

The Bryosphere: An Integral and Influential Component of the Earth's Biosphere

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ABSTRACT

A significant fraction of the Earth's land surface is dominated by bryophytes. Research on carbon and nitrogen budgets of tundra, boreal, and peatland ecosystems has demonstrated the important role of mosses in understanding global change. Bryophytes are also habitat to a highly diverse microbiota that plays a key role in the function of these ecosystems. Here we define the term *bryosphere* to emphasize the combined role of mosses and their associated organisms in the functioning of ecosystems from local to global scales. In this minireview, we emphasize the value of the bryosphere as a spatially bounded, whole ecosystem that integrates aboveground and belowground processes, and we highlight the potential of the bryosphere as a natural model system (NMS) to assist in the study of environmental change on biodiversity and ecosystem functioning. We propose a formal definition of the bryosphere, attempt to summarize the current state of knowledge of the bryosphere, and discuss how the bryosphere can be a complex yet tractable

system under an NMS framework. Recent use of the bryosphere as an NMS has shown how alterations in food web structure can affect ecosystem function in a manner that, although predicted by theory, has remained largely untested by experiment. An understanding of the biodiversity, ecosystem functioning, and adaptation of the bryosphere can be advanced by manipulative experiments coupled with a blend of techniques in molecular, physiological, community, and ecosystem ecology. Although studies described herein have demonstrated the utility of the bryosphere NMS for addressing ecological theory, the bryosphere is an underutilized system with exceptional promise.

Key words: aboveground; belowground; bryobiota; bryophyte; bryosphere; cyanobacteria; detrital food web; global carbon budget; natural model system; mosses.

INTRODUCTION

Mosses (division Bryophyta) are ubiquitous, occurring in aquatic and terrestrial biomes from the tropics to high latitudes, and are currently studied as integral parts of many ecosystems (such as

peatland and boreal forest) because they contribute substantially to aboveground vegetative leaf area (Bond-Lamberty and Gower 2007) and biomass, and are important players in ecosystem processes (Van Cleve and others 1986; Swanson and Flanagan 2001; DeLucia and others 2003), in particular the global carbon (C) cycle (Oechel and Van Cleve 1986; Turetsky 2003; Douma and others 2007; Gornall and others 2007). Mosses, in association with symbiotic cyanobacteria, are also the largest source of biological nitrogen (N) fixation in

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pristine ecosystems (Turetsky 2003) and contribute significantly to global N budgets (Matzek and Vitousek 2003; Zackrisson and others 2004; DeLuca and others 2002, 2007, 2008; Lagerström and others 2007).

In many ecosystems, mosses form expansive ground cover, capturing particulate organic debris and atmospheric nutrients at the surface while transforming soil microclimates and altering decomposition rates below (Chapin and others 1987; Carleton and Dunham 2003; Cornelissen and others 2007). Mosses are habitat for a large diversity of microflora, microfauna, and mesofauna including bacteria, algae, fungi, bacteria, rotifers, tardigrades, nematodes, mites, springtails, and other arthropods, which together form a complex detrital food web (Gerson 1982; Usher and Booth 1986; Döbbeler 1997; Anderson 2006; Boeckner and others 2006; Kausrud and others 2008). In this review we propose the term *bryosphere* to represent the combined complex of living and dead moss tissue and associated organisms. Given the large area and broad distribution of mosses, the bryosphere is likely to be a particularly influential detrital system.

Despite the recognition that detrital systems can have a strong influence on the structure and dynamics of ecosystem-level attributes through above and belowground linkages (Wardle and others 2004), and the processes of decomposition and nutrient cycling, there is a dearth of studies that consider the functional importance of the moss-associated biota (bryobiota) (Davis 1981). A better understanding of the relationship between above and belowground systems at local and regional scales is necessary to understand the controls of bryosphere diversity and maintain ecosystem function (Wardle and others 2004). Key areas for a combined aboveground–belowground approach to modeling ecosystem dynamics are outlined in Van der Putten and others (2009), and here we suggest that a deeper understanding of the functional role of mosses will follow when the moss and associated organisms are itself considered a whole ecosystem—the bryosphere. Additionally, the bryosphere can be studied in the laboratory and greenhouse through the use of moss monoliths, and recent experiments (for example, Staddon and others 2010) have demonstrated the value of this natural model system (NMS; Srivastava and others 2004) as a test bed for the validation of general ecological theory, and as an ideal venue for evaluating the impacts of global change drivers on moss-dominated ecosystems. In this minireview, we (1) propose a formal definition of the bryosphere, (2)

summarize a current state of knowledge for the bryosphere, and (3) discuss how the bryosphere can be a complex yet tractable model system. Furthermore, we propose that the bryosphere can significantly influence ecosystem processes at local to global scales, and represents an important focus of global change biology.

THE BRYOSPHERE

The motivation to define the bryosphere stems from the growing recognition that detrital systems can have a strong influence on the structure and dynamics of ecosystem-level attributes through linked above and belowground processes (Wardle and others 2004). Yet at the same time, comprehensive studies incorporating above and belowground ecosystem components are almost entirely lacking (McGuire and others 2000). The *bryosphere* is defined as the combined complex of living and dead moss tissue and associated organisms, representing a tightly coupled system of both above and belowground processes. It covers a large proportion of the terrestrial Earth's surface and exists at the interface of the lithosphere, pedosphere, atmosphere, and hydrosphere. The nature of the bryosphere can be variable (for example, aquatic or terrestrial, patchy or continuous) but the key functional aspect of the system is governed by the physiological responses, coupling of above and belowground components, and the inquiline nature of the moss plant. Although we focus on the terrestrial bryosphere in temperate, boreal, and polar regions, as this is where the most research has occurred, we also acknowledge that the bryosphere is present in aquatic (Suren 1991), arboreal (Sillett and Antoine 2004), or desert (Neher and others 2009) ecosystems. Although the bryophytes are comprised of three taxa (liverworts, hornworts, and mosses), these are a paraphyletic group, and less is known about the liverworts and hornworts as a whole system. Mosses (Bryophyta) are the dominant taxa within this group, and can contribute a significant proportion to aboveground vegetative biomass in many ecosystems. Thus, we focus our definition on the Bryophyta; however, it is likely that the liverworts and hornworts can be incorporated or similarly defined.

