must respond at relevant temporal and spatial scales. It is not surprising to find weak or no co-variation among bryophytes and other life forms that experience their environments at different spatial or temporal scales. For example, although trends in vascular plants and lichens were identified along an altitudinal gradient in Norway, no trend was detected in bryophyte species richness; this was attributed to differences in the relative importance of fine- versus coarse-scale habitat variability (Grytnes et al., 2006). Neither is it surprising to find co-variation patterns that vary with forest type, history, disturbance factors, gradient length, and spatial scale. Temporal aspects, while receiving increasing attention, are still in the early stages of investigation. For example, the relative importance of continuity is rarely separated from that of microhabitats characteristic of forest age (Nordén and Appelqvist, 2001).

3.3. What is needed to identify operational bryophyte indicators?

While some characteristics of bryophytes hold promise as potential indicators for specific criteria of forest integrity, few are operational and well calibrated. Along with a standardized methodology, we require strategic basic research on bryophyte biology and ecology in the following areas.

3.3.1. Baseline data describing the “target states” of bryophyte communities

Reference standards, i.e. bryophyte community compositions in undisturbed forests, are poorly documented in many regions. In addition, even the basic criteria of the desired endpoint must be inferred (e.g. Sweden’s WKHs, Canada’s “pre-European Acadian forest”) because the long history of anthropogenic forest disturbance has left few or no pristine/undisturbed forests. Unlike large, recognizable and commercially important life forms (e.g. trees), there are no records of bryophyte community composition for forests prior to, or in early stages of, intensive anthropogenic disturbance. Furthermore, there are few databases from long-term monitoring of bryophyte dynamics. With evidence that bryophyte communities are inherently variable over time (e.g. Fenton et al., 2003, Frego unpubl. data), the BACI (Before-After-Control-Impact) approach should be used to account for natural turnover, by using the best available representation of undisturbed conditions as a reference.

3.3.2. Ranges of ecological tolerance and responses to disturbance

Bryophyte communities are often dominated by a few ubiquitous species with similar, apparently very broad, ranges of tolerance, e.g. *Pleurozium schreberi* frequently dominates a wide range of forest types and ages in the northern hemisphere.

In most cases we have insufficient data to understand the widely reported phenomenon of “local rarity” (Humphrey et al., 2002; Pharo and Vitt, 2000). Although the assumption that species with very low occurrence are limited by microclimate or substrate is intuitively attractive, Cleavitt (2005, 2002) has shown that some inherently rare species have broader habitat niches (i.e. ranges of tolerance) than their common counterparts.

Although the habitat changes associated with specific elements of disturbance can be precisely quantified (e.g. Roberts and Zhu, 2002), bryophyte responses are variable. For example, sensitivity to microclimatic change has been invoked to explain bryophyte responses to edge effect (Gignac and Dale, 2005; Hylander, 2005). The different responses of two species (Hylander, 2005) and the wide range of responses reported for putatively substrate-generalist species, ranging from persistence, through slow decline, to death (Fenton et al., 2003) may reflect variability in tolerance of the microclimatic changes associated with canopy removal. However, there are complex interactions among disturbance effects that must be teased apart to predict bryophyte species responses. The degree of canopy removal affects changes in microclimate, including humidity; the latter interacts with log species and diameter and time since disturbance to influence decay state, and hence the relative value of the log for bryophyte species with strong requirements for wood in late stages of decay (Humphrey et al., 2002). Colonial growth form may buffer central shoots, allowing them to survive in an otherwise inhospitable site (e.g. Sollows et al., 2001).

