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Forum

The status of non-vascular plants in trait-based ecosystem function studies

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ABSTRACT

The contributions of non-vascular plants (NVPs) to ecosystem function can be significant in high latitude and high altitude ecosystems and yet their inclusion in trait-based studies is rare. Our aim in this paper is to argue for a more thorough and widespread inclusion of NVPs in trait-based studies of ecosystem function. We focused on three specific objectives, (i) to review and summarize the current knowledge base as to how NVP traits are measured and used in assessing ecosystem function, (ii) to highlight challenges in incorporating vascular plants (VPs) and NVPs together in trait-based studies, and (iii) discuss a framework by which VPs and NVPs can be included in explaining ecosystem function. From a literature search of the Web of Science database we found that the majority of trait-based studies examined mostly vascular plants (VPs), occasionally VPs and NVPs separately, but rarely the two groups together to describe ecosystem function. To date compared to VPs, assessment of the contributions of NVPs to ecosystem function has remained relatively unexplored. Plant communities comprising VPs and NVPs can influence, and in turn be influenced by their habitats. We argue that the response and effect traits of VPs and NVPs are comparable and that classifying NVPs simply as "mosses" and "lichens" and assessing their functions as such is inadequate. We summarized and identified particular measurable traits of both VPs and NVPs that have significant effects on nutrient cycling and community assembly. Future studies in areas where NVPs are abundant should include both VPs and NVPs, aggregated at the finest taxonomic resolution possible to relate ecosystem processes such as cycling of matter and plant community assembly.

1. Introduction

To gain an understanding of the ecosystem functions and services provided by plants, ecologists have been increasingly employing functional trait-based methods to describe the function composition of ecosystems and identify how this links to their properties. From such studies researchers have gained valuable insights into functional properties of ecosystems (Diaz et al., 2004; Lohbeck et al., 2013; Ballantyne and Pickering, 2015; Kumordzi et al., 2015a), ecosystem productivity and stability (Garnier et al., 2004; Lavorel et al., 2011; Paquette and Messier, 2011; Moreau et al., 2015), and how these properties may shift along environmental gradients (Freschet et al., 2010; Holdaway et al., 2011; Amatangelo et al., 2014; Kumordzi et al., 2015b). However, the majority of work to date has focused mainly on vascular plants (VPs), with the contribution of non-vascular plants (NVPs) specifically mosses and lichens, to ecosystem function underrepresented. NVPs encompass all groups defined as "cryptogams", including algae, mosses, liverworts, hornworts, and lichens. However, for brevity we choose to limit this review to mosses and lichens. From a literature search of the Web of Science database (Appendix 1, Table 1), we found that since the year 2000, only 25% of studies that matched our search criteria included NVPs, either on their own or in conjunction with VPs (search criteria and results in Appendix II). Reasons for this exclusion might be (i) low abundance of NVPs in the study area and consequently them having little effect on over all functioning of the ecosystems (Pajunen et al., 2012), (ii) lack of expertise to accurately identify species or relevant groups of species of NVPs, and (iii) difficulty in measuring the relevant traits that influence ecosystem function. Because trait-based studies of ecosystem processes require *a priori* identification of plants' functional role, only the relevant traits of relevant species are assessed (Cadotte et al., 2011). There is some validity for exclusion of NVPs in areas where their abundance is low considering the mass-ratio hypothesis (Grime, 1998). However, the difficulty in measuring traits of NVPs can no longer be considered a valid reason for their exclusion. Much knowledge has been accumulated on the functional significance of NVP traits (see Table 1 of-Cornelissen et al., 2007; Rice et al., 2008). Hence, it is necessary to incorporate both VPs and NVPs in ecosystem function studies to achieve a more complete understanding of ecosystem state.