The Physical Bryosphere

The bryosphere plays a variety of important functional roles in an ecosystem. It may contribute substantially to aboveground biomass and primary production, host N-fixing cyanobacteria, provide

soil N input, control soil chemistry and nutrition through accumulation of recalcitrant polyphenols and through control over soil and vegetation hydrology and temperatures, and prevent soil erosion (Cornelissen and others 2007). Many of these variables, however, are determined by the physical form of the bryosphere, which in turn is governed by the dominant moss species. Mosses are a diverse and wide-spread groups of plants, with over 10,000 described species worldwide (Buck and Goffinet 2000), and growth forms vary from tree-like independent stalks, compact cushions, or tufts, loose to dense mats (wefts), or long tapering strands hanging from branches or rocks. The depth of the bryosphere varies from a few centimeters (for example, those growing on rocks) to meters (for example, those in peatlands).

In general, all mosses share a similar vertical structure separated into the aboveground 'green'

zone of alive, growing, and/or photosynthetically active moss, and a belowground 'brown' zone of senescent, dead, and/or decaying moss, rhizoids, and other detritus (Figure 1). The relative proportions of the above and belowground components depend on the moss species (Oechel and Van Cleve 1986) and the development stage of the bryosphere (Yanoviak and others 2004). Vertical zonation governs photosynthetic activity of the moss and abiotic factors such as moisture availability. Mosses, as non-vascular plants, are poikilohydric; they have no physiological mechanisms to prevent desiccation. Moisture is obtained by directly absorbing water through cell surfaces from nocturnal dew, distillate water vapor from the ground, or by external wicking from wet to dry zones via capillary channels formed by closely appressed dead moss stems (Carleton and Dunham 2003), thus forming three zones of moisture: (1) a top dry zone

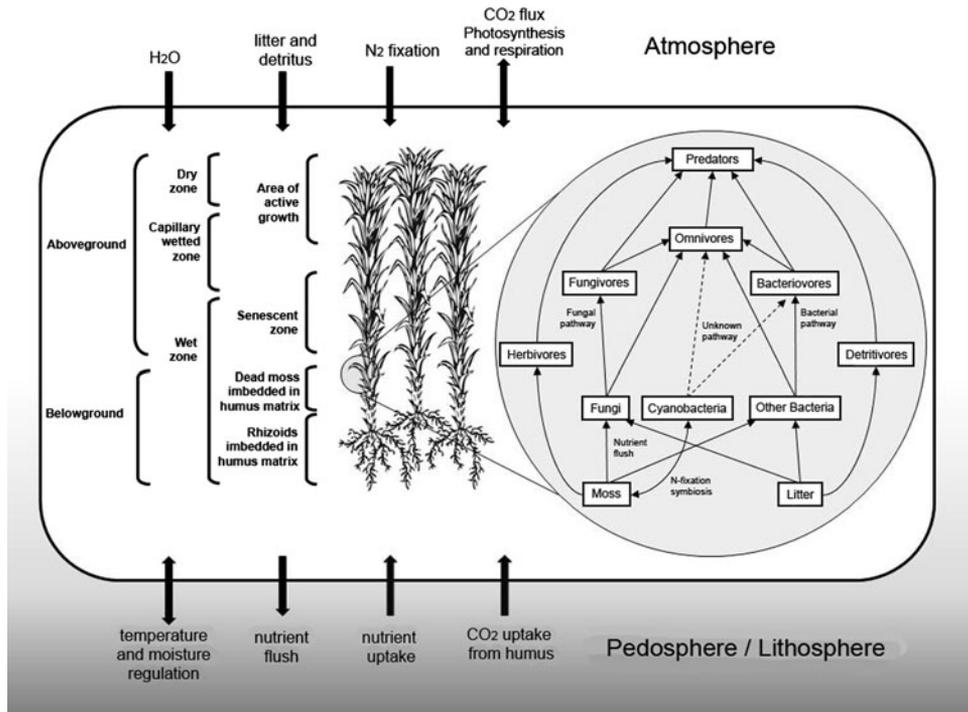


Figure 1. Vertical boundaries and ecosystem-level processes of the physical bryosphere portraying a conceptualized moss species. The bryosphere embodies the ecological linkages between above- and belowground ecosystems, allowing for use as a model system in whole ecosystem ecology. Mosses are a diverse and wide-spread group of plants: growth forms vary from tree-like independent stalks, compact cushions or tufts, loose to dense mats (wefts), or long tapering strands hanging from branches or rocks. In general, all mosses share a similar vertical structure separated into the aboveground 'green' zone of alive, growing and/or photosynthetically active moss, and a belowground 'brown' zone of senescent, dead and/or decaying moss, rhizoids and other detritus. The relative proportions of the above and belowground components will depend on the moss species and the development stage of the bryosphere. Within the bryosphere exists a diverse detrital food web (modeled after the detrital food web by Hunt and others 1987). Food web shown is arbitrarily placed within the bryosphere and is not restricted to the belowground parts of the bryosphere. The size of *circle* drawn represents the small spatial scale at which the diverse community interacts. A potential cyanobacterial nutrient and energy pathway is proposed; highlighted by *dashed lines*.

which experiences frequent wet/dry cycles, (2) a madicolous zone where the mosses are wetted by capillary action, and (3) a water-covered or predominantly wet zone (after Lindegaard and others 1975) (Figure 1).

Moss leaves vary in photosynthetic activity with distance from top of a stem, with the capacity to fix C declining steeply with depth (Zotz and Kahler 2007). Water content strongly influences light attenuation as dry conditions shrivel the plant and allows more light to penetrate deeper into moss, which transiently allows positive CO₂ uptake rates at depth until the entire moss is desiccated (Zotz and Kahler 2007). Combined with high estimates of stand-level leaf area index for boreal and peatland mosses, the contribution of the bryosphere in these zones is substantial to energy, water, and carbon dioxide exchange, and ecosystem productivity (Bond-Lamberty and Gower 2007). However, moisture stress during dry periods can occur even where annual precipitation exceeds net evapotranspiration (for example, boreal zones, Carleton and Dunham 2003; DeLucia and others 2003), during which time the moss will desiccate and remain dormant, but rehydrate when water becomes available.