Although assessment of individual species’ responses is ultimately required to determine the mechanisms of response (e.g. Hylander, 2005), an initial step would be to identify groups of taxa with similar response patterns. One productive approach is to assess patterns of response to perturbations of defined characteristics, then to seek shared biological traits among species with similar responses, e.g. using During’s (1979) classification of life history characteristics. Mechanisms of response could then be inferred from the suite of traits. However, it will be important to integrate further information on species’ ranges of tolerance in order to avoid confounding effects. For example, the co-occurrence of epixylic bryophytes and CWD (e.g. Uotila and Kouki, 2005; Ross-Davis and Frego, 2002) may result from true substrate specificity; it could also arise from the convex form of fallen logs (Hylander et al., 2005), recruitment patterns and (or) biotic interactions that all may differ among species. Furthermore, individual species’ sensitivities to disturbance may vary with colony size, ecotypes, or at the limits of their ranges. It is difficult to avoid circularity: while use of indicators with a known functional relationship to criteria of interest may “suggest entirely new ways of managing a problem” (Simberloff, 1998: 254), choosing such indicators requires understanding the underlying mechanisms of response, which is generally lacking.

One important dimension of ecological tolerance, a species’ time to respond to disturbance, has rarely been documented. If bryophyte metabolism is essentially opportunistic (Schofield, 1985), then species may respond, not only to changes in the

ranges of conditions, but also to changes in duration of conditions that are within the overall range of tolerance (e.g. periods of temperature extremes, or of hydration). For example, metabolism of isolated shoots of *Bazzania trilobata* declined, and did not recover, after hours of dry conditions in the lab (Sollows et al., 2001). In the field, many leafy liverworts in the Acadian forest appear to respond to changes in microclimate within months of canopy removal; others lose vigour and decline over a period of years after harvest (Fenton et al., 2003, Mathieson, unpubl. data). Yet a number of species, including several that declined rapidly in a clear-cut, persisted for at least 4 years in patches of mixed forest with patchy remnant canopy >1.5 m in height, where minimal microclimatic amelioration was detectable (Fenton and Frego, 2005), or where they are buffered in an otherwise dead colony (Sollows et al., 2001). Research to document ranges of ecological tolerance are needed for most species (especially those that show promise as indicators), but must account for interactions among abiotic variables, biological features such as colonial growth form, and temporal aspects.

3.3.3. Biotic factors influencing population processes

While the occurrence of a bryophyte species confirms that a particular microsite falls within a given range of habitat conditions, its absence provides little useful information. It may be intolerant of the habitat, but it may also be critically limited by population level factors, such as mortality, gene flow, recruitment, and other biotic limits on population size and structure. Quantitative information on population processes are lacking for the majority of species (except e.g. *Hylocomium splendens*, Rydgren et al., 1998), and although competitive interactions have been inferred (e.g. Cleavitt, 2003), few studies have explicitly tested biotic interactions among bryophytes in the field.

Recruitment (establishment via spores) is receiving more attention, supported by the association of variability in successional patterns and occurrence of rare species with stand age or time since major disturbance (e.g. Newmaster et al., 2003; Pharo et al., 1999; Crites and Dale, 1998; Jonsson, 1993), and with observations that some bryophytes (especially leafy liverworts) do not appear to recover (e.g. Uotila and Kouki, 2005; Ross-Davis and Frego, 2002), even after environmental conditions return to those of a mature forest. Recruitment may be an infrequent event, requiring the coincidence of several conditions: there must be a source of propagules (e.g. adult plants, buried propagule bank) within dispersal range of a microhabitat that is suitable for germination and establishment. The compositions of the diaspore rain and buried propagule bank vary both spatially and temporally (Ross-Davis and Frego, 2004; Jonsson, 1993); Miller and McDaniel (2004) estimate that some species are capable of routine dispersal over distances of at least 5 km. Limited available data suggest that the forest floor assemblage overall (Jonsson, 1993), and species at greatest risk of loss in managed forests (e.g. leafy liverworts, Uotila and Kouki, 2005; Ross-Davis and Frego, 2002) are not well represented in either propagule reservoir. Recruitment limitations (Hurt and Pacala,

1995) can be expected to become increasingly problematic as stand rotations, already shorter than estimated recovery times (Turner and Pharo, 2005; Ross-Davis and Frego, 2002), are shortened further.