There are many ecosystems around the globe, such as extensive

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mires, bogs, and lichen tundra at high latitudes, where NVPs dominate and perform primary ecosystem functions (Moore and Bellamy, 1974; Gorham, 1990). Worldwide, peatlands cover some 500 million ha, mostly dominated by *Sphagnum* spp. (Gorham, 1990). Mires and bogs have poor drainage with high water tables. The formation of hummocks raises the seedbed above the water table and facilitates colonization by vascular plants tolerant of acidic environments (Hörnberg et al., 1997). *Sphagnum* spp. in bogs host microbial communities that increase the availability of nitrogen and iron in ombrotrophic peatlands. The novel functional traits of these microbial communities associated with the bog and mire species maintain the functioning of peatlands, which provide essential goods and services to humans (as global carbon sinks, water purification systems, fresh water reserves, biodiversity resource, peat resource *etc.*) through nutrient acquisition of the dominant plants (*Sphagnum* spp.) under nutrient-stressed conditions (Bragina et al., 2014). Despite VPs lacking significant cover, these ecosystems are dominated by NVPs performing many ecosystem functions akin to VPs. In arid regions (both hot and cold) the poikilohydric nature of many NVPs provides a high tolerance to prolonged drought (Raggio et al., 2016). The ability to remain productive at low temperatures or in areas with short growing seasons leads to an increase in their occurrence in polar and alpine regions. For example, lichens can photosynthesize in sub-zero temperatures (Schroeter and Scheidegger, 1995) and Smith (1984) reported over 300 lichen species in the Antarctica. In deserts, tundra, and alpine regions, NVPs play numerous functions including soil stabilization (Eldridge and Leys, 2003; Bu et al., 2015), N_2 fixation (Belnap, 2002), stabilization of ecohydrology (Stanton et al., 2014), and carbon assimilation (Street et al., 2013), primary production (Cutler et al., 2008; Ophof et al., 2013), control of successional dynamics (Escudero et al., 2007; Wheeler et al., 2011) and biogeochemical cycles (Cornelissen et al., 2007).

Even where VPs are the dominant life-form, many NVPs can still be abundant and contribute significant functions as subordinates. In tropical cloud forests of Costa Rica, epiphytic bryophytes were reported to have a biomass of over 4000 kg ha^{-1} (Nadkarni et al., 2004), and contribute a significant N retention and cycling (Clark et al., 2005). As in large extent biomes such as the boreal forest, dense tree cover often limits the growth of understorey VPs, allowing shade-tolerant NVPs to flourish and achieve high abundance on the forest floor (DeLuca et al., 2002a). Elevated acidity in boreal soils does not act as a barrier to NVP growth, because their below-ground structures are mainly used for anchorage and they are able to fix atmospheric nitrogen through leaf endophytes (DeLuca et al., 2002b), overcoming nutrient limitations often associated with low soil pH. While nitrogen fixation is less common in lichens, (approximately 10% of lichen species (Nash, 2008), the ubiquitous moss *Pleurozium schreberi* is known to form associations with cyanobacteria of the genus *Nostoc* and contributes significantly to nitrogen pools in boreal forest soils (DeLuca et al., 2002b). The NVPs in this ecosystem also play important roles in early and late-stages of succession. In primary succession, the ability of biological soil crusts consisting of actinomycetes, cyanobacteria, and lichens to fix atmospheric nitrogen, coupled with their ability to chemically weather rocks and release mineral nutrients in ionic form (Harper and Belnap, 2001) allows them to grow in areas with poor or no soil. Through the release of mineral nutrients from parent materials and decomposition of their litter, mosses and lichens contribute significantly to pedogenesis (Jackson, 2015). Mosses are key pioneer species in primary successions following glacier retreat through their effective dispersal, colonization, and lateral growth forming continuous cushions (Cutler et al., 2008). In early phases of secondary successions following canopy removing disturbances, lichens and mosses influence community assembly by inhibiting or facilitating tree seed germination and in late-stage succession by enhancing nutrient cycling (Parker et al., 1997; Escudero et al., 2007; Wheeler et al., 2011; DeLuca et al., 2002b; Kayes, 2016).