Inhabitants of the Bryosphere

The bryosphere can be thought of as similar to an inquiline system whereby mosses host a numerous and diverse community of microorganisms and invertebrates including fungi, bacteria, cyanobacteria, tardigrades, nematodes, mites, and springtails. Yet, the bryosphere community (the bryobiota) as a comprehensive food web has never been formally proposed and defined (but see Davis 1981). The terms previously ascribed to the flora and fauna of the bryosphere (following Gerson 1982) are the 'bryobionts' which occur exclusively in association with mosses; the 'bryophiles' which usually associate with mosses but may survive elsewhere; the 'bryoxenes' that regularly spend part of a life cycle associated with moss; and the 'occasionals' which are found elsewhere regularly, and are not necessarily associated with mosses. Many of these terms are not in general use today, except the term 'bryophilous' which is commonly used among mycologists.

Davey and Currah (2006) give an extensive review of the interactions among mosses and fungi, listing zygomycetes, ascomycetes, basidiomycetes, and oomycetes having a variety of interactions including pathogenic, parasitic, saprobic, and commensal relationships with mosses. Döbbeler

(1997) lists approximately 300 species of ascomycetes alone known to grow obligately on moss gametophytes. Many mycorrhizal fungi (arbuscular and ectomycorrhizal) often colonize dead and senescent portions of the moss (Carleton and Read 1991), and benefit from the nutrient-rich aqueous leachates following wet/dry cycles (Davey and Currah 2006). Although it may not be surprising to observe a diversity of fungi associated with detrital portions of the bryosphere, many different fungal types are associated with the living top few centimeters of boreal forest mosses (Kausrud and others 2008). Kausrud and others (2008) identified 158 genetically distinct fungal species-types associated with shoot tips on only 27 stems of 3 common boreal moss species (*Pleurozium schreberi*, *Hylocomium splendens*, and *Polytrichum commune*), the majority of which were observed only once. The seeming high diversity and rarity of these fungal species was in part attributed to incidental occurrences due to stochastic dispersal events such as mycorrhizal or saprobic fungi associated with falling litter and needle debris. However, citing the possible parasitic associations between fungi and moss, Kausrud and others (2008) invite more experimental studies to investigate the causal relationships and interactions between moss and fungi.

Although there is some knowledge of the fungi associated with mosses, there is a paucity of information on the bacterial component of the bryosphere. The exception, however, is N-fixing cyanobacteria which form symbiotic associations with moss (DeLuca and others 2002). Solheim and Zielke (2002) and Adams and Duggan (2008) give comprehensive reviews of the associations between cyanobacteria and mosses, citing the importance of the N-fixing symbiosis as an important supply of N in local ecosystems of the Arctic, Antarctic, and boreal forest regions (Zielke and others 2005). DeLuca and others (2002) suggest that the symbiotic association of the cyanobacterium, *Nostoc* spp. with the ubiquitous boreal feather mosses, *P. schreberi* and *H. splendens*, contributes significantly to global N budgets.

Gerson (1982) provides an excellent review of the fauna associated with the bryosphere giving the most extensive and detailed information compiled from, albeit now older references, of studies on the invertebrates associated with mosses. Many studies focus on describing the two different groups of fauna that differ in size and spatial position within the moss: the microfauna (<100 µm) that live in the water film around the plant (this includes protozoa, rotifers, nematodes, and tardigrades), or

the mesofauna (100 μm to 2 mm) which inhabit the dry, air-filled pore spaces (this includes collembola, proturans, myriapods, insects, and arachnids, in particular mites) (after Swift and others 1979). More recent studies of the bryo-microfauna include Anderson (2006) which documents approximately 50 morphotypes of naked amoebae from a single site in northeast US region, Boeckner and others (2006) who found 6 rotifer species, 23 nematode species, and 18 tardigrade species from only 3 sample sites on the east coast of Canada, and Jönsson (2003) who found 16 species of tardigrades in northern Sweden. Many of these studies document new species, and new species records for their region indicating that the bryosphere contains a highly diverse but understudied fauna.

One group of arthropods so ubiquitous to the bryosphere that they have been referred to as 'moss mites' is the oribatid mites (Acari: Oribatida, also Oribatei, Cryptostigmata, and Moosmilben) which are typically the dominant mesofauna in arctic, boreal, and arboreal mosses (Seniczak and Plichta 1978; Behan-Pelletier and Bissett 1994; Lindo and Visser 2003; Lindo and Winchester 2006; Schatz and Behan-Pelletier 2008). Other dominant groups include prostigmatid mites (Acari: Prostigmata) and Collembola whose density in the bryosphere can reach 100,000 individuals/ m^2 even in Antarctic regions (Block 1982). By comparison, Collembola densities have been found to range between 100 individuals and 670,000 individuals/ m^2 from desert and tropical grasslands to temperate and boreal coniferous forests (Petersen and Luxton 1982). Collembola densities tend to be greatest in raw humus and moss layers of the boreal conifer forest where densities can exceed 225,000 individuals/ m^2 , whereas temperate deciduous forest floors without mosses range between 40,000 and 70,000 individuals/ m^2 (Petersen and Luxton 1982). In isolated areas where mosses produce and possess their own humus regions, like saxicolous (on rocks) (Materna 2000) or arboreal (in trees) (Lindo and Winchester 2006) systems, species richness and abundance of microarthropods increase with humus development produced by the bryosphere itself, as well as through the accumulation of litter (Yanoviak and others 2004; Lindo 2010).