Experimental manipulations are needed to test the predictions of habitat-limited versus recruitment-limited community assembly models. For example, will provision of a limiting habitat such as large diameter logs hasten reestablishment of epixylic species, or is colonization ultimately limited by the microclimate (which in turn alters decay rate), or by propagule availability? What are the probabilities that biological and structural legacies preserve source populations (Fenton and Frego, 2005), and that source populations accelerate colonization of adjacent areas? If some bryophyte assemblages are critically limited by recruitment (dispersal and establishment), their maintenance may require forest continuity, i.e. uninterrupted site-specific presence in time of a particular forest type, or critical components thereof (Nilsson et al., 1995). Such thresholds, if they exist (Huggett, 2005), must be determined.

In the meantime, Rolstad et al. (2002) call for inventories of forests of known continuity, to identify potential surrogates for continuity: putatively dispersal-limited species that consistently occur only in the oldest stands, and not in otherwise suitable habitats in younger stands. The dispersal abilities of these species could then be tested in controlled experiments.

3.4. Challenges in monitoring bryophytes

The effective implementation of reliable indicators requires consistent monitoring (Lindenmayer, 1999). Once bryophyte indicators of forest integrity are developed, protocols for monitoring them require attention. As with many small, taxonomically challenging organisms, bryophytes are time-consuming to assess (e.g. Steel et al., 2004), especially over large spatial scales, because they vary on a very fine scale, with a few species extremely abundant and a relatively large proportion inherently infrequent (e.g. Fenton et al., 2003; Humphrey et al., 2002; Pharo and Vitt, 2000). They require expertise and the use of microscopic characters to identify, but there is insufficient expertise available to make bryophyte sampling practical for forest managers: few herbaria have cryptogamic collections, many regional identification manuals are long out of print, and there are relatively few specialists trained in bryophyte identification, especially in North America. Summary indices such as total cover and species richness, which do not require taxonomic expertise, have proven to be unreliable predictors of forest integrity (e.g. Lindenmayer, 1999; Glenn et al., 1998). Although Scandinavian ecologists report success in training of non-experts to identify selected species or groups, most North American foresters have neither the time nor the expertise to assess the bryophyte community. The few bryophyte taxa that they learn to identify on sight are typically large, distinctive and ubiquitous species (e.g. Schreber's moss, *Pleurozium schreberi*; Broom-moss, *Dicranum scoparium*, the genus *Sphagnum*) with limited indicator value. Given these challenges,

bryophytes may be more difficult or expensive to monitor than many of the criteria themselves.

3.5. Indicators of bryophyte community integrity

The converse of this paper's title is also worth considering: what indicators predict bryophyte community integrity? As components of the native biota and ecosystem functioning, bryophytes must be conserved to maintain forest integrity, however monitoring of bryophytes by non-specialists requires reliable, well-calibrated but easily-assessed surrogates.

Species composition may be much more important to ecosystem integrity than mere species richness (Simberloff, 1999), however few predictors have proven sensitive to individual bryophyte species' presence, especially for rare species. While Vitt et al. (2003) found that occurrence of rare bryophyte species was correlated with bryophyte species richness at both site and stand scales, the relationship is not transitive: stands rich in locally rare species were also generally species rich, but not all species-rich stands contained many locally rare species.

Furthermore, other putative indicators of bryophyte species composition are scale sensitive. For example, richness of rare species was significantly correlated with forest cover, pebbly soil, and water near the soil surface (Vanderpoorten and Engels, 2003), but the coarse scale of the study (units of 16 km²) limits its value for monitoring. Similarly compositional gradients have been linked to overriding environmental gradients of e.g. moisture, but few patterns are predictable at finer scales. In montane forests, Pharo and Vitt (2000) reported that ground layers were highly variable with little local distinctiveness and no strong environmental correlations with species patterns at a local scale. In the Acadian forest, composition varied on the scale of meters, and was only weakly associated with stand-scale environmental features (Fenton et al., 2003). This may reflect the choice of features tested, but more likely it stems from real ecological factors, and our knowledge gaps concerning them. For example, broad ranges of tolerance may be far more common than expected, or community assembly may be critically limited by factors other than habitat availability.