In light of global climate change, it is likely that many polar regions will become more temperate and temperate regions more arid creating a shift in plant community composition and structure (Elmendorf et al., 2012; Dawes et al., 2015). Landscapes dominated by NVPs will likely become dominated by VPs and *vice versa* (Lang et al., 2012). It would be difficult to assess the overall impact on future ecosystems if we cannot measure VP and NVP traits simultaneously. For these reasons we emphasize the need for a more widespread and effective use of NVPs in trait-based ecosystem function studies in light of (i) a review of the current knowledge base as to how NVP traits are measured and used in assessing ecosystem function, (ii) challenges in incorporating VPs and NVPs together in trait-based studies, and (iii) a framework (centered on nutrient cycling and community assembly) by which VPs and NVPs can be included in trait-based studies.

2. NVP trait-based research

Significant advances have been made in our understanding of NVP traits and how they relate to abiotic and biotic components of habitats. This relationship between NVP traits and habitat includes knowledge of both response traits (how a species responds to habitat change or environmental gradients) (Rice et al., 2008; Waite and Sack, 2010), and effect traits (how a species may impact its surroundings once established) (Cornelissen et al., 2007; Michel et al., 2012). Studies examining NVP response traits found species exhibit intraspecific variation along environmental gradients, and NVP community composition is subject to both biotic and abiotic habitat filters. Non-*Sphagnum* moss leaves were shown to respond to light levels in terms of photosynthetic rate (Waite and Sack, 2010; Wang et al., 2017) in accordance with the leaf economic spectrum described for VPs (Wright et al., 2004). However, this relationship was not found in ten species of *Sphagnum* (Rice et al., 2008). Tissue N and P concentrations in moss leaves fluctuate along temperature and soil fertility gradients in accordance with stoichiometric hypotheses developed using VPs (Waite and Sack, 2011). Lichen community assembly is shown to be driven by morphology and type of photobiont responding to aridity (Matos et al., 2015), light (Pardow et al., 2010), and soil pH gradients (Robinson et al., 1989) and in tree bark (Kermit and Gauslaa, 2001) indicating habitat preferences among specific groups of lichens. In subarctic regions, warmer and wetter conditions increase the growth rate of *Sphagnum* species. This high *Sphagnum* growth generates a biotic filter and results in a decline in all other NVP diversity as the non-*Sphagnum* spp. are unable to compete with the higher growth rates of *Sphagnum* moss (Lang et al., 2009a). Interestingly, Laine et al. (2011) found that mire succession was characterized by seres dominated by *Sphagnum* species that function in accordance with Grime's C-S-R description of plant strategies.

In terms of effect traits, NVPs can impact ecosystem processes and properties such as nutrient cycling, ecosystem hydrology, soil stability, and community assembly. By housing cyanobacteria in plant tissue, atmospheric N_2 fixation occurs in both mosses (DeLuca et al., 2002b) and lichens (Belnap, 2002). NVP litter decomposition plays a significant role in nutrient cycling (Cornelissen et al., 2007), while the litter of lichen species displayed mass loss rates comparable to those of VPs, rates observed in bryophytes are much lower (Lang et al., 2009b). The lowest rates were observed in *Sphagnum*; litter of *Sphagnum* spp. are highly resistant to decay due to the direct effects of their tissue chemistry as well as indirect effects on soil microbes (Hájek et al., 2011). Epiphytic lichens can stabilize water relations of their host plants, an effect that can translate to the ecosystem-level in arid regions (Stanton et al., 2014). Canopy structure of bryophytes influences rates of evaporative water loss (Rice et al., 2001). This effect can influence ecosystem level hydrology as co-occurring mosses conform their individual morphologies to those of their neighbors, essentially reducing moss cushion surface area and limiting water loss (Michel et al., 2010). The water retention capacities of moss carpets can also have facilitative effects on the performance of co-occurring lichens (Colesie et al., 2011). NVPs alongside algae and cyanobacteria in arid environ-

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