The extent and development stage of the bryosphere, particularly in these isolated habitats, is important for the invertebrate assemblages for three reasons: (1) buffering abiotic conditions at depth (Berg and Bengtsson 2007), (2) habitat heterogeneity of resources (Lawton and Schröder 1977; Southwood 1996), and (3) colonization

events (MacArthur and Wilson 1967; White and others 2006). Increased stability of bryosphere microclimates with increasing depth (Wallwork 1983), greater moisture-holding capacity of large moss areas (Lindo and Winchester 2007; Lindo and others 2008), and vertical stratification of species associated with differences in the structural aspects within different bryosphere layers (Yanoviak and others 2004) are parameters that contribute to increased species richness of bryophilous microarthropods (Lindo and Winchester 2007; Salmane and Brumelis 2008). As mosses are pioneering species on hard substrates and newly formed soils (Turetsky 2003), the successional patterns of the bryofauna can provide interesting insight regarding the dispersal patterns and processes that generate and maintain patterns of invertebrate diversity. First colonizers are usually smaller, passively dispersed individuals arriving by wind (rhizopods, rotifers, tardigrades, nematodes, and ciliates) (Gerson 1982). As decaying material forms under the moss, the detrital food web begins to develop; rotifers, tardigrades, and nematodes increase, while arthropods (collembola and mites) begin to colonize the bryosphere (Neher and others 2009). Eventually, rotifers and tardigrades decline as the development time and development stage of the moss continue and the fauna becomes more similar to organic soil communities.

THE BRYOSPHERE DETRITAL FOOD WEB

The food web that develops within the bryosphere is complex (Figure 1), consisting of multiple assemblages of species that are supported by detritus and the by-products of the moss plant itself. The moss plant forms the arena for a detrital food web that frequently houses symbiotic cyanobacteria, and supports microflora through the flush-release of nutrient associated with wet/dry cycles. Detritus from aboveground litter input, moss senescence, and belowground soil humus layers form the base of at least two linked energy channels: the bacterial and fungal pathways, as in other detrital systems (see Hunt and others 1987) (Figure 1). These channels differ in ways that are important to the availability of nutrients. The bacterial energy channel is composed of bacteria, protozoa, rotifers, nematodes, and a few arthropods. The fungal energy channel largely consists of the saprophytic and arbuscular- and ecto-mycorrhizal fungi, fungivorous arthropods, and nematodes. The fungal pathway is considered to be a slower, more stable pathway exploiting recalcitrant resources over a larger spatial scale than the bacterial pathway

which has fast turnover times associated with labile resources that are patchily distributed spatially and temporally (Coleman and others 1983, 2004).

Trophically, the invertebrate groups within the bryosphere span multiple levels and include complex feeding relations such as herbivory, fungivory, detritivory, omnivory, coprophagy, necrophagy, and opportunistic scavenging (Luxton 1972). Mites of the suborder Mesostigmata along with small spiders, pseudoscorpions, and some insect larva (Diptera and Coleoptera) comprise the majority of top predators. As the role of many microarthropods in decomposition and nutrient cycling processes is mainly indirect via the microbial components (Seastedt 1984), the absolute contribution of many groups to ecosystem function remains unquantified. However, there is a strong interaction between organismal abundance and diversity, and energy and nutrient flux within the bryosphere that occurs sometimes in surprising ways. For instance, Cronberg and others (2006) demonstrated that the presence of microarthropods within the bryosphere directly facilitated moss sperm transfer. Similarly, microarthropod feeding activities may disperse microbial propagules and spores, and may alter microbial community structure (Maraun and others 1998; Bardgett and Chan 1999).

Given the important role of cyanobacteria for atmospheric N fixation in the bryosphere (DeLuca and others 2002), it is evident then that organisms which feed or otherwise interact with cyanobacteria would also form an energy pathway that could have major implications for nutrient cycling at the ecosystem level (Figure 1). For example, Collembola feeding on cyanobacterial mats in the Arctic have been shown to decrease N-fixation rates at high grazing densities (Birkemoe and Liengen 2000). Patterns of N-fixation, similar to fungal biomass patterns, conform to the grazing optimization hypothesis (McNaughton 1979; Hilbert and others 1981) whereby the highest fixation rates are observed at low-to-intermediate grazing pressure (Birkemoe and Liengen 2000). The wide variety of trophic interactions and feeding strategies would support multiple pathways for energy and nutrient cycling within the bryosphere (Merrifield and Ingham 1998), and further research into the dynamics of a potential cyanobacterial pathway is warranted.

A combined above- and belowground approach to community and ecosystem ecology will enhance our understanding of the regulation and functional significance of biodiversity. The interdependence between the above- and belowground realms within the bryosphere can also be explained in

terms of the patterning of the trophic interactions and the influence of these interactions on the supply of nutrients and rates of nutrient uptake by the mosses themselves (Moore and others 2004; Wardle and others 2004). Aboveground communities are affected by both direct and indirect consequences of detrital food web organisms (Wardle and others 2004). Trophic interactions in detrital systems, like the bryosphere, have a large potential to influence ecosystem processes because the abundance and biomass of the microbial and microbivorous communities, which may be limited by predators, control energy flow, and nutrient cycling (Seastedt 1984; Wardle 2002). Furthermore, cascading functional effects in detrital food webs are expected to significantly alter ecosystem processes from local-to-global scales despite high levels of functional diversity and degeneracy (Schimel and Gullledge 1998; Swift and others 1998; Wolters and others 2000, 2003; Allison and Martiny 2008).

The increasing interest in biodiversity–ecosystem function relationships in ecology has stimulated research on food webs. The parameterization of real and model detrital food webs which incorporate energy and nutrient flow rates based on observations of population sizes, feeding preferences, N contents, life spans, assimilation efficiencies, and production:assimilation ratios have been useful for elucidating the mechanisms that maintain biodiversity and regulate nutrient dynamics in detrital systems (for example, Hunt and others 1987; de Ruiter and others 1998; Neutel and others 2002). A similar approach for the bryosphere is feasible, whereby attention paid to ecostoiometric ratios (C:N:P) during trophic transfer (Pokarzhevskii and others 2003) along with a mass balance approach (Bowden 1991) would help identify the limiting factors and processes that maintain patterns in bryosphere biodiversity.

NUTRIENT CYCLING WITHIN THE BRYOSPHERE

The poikilohydric nature of mosses combined with long periods of desiccation and moisture stress has important implications for nutrient dynamics within the bryosphere. For example, nutrients are released from moss following periods of desiccation (Wilson and Coxson 1999). The amount of nutrients released depends on a suite of abiotic events such as the intensity and duration of the rain event, the duration of the period of desiccation, and the rate of drying after the preceding rain event (Wilson and Coxson 1999). Yet significant amounts of dissolved organic carbon, N, and phosphorus (P)

are released from moss shoots upon rewetting (Carleton and Read 1991) and these nutrient flushes can be an important source for microbes (for example, mycorrhizal fungi, Moore and Dalva 2001; Davey and Currah 2006).