The search for indicators of bryophyte community composition may be inherently difficult: surrogates with body sizes that are large enough to be easily monitored, such as vascular plant composition, are unlikely to be as sensitive to the fine-scale changes to which small organisms such as bryophytes respond.

4. Conclusions

Are bryophytes potentially suitable indicators for forest integrity, i.e. is their presence or composition a reliable and practical surrogate for key ecological entities or processes (Rolstad et al., 2002)? It is imperative to first acknowledge the limitations inherent in both the definition of "forest integrity" and the indicator approach in the broadest sense; at best, a given indicator provides a surrogate for a defined subset of criteria within a defined range of ecosystems. Forest bryophytes as a

group possess features that are desirable in potential indicators of forest integrity. They are important components of forest integrity, and extremely sensitive to anthropogenic disturbance, however, much research is needed in order to formulate operational indicators based on bryophytes. Patterns of co-variation must be quantified, rigorous statistical selection processes applied, tested and refined to determine under what scales and under what conditions they are reliable. Strategic research should address ranges of ecological tolerance, mechanisms of response to disturbances, and the relative limits to populations arising from habitat, biotic interactions, and recruitment—all considering spatial and temporal scales. Given the circumpolar distribution of many species, it would also be instructive to explicitly compare their applicability in eastern and western hemispheres, in order to explore the possibility of ecological divergence between isolated populations (e.g. different ecotypes). We need documentation of the basic biology and ecology of species that previous research suggests are potential indicators, and those that are vulnerable because they are inherently infrequent, sensitive to disturbance, and (or) limited in recovery potential.

While it is certainly valuable to compile lists of putatively rare species (e.g. Red List species), and to preserve the habitats that contain them, it would be dangerous to expect such species to serve as umbrella species. Without more extensive understanding of the critical factors governing their distribution – in particular, ranges of ecological tolerance, and life cycle processes such as dispersal and establishment – they have limited predictive value.

The greatest challenge in using bryophytes as indicators of forest integrity is the apparent contradiction between the critical requirements of strong predictive value for key ecological attributes vs. ease of monitoring. Unfortunately, the widespread, abundant and easily recognized bryophyte species are not strongly associated with the criteria defining forest integrity. Conversely, factors controlling the distribution of species that are especially vulnerable, because they show a high degree of sensitivity to microclimatic change, or of habitat affinity, are largely unknown, and most of these species require labour-intensive searching and specialized knowledge for identification. Evidence of low resilience of many forest floor species suggests that forest continuity, which incorporates ecological legacies, specialized microhabitats, and a temporal aspect, may be critical.

The increasing exploitive pressure on forests adds a sense of urgency to this research agenda, based on the potential for further reduction of full ranges of distribution (hence loss of documentation of ranges of tolerance), and for loss of genetic diversity of inherently rare species. Although the identification of operational indicators of forest integrity may not yet be a reality, strategic bryophyte research to accomplish that goal would, in the shorter term, aid development of methods to assess the status of forest bryophyte assemblages themselves.

Acknowledgements

I appreciate the collegiality of Y. Bergeron, S. Gachet, S. Haeussler, and E. MacDonald who organized the oral paper

session on forest integrity at the annual meeting of the Ecological Society of America (August 2005), from which this paper developed. My students, past and present, provided the foundation for this synthesis; Z. Fang, K. Mathieson, J. Mudge, M. Pokorski, and A. Witkowski made valuable suggestions to improve the manuscript. The generous and constructive comments of J. Houlahan, M.R. Roberts and two anonymous reviewers stimulated a more productive approach to the subject.

