# Lichens as drivers of community and ecosystem properties in terrestrial ecosystems

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## Abstract

Lichens occur in most terrestrial ecosystems; they are often present as minor contributors, but in some forests, grasslands and tundras they can make up most of the ground layer biomass. As such, lichens dominate approximately 8% of the Earth's land surface. Despite their potential importance in driving ecosystem biogeochemistry, the roles of lichens as drivers of community processes and ecosystem functioning have attracted comparatively little attention. Here, we review the role of lichens in terrestrial ecosystems and draw attention to the important, but often overlooked role of lichens as ecological drivers. We start by assessing characteristics that vary among lichens and that may be important in determining their ecological role; these include their growth form, the types of photobionts that they contain, their key functional traits, their water holding capacity, their colour, and the levels of secondary compounds in their thalli. We then assess how these differences among lichens influences their impacts on ecosystem and community processes. As such, we consider the consequences of these differences for determining the impacts of lichens on ecosystem nutrient inputs and fluxes, on the loss of mass and nutrients during lichen thallus decomposition, and on the role of lichenivorous invertebrates in moderating decomposition. We then consider how differences among lichens impacts on their interactions with consumer organisms that utilize lichen thalli, and that range in size from microfauna (for which the primary role of lichens is habitat provision) to large mammals (for which lichens are primarily a food source). We then address how differences among lichens impact on plants, through for example increasing nutrient inputs and availability during primary succession, and serving as a filter for plant seedling establishment. Finally we identify areas in need of further work for better understanding the role of lichens in terrestrial ecosystems. These include understanding how the high intraspecific trait variation that characterizes many lichens impacts on community assembly processes and ecosystem functioning, how multiple species

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

mixtures of lichens affect the key community- and ecosystem-level processes that they drive, the extent to which lichens in early succession influence vascular plant succession and ecosystem development in the longer term, and how global change drivers may impact on ecosystem functioning through altering the functional composition of lichen communities.

**Keywords (5-10):** Decomposition; Functional traits; Invertebrate food-webs; Lichenized fungi; Nutrient cycling; Trophic interactions

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

## Contents

I. Introduction ..... 4
II. Characterizing the diversity of lichen growth forms and functional characteristics ..... 6
III. How variation among lichens affect ecosystem nutrient and carbon flux ..... 11
(1) Biogeochemical nutrient cycling ..... 11
(2) Litter decomposition ..... 13
IV. How variation among lichens affects their interactions with consumers ..... 17
(1) Lichen food webs ..... 17
(2) Defence ..... 23
V. How variation among lichens affects their impacts on plants ..... 26
VI. Conclusions and future directions ..... 28
VII. Acknowledgements ..... 30
VIII. References ..... 30

## I. Introduction

Lichens are symbiotic associations between a heterotrophic mycobiont (i.e., fungus) and one or more autotrophic photobionts (green algae and/or cyanobacteria). Lichens are generally slow-growing, long-lived and stress-tolerant, but they show a wide diversity of growth forms (Fig. 1). As such, some are prostrate and have leaf-like structures, while others have complex three-dimensional structures that resemble minute forests. Lichens occur in most terrestrial ecosystems; often they occur as minor contributors, but in some forest, grassland and tundra ecosystems they make up a large proportion of the ground layer biomass. Further, they frequently dominate in habitats that are too nutrient-poor, too dry, or too cold to support a complete or permanent cover of plants. As such, lichens dominate approximately 8% of the Earth’s land surface (Ahmadjian,

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

1995), and most of the land surface in xeric high latitude and high elevation ecosystems. More than 18,000 species of lichens exist world-wide and at higher latitudes the number of lichen species exceeds the number of vascular plant species (Nash, 2008). As such, Norway host 1.5 times more lichen than vascular plant species and there are 190 times more lichen than vascular plant species in Antarctica.

Most literature about how autotrophs affect ecosystem processes has focused on vascular plants, and over the past 25 years an enormous literature has emerged on how plant species differences drive ecosystems (Hobbie, 1992; Grime, 2001; Wardle, 2002). As such, it is well recognized that vascular plant species identity influences biogeochemical processes through determining the quantity and quality of litter that enters the soil, and inputs of nitrogen (N) through biological $N_2$ fixation. In contrast, despite their importance in many ecosystems worldwide, the roles of lichens as drivers of community processes and ecosystem functioning have attracted less attention and are often overlooked. This is despite their potential importance in driving ecosystem biogeochemistry. As such, most lichen species capture nutrients from the air and roughly 10% of them fix atmospheric $N_2$ through their association with cyanobacteria. These nutrients trapped by lichens reach other ecosystem components through leaching, decomposition and consumption by animals. Further, lichens also provide habitats for various invertebrates that may or may not use them as a food source.