Turetsky (2003) gives a detailed review of the C and N dynamics which occur in the bryosphere, but generally mosses play an important role in nutrient cycling as they capture and accumulate detritus (Chapin and others 1987), fix C from atmospheric pools (Zotz and Kahler 2007), compete with vascular plants for N availability (Ayres and others 2006), and influence local soil climates and decomposition processes by increasing soil moisture and decreasing soil temperatures (Van Cleve and others 1983; Sveinbjornsson and Oechel 1991; Eckstein 2000; Gornall and others 2007) (Figure 1). In areas where mosses blanket the forest floor such as boreal or temperate rain forests, net primary productivity of the bryosphere can equal or exceed overstory vegetation (Oechel and Van Cleve 1986), although often limited by light, water, N, or P (Turetsky 2003).

Mosses which have low foliar N content are slow to decompose (Oechel and Van Cleve 1986; Carleton and Dunham 2003; Turetsky 2003), and have high N-use efficiency due to their ability to recycle N within stems during senescence (Eckstein and

Karlsson 1999). As such, a large proportion of N content is located in the non-productive, deeper tissues of mosses (Zotz and Kahler 2007). Furthermore, mosses may slow decomposition rates of belowground organic matter by keeping soil temperatures cool. Combined with recently observed symbiosis between moss and N-fixing cyanobacteria (DeLuca and others 2002), the bryosphere is an important C and N sink.

Global Contribution of the Bryosphere: C Budgets

Carbon stored globally in the bryosphere represents a large terrestrial pool, which is both a C sink and a C source. The factors affecting the net balance between C uptake and C release in terrestrial mosses are critical to the understanding of future atmospheric CO₂ concentrations and global climate change. Factors affecting whether mosses act as a net CO₂ sink (C uptake through process of photosynthesis and net primary productivity (growth)) or a CO₂ source (C release through plant respiration, decomposition, and heterotrophic soil respiration) include broad abiotic conditions such as light, temperature, moisture, and local atmospheric CO₂ conditions (Figure 2). Physiological photosynthetic

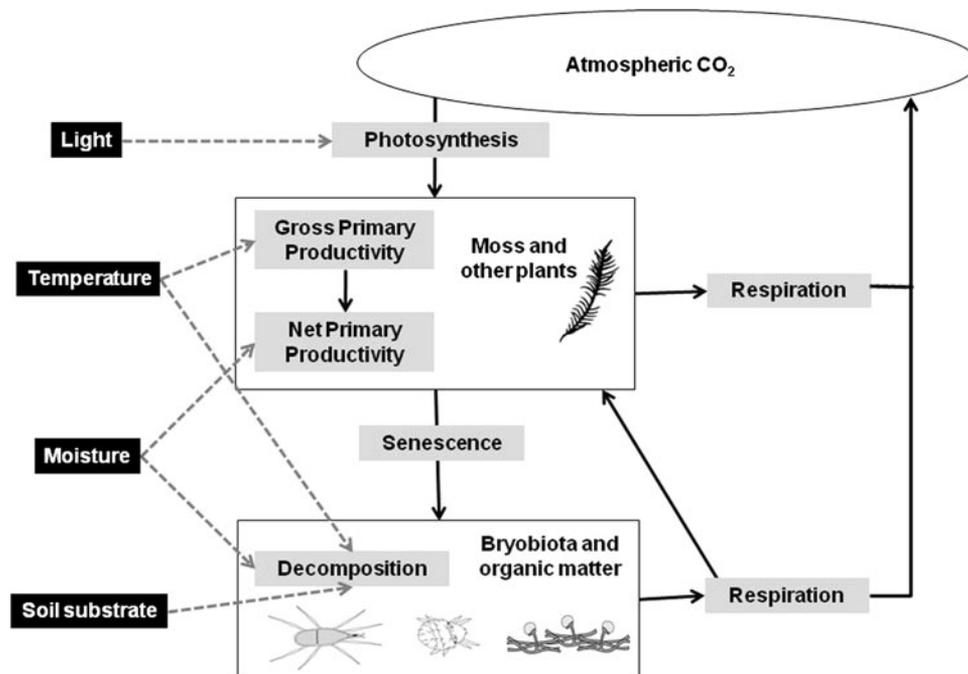


Figure 2. The generalized C cycle for the bryosphere at local to global scales. The processes that couple the bryosphere to regional conditions (through climate and soil type) and to global climate (through C flux) are modeled after Chapin and others (2000). C sources/sinks are in bounded boxes spanning above- and belowground ecosystem realms. Arrows connecting boxes indicate C pathways only and do not represent quantities or relative rates of C flux. Processes are in gray shade, whereas factors affecting processes are in black.

responses of mosses to light, temperature, and atmospheric CO₂ concentrations are essentially the same as other plants, interacting to produce a complex but tractable four-dimensional response curve (see Proctor 1982). Net photosynthesis (gross photosynthesis minus respiration of the plant) can generally occur as long as temperatures are above zero with temperature optima ranging 5–20°C for most species (Proctor 1982). The poikilohydric nature of moss plants and consequently the availability of water regulate most physiological responses including photosynthesis, and as such is the most important factor influencing C balance in mosses (Harden and others 1997; DeLucia and others 2003; Rice and others 2008; Dise 2009). Mosses fix CO₂ during photosynthesis in similar fashion to C₃ plants; however, an ability to utilize other C sources, such as methane (CH₄), has been demonstrated for peatlands (Raghoebarsing and others 2005). In addition to utilizing atmospheric CO₂, the bryosphere, existing within the boundary layer next to the ground, also captures an estimated 10–36% of total forest floor CO₂ efflux from decomposition and heterotrophic soil respiration (Morén and Lindroth 2000; Swanson and Flanagan 2001; DeLucia and others 2003).