References

- Aboal, J.R., Real, C., Fernández, J.A., Carballeira, A., 2006. Mapping the results of extensive surveys: the case of atmospheric biomonitoring and terrestrial mosses. *Sci. Total Environ.* 356, 256–274.
- Åström, M., Dynesius, M., Hylander, K., Nilsson, C., 2005. Effects of slash harvest on bryophytes and vascular plants in southern boreal forest clearcuts. *J. Appl. Ecol.* 42, 1194–1202.
- Billington, M., Alexander, V., 1978. Nitrogen fixation in a black spruce (*Picea mariana* [Mill] B.S.P.) forest in Alaska. *Ecol. Bull. (Stockholm)* 26, 209–215.
- Brooks, R.P., O'Connell, T.J., Wardrop, D.H., Jackson, L.E., 1998. Towards a regional index of biological integrity: the example of forested riparian ecosystems. *Environ. Monit. Assess.* 51, 131–143.
- Canadian Council of Forest Ministers, 1999. Compendium of Canadian Forestry Statistics 1998. Natural Resources Canada, Ottawa.
- Carignan, V., Villard, M.-A., 2002. Selecting indicator species to monitor ecological integrity: a review. *Environ. Monit. Assess.* 78, 45–61.
- Caro, T.M., O'Doherty, G., 1998. On the use of surrogate species in conservation biology. *Conserv. Biol.* 13, 805–814.
- Cleavitt, N.L., 2002. Stress tolerance of rare and common moss species in relation to their occupied environments and asexual dispersal potential. *J. Ecol.* 90, 785–795.
- Cleavitt, N.L., 2003. Controls on the distribution of *Mnium arizonicum* along an elevation gradient in the Front Ranges of the Rocky Mountains, Alberta. *J. Torrey Bot. Soc.* 131, 150–160.
- Cleavitt, N.L., 2005. Patterns, hypotheses and processes in the biology of rare bryophytes. *Bryologist* 108, 554–566.
- Crites, S., Dale, M.R.T., 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. *Can. J. Bot.* 76, 641–651.
- Dale, V.H., Beyeler, S.B., 2001. Challenges in the development and use of ecological indicators. *Ecol. Indicators* 1, 3–10.
- Deluca, T.B., Zackrisson, O., Nilsson, M.-C., Sellstedt, A., 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature* 419 (October), 917–920.
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- During, H., 1979. Life strategies of bryophytes: a preliminary review. *Lindbergia* 5, 2–18.
- Ericsson, T.S., Berglund, H., Östlund, L., 2005. History and forest biodiversity of woodland key habitats in south boreal Sweden. *Biol. Conserv.* 122, 289–303.
- Fenton, N.J., Frego, K.A., 2005. Bryophyte conservation under remnant canopy in managed forests. *Biol. Conserv.* 122, 417–430.
- Fenton, N.J., Frego, K.A., Sims, M.R., 2003. Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. *Can. J. Bot.* 81, 714–731.
- Ferretti, M., 1997. Forest health assessment and monitoring—issues for consideration. *Environ. Monit. Assess.* 48, 45–72.
- Forbes, G., Veen, H., Loo, J., Zelazny, V., Woodley, S., 1998. Ecological change in the Greater Fundy Ecosystem. In: Woodley, S., Forbes, G., Skibicki, A. (Eds.), *State of the Greater Fundy Ecosystem*. Greater Fundy Ecosystem Research group, University of New Brunswick, Fredericton, pp. 55–74.
- Gerdol, R., Bragazza, L., Marchesini, R., Alber, R., Bonetti, L., Lorenzoni, G., Achilli, M., Buffoni, A., De Marco, N., Franchi, M., Pison, S., Giaquinta, S.,