Many studies on vascular plants have shown that the effect of species on ecosystem processes depends on their functional traits (Cornelissen *et al.*, 1999; Díaz *et al.*, 2004; Kurokawa, Peltzer, & Wardle, 2010), and that variation in functional traits may have a more important direct role than macroclimate in driving ecosystem processes (Cornwell *et al.*, 2008). This has led to calls for a shift from species-centred to traits-centred approaches in understanding community and ecosystem processes (McGill *et al.*, 2006; Violle & Jiang, 2009). However, the

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

importance of functional traits for driving ecological processes in other ecologically important autotrophs such as lichens has seldom been acknowledged (e.g. Lang *et al.*, 2009; Asplund & Wardle, 2013). Despite this, lichens have a distinct suite of functional traits that are analogous to the types of functional traits frequently studied for vascular plants (Cornelissen *et al.*, 2007), and that potentially provide a mechanistic framework for understanding their contribution to community and ecosystem processes.

In this paper we will review the role of lichens in terrestrial communities and ecosystems. We will start by discussing the functional characteristics of lichens, with particular focus on their traits and functional groupings because of their potential importance in driving lichen species effects on community and ecosystem processes. We will then explore the role that variation among lichens has in determining ecosystem carbon (C) and nutrient fluxes, for instance by affecting the decomposition and nutrient loss from their residues. Following that, we will discuss how differences among lichens affect their interactions with animals and plants, and the ecological consequences of these effects. By addressing these topics in combination we will draw attention to the important but often overlooked role of lichens as community and ecosystem drivers, and will identify areas which are in need of further work for better understanding the role of lichens in terrestrial ecosystems.

## II. Characterizing the diversity of lichen growth forms and functional characteristics

How lichens drive communities and ecosystems are regulated by a number of ways in which lichens differ. These include their growth form, associations with symbionts, functional traits,

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

capacity for water retention, colour and secondary chemistry (Fig. 2). We now explore each of these characteristics in turn.

Lichenized fungi form vegetative structures that are much more complex than those of other fungi. There is a great variability in the physical structure of lichens and they are traditionally divided into three main morphological groups: crustose, foliose and fruticose. However, there is a high level of morphological diversity within these groups which results in contrasting functional characteristics. Crustose lichens are tightly adhered to their substrate (often tree bark or rock, but sometimes evergreen tree leaves in moist forests) from which they cannot be removed without destruction. Some are very thin and do not produce much biomass, suggesting that their direct role in biogeochemical cycling probably is limited. However, other crustose lichens, particularly those that are endolithic (i.e., growing inside rocks), may induce rock weathering through both physical processes (via hyphal penetration and expansion/contraction of lichen thalli) and chemical processes (via excretion of various organic acids) (Chen, Blume, & Beyer,  2000). Furthermore, many crustose lichens are grazed by invertebrates (Baur, Fröberg, & Baur,  1995). Meanwhile foliose (i.e., leaf-like) lichens are loosely or tightly attached to their substrate. The lobes of these lichens sometimes overlap like tiles, and the lower side often has a tomentum or anchoring rhizinae, which helps generate favourable microclimate and microhabitat conditions for different invertebrates. Fruticose lichens always stand out from the surface of their substrate. These are hair-like, strap-shaped or shrubby, with considerable variation in branching pattern. Their size varies from minute species of 1-2 mm to species up to 10 m long. An extreme growth form of these fruticose lichens includes vagrant epiphytic lichens that lack holdfasts in mature specimens, and that occupy the air spaces between branches of trees. Such lichens (e.g. *Usnea longissima)* can be >1 m long and their hair-like tissues tend to degrade when in direct contact with the tree branch (Gauslaa,  1997).