Carbon sequestration is further promoted in moss systems through the production of highly recalcitrant litter containing low N, and high phenolics and structural carbohydrates (Jonsson and Wardle 2010). As such, decomposition rates of mosses are generally lower than for vascular plants (Lang and others 2009) leading to organic matter accumulation and C sequestration of a globally significant magnitude (Gorham 1991). Climate (temperature and moisture) and litter quality are the primary drivers of decomposition, but soil substrate (CaCO₃ concentrations and soil pH) can also regulate the flux of nutrients in detrital systems (Adl 2003; Wall and others 2008). Other plants co-occurring with the bryosphere may affect C accumulation as relative C:N ratios of litter (litter quality) affect decomposition rates and subsequently soil respiration efflux. Additionally, the microbial and faunal community within the soil and bryosphere play an important role in C uptake and contribute to overall respiration rates within the bryosphere (Anderson 2008).

The bryosphere plays an important global role in C cycling, through the storage of C, the efflux of CO₂, the production of dissolved organic C, and the emission of CH₄. There is thus an obvious need to understand how the bryosphere will be affected by increased atmospheric concentration of CO₂, climate warming, and other disturbances (for

example, fire) over the coming century (Turetsky and others 2002). Currently, there is uncertainty in predicting the effect of climate change on the C cycling in the bryosphere, and in particular whether it will switch from a net C source to C sink (Chapin and others 2000). Three main results have come from manipulative elevated CO₂ experiments in peatlands: (1) the specific response to elevated CO₂ differs among bryophyte species (Van der Heijden and others 2000b; Berendse and others 2001; Toet and others 2006), (2) specific responses are influenced by the interaction of CO₂ and N availability (Van der Heijden and others 2000a), and (3) community-level outcomes are a complex interaction of the specific responses of mosses, vascular plants, and nutrient availability. For example, Heijmans and others (2001) transplanted intact monoliths of *Sphagnum magellanicum* from a heathland bog to a grassland miniFACE experiment where monoliths were exposed to ambient and elevated CO₂ concentrations at 560 ppm. High CO₂ increased *Sphagnum* growth in the second and third growing seasons, a response that negatively affected vascular plant species growing close to the moss surface. However, the addition of N favored vascular plant growth, which subsequently reduced *Sphagnum* growth by 32% in the third growing season.

As the bryosphere represents a significant global C pool, the potential for feedback effects of global climate change including increased temperatures and elevated CO₂ levels are large. Areas of most concern include boreal (Hollingsworth and others 2008) and subarctic (Goulden and Crill 1997; Campioli and others 2009) ecosystems with high accumulations of feathermosses (*Pleurozium* and *Hylocomium*) and peatlands (*Sphagnum*). The diversity of *Sphagnum* moss species is an important predictor of soil C sequestration in boreal forests (Hollingsworth and others 2008). *Sphagnum* species, the dominant species in peatlands, act as ecosystem engineers, creating conditions that favor C sequestration. Anaerobic decomposition under waterlogged conditions in peatlands leads to extremely low levels of decomposition and C release (CH₄ and CO₂). Gorham (1991) reviewed the response of peatlands in boreal and subarctic systems to climate warming with respect to the global C cycle, and concluded that the interaction of multiple direct human habitat alterations, such as land-use change and global climate change can produce idiosyncratic outcomes for many variables of the bryosphere C cycle (Figure 2). More recently, Turetsky and others (2002) emphasized the importance of understanding anthropogenic

disturbance on peatlands as a C sink. Particular threats to peatlands include draining, peat extraction, peatland conversion for industry, as well as increases in temperatures (Turetsky and others 2002). Peatlands have been suggested as complex adaptive systems, resilient to change at some levels of perturbation, but shifting to new states at higher levels of perturbation (Dise 2009). More research on the existence of multiple stable states in the bryosphere is required.

Global Contribution of the Bryosphere: N Fixation

Biological N₂ fixation (BNF) is the main pathway by which reactive N enters into terrestrial ecosystems and is a major source of N input to many natural systems (Cleveland and others 1999; DeLuca and others 2002; Turetsky 2003). Recent studies show cyanobacteria form symbiotic associations with mosses which fix N in boreal forest systems, contributing significantly to whole forest-level or even global N budgets (DeLuca and others 2002). BNF rates by cyanobacteria of 1–41 kg/ha/y have been reported for terrestrial environments (Cleveland and others 1999) contributing an important supply of N in Arctic, Antarctic, and boreal ecosystems (Zielke and others 2005). Moisture, temperature, light, and nutrient conditions are thought to be the foremost environmental factors influencing N₂ fixation in Arctic and sub-arctic ecosystems (Gentili and others 2005), and are the primary limits on bryophyte growth (Turetsky 2003). In boreal and temperate systems, soil nutrient status is thought to be most important, particularly N, P, and their combined ratios (Matzek and Vitousek 2003; Benner and Vitousek 2007; DeLuca and others 2007). Evidence supporting that N availability governs N-fixation rates (DeLuca and others 2007) comes from nutrient addition experiments (but see Markham 2009 for non-significant results of nutrient additions) and field-based correlations of nutrient status and BNF rates as measured by acetylene reduction assays (Matzek and Vitousek 2003; Zackrisson and others 2004; DeLuca and others 2007, 2008; Lagerström and others 2007).

This negative relationship between BNF rate and N availability (termed ‘nitrostat’ by Menge and Hedin 2009) is generally accepted, as the process of N-fixation is energetically expensive. However, recent findings suggest that BNF contributions from sources that are ‘spatially decoupled’ from forest floor N pools (for example, arboreal mosses)

perform BNF regardless of soil N conditions, responding only to local conditions (Menge and Hedin 2009). Menge and Hedin (2009) further suggest that BNF from arboreal sources may create a positive N feedback loop, as high soil N could indirectly increase epiphytic biomass and consequently arboreal BNF. Feedback loops, whether positive or negative, for C or N, within the bryosphere and among other components of forest systems may occur over hierarchically structured spatial scales. Unraveling the complexities of the bryosphere N cycle over these scales provides many avenues for future research.