- Palmieri, F., Spezzano, P., 2000. Monitoring of heavy metal deposition in Northern Italy by moss analysis. *Environ. Pollut.* 108, 201–208.
- Gignac, L.D., Dale, M.R.T., 2005. Effects of fragment size and habitat heterogeneity on cryptogam diversity in the low-boreal forest of western Canada. *Bryologist* 108, 50–66.
- Glenn, M.G., Webb, S.L., Cole, M.S., 1998. Forest integrity at anthropogenic edges: air pollution disrupts bioindicators. *Environ. Monit. Assess.* 51, 163–169.
- Grumbine, R.E., 1994. What is ecosystem management? *Conserv. Biol.* 8, 27–38.
- Grytnes, J.A., Heegaard, E., Ihlen, P.G., 2006. Species richness of vascular plants, bryophytes and lichens along an altitudinal gradient in western Norway. *Acta Oecol.* 29, 241–246.
- Gustafsson, L., Hylander, K., Jacobson, C., 2004. Uncommon bryophytes in Swedish forests—key habitats and production forests compared. *Forest Ecol. Manage.* 194, 11–22.
- Heino, J., Virtanen, R., Vuori, K.-M., Saastamoinen, J., Ohtonen, A., Muotka, T., 2005. Spring bryophytes in forested landscapes: land use effects on bryophyte species richness, community structure and persistence. *Biol. Conserv.* 124, 539–545.
- Huggett, A.J., 2005. The concept and utility of ‘ecological thresholds’ in biodiversity conservation. *Biol. Conserv.* 124, 301–310.
- Humphrey, J.W., Davey, S., Peace, A.J., Ferris, R., Harding, K., 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. *Biol. Conserv.* 107, 165–180.
- Hurt, G., Pacala, S., 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *J. Theor. Biol.* 176, 1–12.
- Hylander, K., Dynesius, M., Jonsson, B.G., Nilsson, C., 2005. Substrate form determines the fate of bryophytes in riparian buffer strips. *Ecol. Appl.* 15, 674–688.
- Hylander, K., 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *J. Appl. Ecol.* 42, 518–525.
- Ingerpuu, N., Vellak, K., Kukk, T., Pärtel, M., 2001. Bryophyte and vascular plant species richness in boreo-nemoral moist forests and mires. *Biodiversity Conserv.* 10, 2153–2166.
- Jalonen, J., Vanha-Majamaa, I., 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. *Forest Ecol. Manage.* 146, 25–34.
- Jonsson, B.G., 1993. The bryophyte diaspore bank and its role after small-scale disturbance in a boreal forest. *J. Vegetat. Sci.* 4, 819–826.
- Jonsson, B.G., Jonsell, M., 1999. Exploring potential biodiversity indicators in boreal forests. *Biodiversity Conserv.* 8, 1417–1433.
- Karr, J.R., Dudley, D.R., 1981. Ecological perspective on water quality goals. *Environ. Manage.* 5, 55–68.
- Kolari, P., Pumpanen, J., Kulmala, L., Ilvesniemi, H., Nikinmaa, E., Grönholm, T., Hari, P., 2006. Forest floor vegetation plays an important role in photosynthetic production of boreal forests. *Forest Ecol. Manage.* 221, 241–248.
- Lindenmayer, D.B., 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *Forest Ecol. Manage.* 115, 277–287.
- Lindenmayer, D.B., Manning, A.D., Smith, P.L., Possingham, H.P., Fischer, J., Oliver, I., McCarthy, M.A., 2002. The focal-species approach and landscape restoration: a critique. *Conserv. Biol.* 16, 338–345.
- Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecological sustainable forest management. *Conserv. Biol.* 14, 941–950.
- Longton, R., 1984. The role of bryophytes in terrestrial ecosystems. *J. Hattori Bot. Lab.* 55, 147–163.
- Lundquist, J.E., Beatty, J.S., 1999. A conceptual model for defining and assessing condition of forest stands. *Environ. Manage.* 23, 519–525.
- MacNally, R., Fleishman, E., 2004. A successful predictive model of species richness based on indicator species. *Conserv. Biol.* 18, 646–654.
- McCune, B., Mefford, M.J., 1999. PC-Ord. Multivariate Analysis of Ecological Data. Vers. 4. MjM Software Design. Gleneden Beach, Oregon.
- Miller, N.G., McDaniel, S.F., 2004. Bryophyte dispersal inferred from colonization of an introduced substratum on Whiteface Mountain, New York. *Am. J. Bot.* 91, 1173–1182.