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

In addition to their growth form, lichenized fungi also vary in their associations with their photobionts, and this can have important ecosystem-level implications. Chlorolichens have green algae as their only photobiont, whereas cyanolichens have cyanobateria as their only photobiont, while cephalolichens have green algae as their main photobiont but also contain cyanobacteria in localized internal or external structures (i.e., cephalodia). The most obvious difference between these groups is that those lichens which contain cyanobacterial symbionts commonly fix $N_2$ and thus have a higher N concentration. However, these groups also differ in their water relations, which in turn influence both their physical structure and water holding capacity. As such, chlorolichens and cephalolichens readily activate their photosynthesis in equilibrium with high ambient air humidity (Lange, Kilian, & Ziegler, 1986), and some of them even prefer habitats that are deficient in liquid water such as below overhanging rocks or on the leeside parts of lower old spruce trunks. Meanwhile, cyanolichens need liquid water to activate photosynthesis (Lange *et al.*, 1986), which explains why they are most abundant in rain forests and open sites with frequent heavy dewfall.

Lichens have a high diversity of functional traits associated with resource uptake and retention (Cornelissen *et al.*, 2007; Asplund & Wardle, 2013), which may potentially play an important role in determining their effects on ecological processes (Lang *et al.*, 2009) and associated invertebrate communities (Bokhorst *et al.*, 2015). These traits include thallus nutrient content, defence compounds, specific thallus mass (STM; the equivalent of plant's specific leaf mass or the reciprocal of specific leaf area) and water-holding capacity, and are analogous to vascular plant leaf functional traits that are widely recognized as important ecological drivers (Table 1). However, very few studies have sought to characterize the variation of lichen functional traits that occur in natural communities, or whether lichens show trade-offs in traits between those that are characteristic of rapid resource acquisition versus resource conservation in

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

the manner frequently shown for vascular plants (Grime *et al*. 1997; Díaz *et al*. 2004; Grime *et al.*, 1997; Wright *et al.*, 2004; Díaz *et al.*, 2004). Recently, it has been shown that within species variation in lichen functional traits can be more important than variation among species (and thus species turnover) in determining overall community-level measures of trait variation (Asplund & Wardle, 2014). This contrasts with what is usually found for vascular plants where across-species variation species turnover is usually more important (Kichenin *et al.*, 2013; Siefert *et al.*, 2015). For example, thallus nutrient concentration, a functional trait known to be important in driving thallus decomposability (Lang *et al.*, 2009; Asplund & Wardle, 2013), can show tremendous variation not only across but also within species (Palmqvist *et al.*, 2002; Asplund & Wardle, 2014). This high intraspecific variability is linked to the considerable ability of lichens to absorb and accumulate nutrients from atmospheric sources (Nash, 2008). Likewise, several studies have revealed that STM can show considerable variation within species (Snelgar & Green, 1981; Gauslaa *et al.*, 2009; Solhaug *et al.*, 2009; Asplund, Sandling, & Wardle, 2012).

Lichens vary greatly in their ability to retain moisture, and this has important ecological implications. Some lichens (e.g. those that are thin and pendulous) generally have a limited ability to retain water (Esseen *et al.*, 2015), even though they quickly take up water from humid air. Meanwhile, some other lichens (typically thick or gel-like foliose cyanobacterial lichens) have the ability to retain water for lengthy periods (Lange *et al.*, 1993; Lange, Belnap, & Reichenberger, 1998; Gauslaa & Solhaug, 1998; Lange, 2000). The water holding capacity of lichens is strongly positively correlated with their STM both within and across species (Gauslaa & Coxson, 2011; Merinero, Hilmo, & Gauslaa, 2014; Esseen *et al.*, 2015). There appears to be a trade-off between the flexible and rapid moisture uptake strategy characteristic of thin chlorolichens that utilize humid air every night, and the conservative water storage strategy of

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

cyanolichens that limit their photosynthesis to rarer rainy periods (Gauslaa, Coxson, & Solhaug, 2012). In lichen-dominated epiphytic communities, there is a need for frequent rain to sustain high cyanolichen and cephalolichen biomass and thus high $N_2$-fixation rates. In this light, epiphytic lichens may play an important role in the partitioning of moisture derived from precipitation and thus the humidity of the forest interior (Van Stan II & Pypker, 2015). In some sites with low rainfall, fruticose epiphytic lichens absorb moisture from fog and thereby supply underlying soils with water, in turn enhancing the availability of soil moisture for tree growth (Stanton & Horn, 2013; Stanton, Armesto, & Hedin, 2014).