EXPERIMENTAL MODEL SYSTEMS FOR THE BRYOSPHERE

Despite the recognition that detrital food webs can have a strong influence on the structure and dynamics of ecosystem attributes, and for their coupling to the aboveground food web, many ecological models are inept to explain the structure and function of detrital systems. Furthermore, our lack of understanding of detrital systems has global consequences regarding C storage, nutrient translocation, environmental pollution, and climate change (Swift and others 1998; Wardle and others 1998; Wolters and others 2000; Bardgett 2005; Wall 2007). There is a need for comprehensive models which are interdisciplinary, which model relationships across scales, and which simulate future scenarios for detrital systems and overall ecosystem function (Wardle 2002; Hooper and others 2005). A promising approach is the use of the bryosphere as a complex yet tractable model system to study the impact of environmental change on biodiversity and ecosystem function.

The bryosphere even as an isolated model system offers the opportunity to study many facets of ecosystem processes. The layered and compact spatial structure of the bryosphere means that it can be sampled and manipulated as a whole system in the field, or easily transported and grown in the laboratory or greenhouse for carefully controlled experimentation. These structural properties suggest that mosses may be used as an NMS (Srivastava and others 2004). The bryosphere, whether studied in the field as part of a larger ecosystem, or in the lab/greenhouse as a model system can reveal central and relevant information on (1) the processes which generate, maintain, or alter patterns of biodiversity, (2) the relationship between biodiversity and ecosystem processes such as decomposition and nutrient cycling, and (3) the issue of scale (spatial,

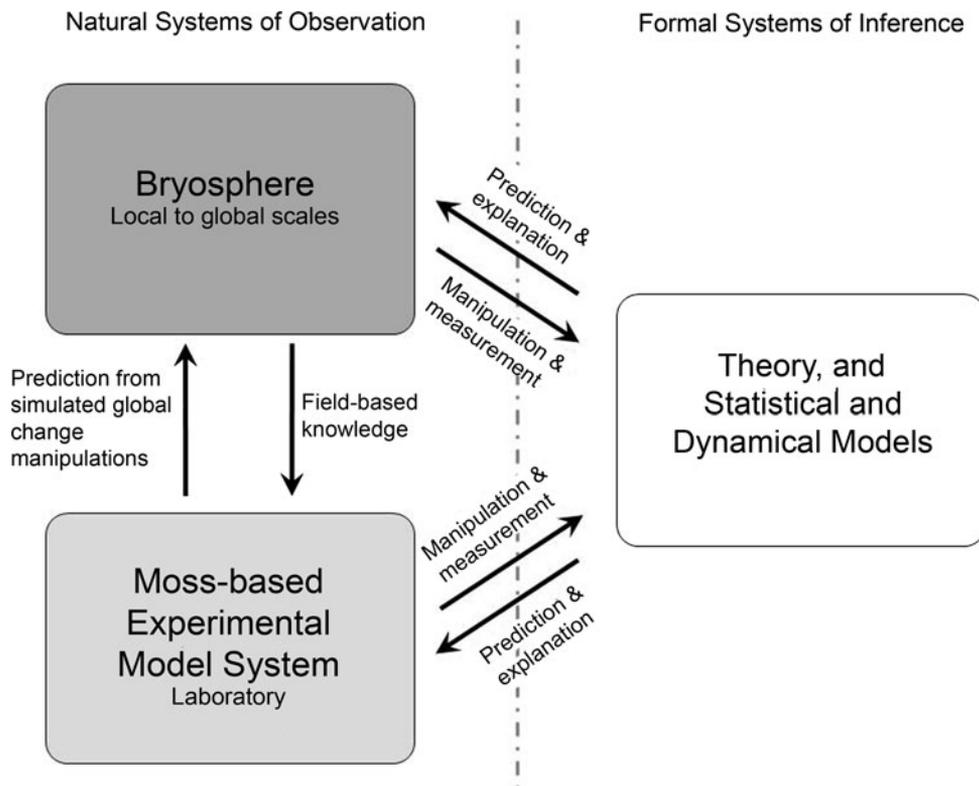


Figure 3. The modeling relation (Rosen 1991) that underpins the framework for establishing a natural or experiment model system (NMS) as a successful component of the scientific process. Measurements on the bryosphere are encoded in models (top left to center right). Study of these models generates inference about the functioning of the bryosphere. Repeated cycles of measurement, manipulation, and prediction leads asymptotically to improved models and greater understanding of the functioning of the bryosphere. The NMS (lower left) is distinct from artificial or synthetic model systems because it is maintained and manipulated as an intact ecosystem. Because of this the theory and models previously developed can also be used to explain and predict the functioning of the NMS. The NMS can be experimentally manipulated to inform further modification and improvement of the models and improve understanding of the bryosphere itself. Manipulation of the NMS under controlled conditions can be used to generate a range of future scenarios of environmental change. The measured response of the NMS to these scenarios can be used to directly inform the likely response of the bryosphere to environmental change (from lower left to upper left), and to improve the models (lower left to center right), that can then be used to integrate missing but crucial features of scale to predict the future response of the bryosphere to environmental change (moving from center right to upper left).

temporal, functional, and phylogenetic) in ecological research which can confound the inference of process from patterns of biodiversity.

Figure 3 shows the modeling relation (Rosen 1991) that underpins the framework for establishing an NMS as a successful component of the scientific process. To date most progress in our understanding of the bryosphere has been achieved by observing it directly under field conditions (upper left in Figure 3) without too much inference from theoretical perspectives (right side Figure 3), and vice versa. The NMS (lower left in Figure 3) is distinct because it is maintained and manipulated as an intact ecosystem, yet isolated from many confounding variables. Theory and models can be

developed to explain and predict the functioning of the NMS, and the NMS can be used to test the theory and models. Field observations and experiments can validate the findings of the iterative cycle between the NMS and theory. The repeated use of the NMS, field experiments, and mathematical modeling leads asymptotically to a greater understanding of the bryosphere. Crucially, the small scale of the NMS lends it to relatively short-term studies of the response of the system to entirely novel environmental conditions. For example, consider a press or pulse manipulation of the bryosphere NMS under controlled conditions (lab or greenhouse). Such manipulations can be used to generate a range of future scenarios of

environmental change, and the measured response of the bryosphere NMS to these scenarios can be used to directly inform the likely response of the natural bryosphere to environmental change (from lower left to upper left in Figure 3). In addition, the measured response of the bryosphere NMS to environmental change can inform new theoretical models (lower left to centre right) that can then be used to integrate missing but crucial features of scale to predict the future response of the bryosphere to environmental change (moving from center right to upper left).