- Mills, S.E., MacDonald, S.E., 2004. Predictors of moss and liverwort species diversity of microsites in conifer-dominated boreal forest. *J. Vegetat. Sci.* 15, 189–198.
- Moen, J., Jonsson, B.G., 2003. Edge effects on liverworts and lichens in forest patches in a mosaic of boreal forest and wetland. *Conserv. Biol.* 17, 380–388.
- Moser, D., Zeichmeister, H.G., Plutzer, C., Sauberer, N., Wrba, T., Grabherr, G., 2002. Landscape patch shape complexity as an effective measure for plant species richness in rural landscapes. *Landscape Ecol.* 17, 657–669.
- Müller, F., Lenz, R., 2006. Ecological indicators: theoretical fundamentals of consistent applications in environmental management. *Ecol. Indicators* 6, 1–5.
- Newmaster, S.G., Bell, F.W., 2002. The effects of silvicultural disturbances on cryptogam diversity in the boreal-mixedwood forest. *Can. J. Forest Res.* 32, 38–521.
- Newmaster, S.G., Belland, R.J., Arsenault, A., Vitt, D.H., 2003. Patterns of bryophyte diversity in humid coastal and inland cedar-hemlock forests of British Columbia. *Environ. Rev.* 11 (Supplement), 159–185.
- Nicholson, B.J., Gignac, L.D., 1995. Ecotope dimensions of peatland bryophyte indicators species along gradients in the Mackenzie River Basin, Canada. *Bryologist* 98, 437–451.
- Niemi, G.J., McDonald, M.E., 2004. Application of ecological indicators. *Annual Rev. Ecol. Syst.* 35, 89–111.
- Nilsson, S.G., Arup, U., Baranowski, R., Ekman, S., 1995. Tree-dependent lichens and beetles as indicators in conservation forests. *Conserv. Biol.* 9, 1208–1215.
- Norden, B., Appelqvist, T., 2001. Conceptual problems of ecological continuity and its bioindicators. *Biodiversity Conserv.* 10, 779–791.
- Parrish, J.D., Braun, D.P., Unnasch, R.S., 2003. Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioScience* 53, 851–860.
- Pesch, R., Schroeder, W., 2006. Mosses as bioindicators for metal accumulation: statistical aggregation of measurement data to exposure indices. *Ecol. Indicators* 6, 137–152.
- Pharo, E.J., Beattie, A.J., Binns, D., 1999. Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conserv. Biol.* 13, 282–292.
- Pharo, E.J., Vitt, D.H., 2000. Local variation in bryophyte and macro-lichen cover and diversity in montane forests of western Canada. *Bryologist* 103, 455–466.
- Pykälä, J., 2004. Effects of new forestry practices on rare epiphytic macro-lichens. *Conserv. Biol.* 18, 831–838.
- Rambo, T.R., 2001. Decaying logs and habitat heterogeneity: Implications for bryophyte diversity in Western Oregon forests. *Northwest Sci.* 75, 270–279.
- Rambo, T.R., Muir, P.S., 1998. Bryophyte species associations with coarse woody debris and stand ages in Oregon. *Bryologist* 101, 366–376.
- Rieley, J., Richards, P., Bebbington, A., 1979. The ecological role of bryophytes in a North Wales woodland. *J. Ecol.* 67, 497–527.
- Roberts, M., Zhu, L.-X., 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. *Forestry Ecol. Manage.* 155, 17–31.
- Rolstad, J., Gjerde, I., Gundersen, V.S., Saetersdal, M., 2002. Use of indicator species to assess forest continuity: a critique. *Conserv. Biol.* 16, 253–257.
- Ross-Davis, A.L., Frego, K.A., 2002. Comparison of three managed forest types in the Acadian forest: diversity of forest floor bryophyte community and habitat features. *Can. J. Bot.* 80, 21–23.
- Ross-Davis, A.L., Frego, K.A., 2004. Propagule sources of forest floor bryophytes: spatiotemporal composition patterns. *Bryologist* 107, 88–97.
- Rydgren, K., Økland, R.H., Økland, T., 1998. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal forests. 4 Effects of experimental fine-scale disturbance. *Oikos* 82, 5–19.
- Saetersdal, M., Gjerde, I., Blom, H.H., 2005. Indicator species and the problem of spatial inconsistency in nestedness patterns. *Biol. Conserv.* 122, 305–316.
- Saetersdal, M., Gjerde, I., Blom, H.H., Ihlen, P.G., Myrseth, E.W., Pommeresche, R., Skartveit, J., Solhøy, T., Aas, O., 2003. Vascular plants as a surrogate species group in complementary site selection for bryophytes,