The bryosphere has a recent history of use as an NMS for addressing ecological theory in community ecology (Gilbert and others 1998; Gonzalez and Chaneton 2002; Hoyle 2004; Starzomski and Srivastava 2007). Experimental fragmentation of extensive carpets of moss, both in the field and greenhouse, has validated theories of extinction, and how immigrations mediate the relative abundance and distribution of the bryobiota (Gonzalez 2000; Hoyle 2004). Experiments with the moss NMS have also revealed the importance of moss diversity and fragmentation for various facets of bryosphere ecosystem function (Mulder and others 2001; Jonsson and Wardle 2010). In these experiments, the small size of the bryosphere provided a terrestrial system, with a highly diverse and complex food web, that was replicated quickly, easily, and cheaply in the field and in the greenhouse, and which provided results near analogous to whole forest experimental treatments at a fraction of the scale. We suggest that the use of the bryosphere, and other similar model experimental systems, can be invaluable for testing predictions generated from theoretical models prior to embarking on larger-scale experimental projects.

THE CAVEATS, CHALLENGES, AND LIMITATIONS

The small size, high diversity, and ease of manipulation and handling make the bryosphere NMS a relatively low cost, readily available, and attractive NMS. However, all models have limitations; the small size of the moss NMS limits inferences about large-scale phenomena, the high diversity of the system highlights significant limits in taxonomic knowledge, and specific physiological traits of the moss plant itself can reduce the transferability of results to other systems. The importance of using appropriate model systems to ask questions in ecology and biology is acknowledged, and Srivastava and others (2004) discuss in detail the unique challenges and benefits of using NMSs. One

important point raised is that not all assumptions regarding natural systems will be met by all taxa within an NMS context, and small-scale experiments may not capture the effect of some larger-scale-dependent processes. For instance, the bryosphere NMS within a laboratory or greenhouse setting cannot incorporate all species that might interact with the moss-detrital food web under natural conditions.

High species richness and the small size of organisms within the moss NMS require at least a moderate degree of taxonomic expertise. Closer collaboration between taxonomic specialists and ecologists, more easily accessible taxonomic information, and joint grant proposals that incorporate the expense of taxonomic specialists are various suggestions for overcoming the limitations of non-specialists (Gotelli 2004) in utilizing the bryosphere as a model system. However, as with soil-dwelling fauna (Behan-Pelletier and Bissett 1992), knowledge of microbial and arthropod diversity in the bryosphere varies in completeness. Many groups are poorly understood taxonomically and details of their natural history and biology are unknown; the situation is especially true for hyper-diverse groups like bacteria and nematodes. However, the use of functional groups (that is, species sharing similar life history characteristics, such as same prey and predators, reproductive output, and body size) has been used extensively successfully for soil food webs (Hunt and others 1987; Moore and others 1988; de Ruiter and others 1993; Hunt and Wall 2002) and demonstrates that accurate parameterization of physiological variables and population sizes at the functional group level can generate precise and reliable prediction of nutrient mineralization rates in modeled scenarios (de Ruiter and others 1993).

Although it has been demonstrated that small-scale moss NMS studies can be representative of larger-scaled trends in moss systems (Wiedermann and others 2009), it may not be an accurate representation of terrestrial systems beyond the bryosphere. Mosses are relatively slow-growing, adapted to infertile areas, and have few direct consumers, parasites, or pathogens. High C allocation to secondary metabolites, low specific leaf area, long leaf life span, and low forage quality leading to low rates of herbivory, signify that a low proportion of the net primary productivity of the bryosphere is consumed and converted to fecal material before entering the belowground food web (see Figure 1 of Wardle and others 2002). As such, litter that is produced from mosses is highly recalcitrant containing low N, and high phenolics,

and structural carbohydrates. Plant functional traits are major drivers of belowground food web structure and overall functioning in detrital systems, which may limit the transfer of bryosphere-derived nutrients to systems with high productivity (Jons-son and Wardle 2010).

The bryophyte NMS may not always be a good model for other ecosystems beyond the bryosphere, but the functional integrity of the system, and the ease of manipulation make it a valuable experimental model that overcomes many of the logistical and financial challenges of large-scale field experiments, while retaining the complexity that over-simplified artificial systems lack. Rather than extrapolating directly from the bryosphere to other systems, it will be important to couple results from the moss NMS to good theory and mathematical models. An example of this is the use of the moss NMS to verify predictions from metacommunity theory and thus infer the effects of habitat fragmentation on biodiversity at larger spatial scales (Gonzalez and others 1998; Lawton 1999). The combination of the NMS and theory allows a more convincing test of hypotheses that do not strictly relate to the bryosphere but pertain to the dynamics of ecological systems in general.

CONCLUSION

The motivation to define the bryosphere stems from the growing recognition that a significant fraction of the Earth's land surface, dominated by mosses, are places of high biodiversity, and strongly influence the structure and dynamics of ecosystem-level attributes through linked above- and belowground processes from local-to-global scales. C and N budgets of tundra, boreal, and peatland ecosystems have demonstrated the important role of the bryosphere (mosses plus bryobiota) in understanding global change, and current research has raised the concern that climate change, in conjunction with increased disturbance, will see the bryosphere switch from a net C sink to C source. In this mini-review, we have reviewed a broad section of the literature relating to the bryosphere. We have also indicated the potential of the bryosphere as an NMS. We emphasized the value of mosses as a spatially bounded, whole ecosystem model that integrates above- and belowground processes, and facilitates the study of the impacts of environmental change on the biodiversity and activity of the bryosphere. Recent use of the bryosphere as an NMS has shown how alterations in food web structure can affect ecosystem function in a manner that, although predicted by theory, has remained largely

untested by experiment. Experimental research coupled to ongoing field studies will enhance our understanding of the contribution of the bryosphere to the Earth's biosphere under ongoing global change.

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