- macrolichens, spiders, carabids, staphylinids, snails and wood living pore fungi in a northern forest. *Biol. Conserv.* 115, 21–31.
- Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.-M., Bieringer, G., Milasowsky, N., Moser, D., Plutzar, C., Pollheimer, M., Storch, C., Tröstl, R., Zechmeister, H., Grabherr, G., 2004. Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. *Biol. Conserv.* 117, 181–190.
- Schaffers, A.P., Sýkora, K.V., 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *J. Vegetat. Sci.* 11, 225–244.
- Schofield, W.B., 1985. *Introduction to Bryology*. Macmillan Publishing, New York.
- Shacklette, H.T., 1965. Bryophytes associated with mineral deposits and solutions in Alaska. *Contributions to geochemical prospecting for minerals. Geol. Survey Bull.* 1198C, 17–18.
- Shacklette, H.T., Erdman, J.A., 1982. Uranium in spring water and bryophytes at Basin Creek in central Idaho. *J. Geochem. Explor.* 17, 221–236.
- Simberloff, D., 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Biol. Conserv.* 83, 247–257.
- Simberloff, D., 1999. The role of science in the preservation of forest biodiversity. *Forest Ecol. Manage.* 115, 101–111.
- Sollows, M.C., Frego, K.A., Norfolk, C., 2001. Recovery of *Bazzania trilobata* following desiccation. *Bryologist* 104, 421–429.
- Steel, J.B., Wilson, J.B., Anderson, B.J., Lodge, R.H.E., Tangney, R.S., 2004. Are bryophyte communities different from higher-plant communities? Abundance relations. *Oikos* 104, 479–486.
- Stork, N.E., Boyle, T.J.B., Dale, V., Eeley, H., Finegan, B., Lawes, M., Manokaran, N., Prabhu, R., Soberon, J., 1997. Criteria and indicators for assessing the sustainability of forest management: conservation of biodiversity. Working paper no. 17. Center for International Forestry Research, Jakarta, Indonesia.
- Turner, P.A.M., Pharo, E.J., 2005. Influence of substrate type and forest age on bryophyte species distribution in Tasmanian mixed forest. *Bryologist* 108, 67–85.
- Uotila, A., Kouki, J., 2005. Understorey vegetation in spruce-dominated forests in eastern Finland and Russian Karelia: successional patterns after anthropogenic and natural disturbances. *Forest Ecol. Manage.* 215, 113–137.
- Vanderpoorten, A., Engels, P., 2003. Patterns of bryophyte diversity and rarity at a regional scale. *Biodiversity Conserv.* 12, 545–553.
- Vanderpoorten, A., Engels, P., Sotiaux, A., 2004. Trends in diversity and abundance of obligate epiphytic bryophytes in a highly managed landscape. *Ecography* 27, 567–576.
- Vellak, K., Paal, J., 1999. Diversity of bryophyte vegetation in some forest types in Estonia: a comparison of old unmanaged and managed forests. *Biodiversity Conserv.* 8, 1595–1620.
- Vitt, D.H., Halsey, L.A., Bray, J., Kinser, A., 2003. Patterns of bryophyte richness in a complex boreal landscape: identifying key habitats at McClelland Lake Wetland. *Bryologist* 106, 372–382.
- Weetman, G., 1968. The relationship between feather moss growth and the nutrition of black spruce. In: *Proceedings of the Third International Peat Congress, Quebec*, pp. 366–370.
- White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Inc., pp. 3–13.
- Zechmeister, H.G., Moser, D., 2001. The influence of agricultural land-use intensity on bryophyte species richness. *Biodiversity Conserv.* 10, 1609–1625.