Lichens vary hugely in colour from almost white to black. This variation in spectral characteristics results in large differences in thallus surface temperatures (Kershaw, 1975; Gauslaa, 1984). As such, in cold environments dark pigmented lichens may elevate temperatures above 0 ºC and induce melting of the surrounding snow, thereby enabling them to utilize snow-melt water (Kershaw, 1983). Variation in pigmentation among lichens may also affect microclimate at the soil surface (Kershaw, 1978). As such, the light-coloured, mat-forming lichens can increase the albedo of the land surface by around 1 % (Stoy *et al.*, 2012). Further, the surface and internal temperature of limestones are higher below the black-coloured *Verrucaria nigrescens* than below the light grey *V. baldensis*, and this contributes to increased rock weathering (Carter & Viles, 2003, 2004).

There is considerable variation among lichens in their production of carbon based secondary compounds (CBSC), and in total more than 800 compounds have been described (Huneck & Yoshimura, 1996; Huneck, 2001). These are commonly week phenolic acid derivatives and all are produced by the fungal partner. Most of them are unique to lichenized fungi with only a few also produced by non-lichenized fungi. These compounds have likely evolved to protect the lichens from a suite of physical and biotic stressors, such as light damage and attack by predators and pathogens (Lawrey, 2009; Solhaug & Gauslaa, 2012). Further, they likely play a key role in driving lichen-mediated ecosystem processes and community assembly (Asplund & Wardle, 2013; Asplund, Bokhorst, & Wardle, 2013; Asplund *et al.*, 2015). These CBSCs are often present in concentrations ranging from 1 to 5 % of thallus dry mass, but in the widespread epiphyte *Hypogymnia physodes* can reach over 20% (Solhaug *et al.*, 2009). Considerable variation in CBSC concentration exists not only among but also within lichen species (Culberson & Culberson, 1958; McEvoy, Gauslaa, & Solhaug, 2007; Vatne, Asplund, & Gauslaa, 2011; Asplund & Wardle, 2014). For instance, concentrations of CBSCs in the lichen *Lobaria pulmonaria* varies from 0.7 to 13 % depending on thallus size, elevation and pH (Asplund & Gauslaa, 2007; Vatne *et al.*, 2011). In addition to phenolic compounds, some cyanobacteria (*Nostoc* sp.) in lichen symbioses produce microcystins which are a group of cyclic petide hepatotoxins (Oksanen *et al.*, 2004; Kaasalainen *et al.*, 2012), although the ecological role of these toxins is not well established.

## III. How variation among lichens affect ecosystem nutrient and carbon flux

### *(1) Biogeochemical nutrient cycling*

While plant dominated communities gets most of their nutrients from the soil or from nutrients cycled within the system, lichen-dominated ecosystems obtain a relatively larger part of their nutrients from outside the ecosystem. This is because lichens lack roots and instead take up significant nutrient pools from wet and dry depositions that originate primarily from outside the ecosystem. They do this efficiently because they have a large surface area relative to their biomass, and because their surfaces lack cuticles and stomata, which make them very effective at absorbing nutrients. In addition, lichens can accumulate concentrations of these captured

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

nutrients that are vastly in excess of their physiological needs. However, lichens differ tremendously in their capacity to capture nutrients from outside the ecosystem and this depends on their characteristics. Some lichen growth forms, especially fruticose hair-like lichens, are particularly effective at capturing both dew and fog, which is often more rich in nutrients than is rain (Nash, 2008). For example, the epiphytic chlorolichen *Ramalina menziesii* in an oak woodland was shown to capture 2.85 and 0.15 kg ha$^{-1}$ y$^{-1}$ of N and phosphorus (P), respectively, from sources outside the ecosystem (Knops, Nash, & Schlesinger, 1996). Another study showed that this species alone was responsible for 13 % of the total annual canopy turnover of N, 4 % of P, 7 % of potassium (K), 1 % of calcium (Ca), 3 % of magnesium (Mg) and 8 % of sodium (Boucher & Nash, 1990). Further, fruticose lichens, which have a relative large surface area, appear to be better at capturing elements than are foliose lichens (Yemets, Solhaug, & Gauslaa, 2014). However, foliose lichens are generally richer in N, P and Ca than are fruticose lichens (Mangelson *et al.*, 2002; Asplund & Wardle, 2013). Because of their capacity to take up and accumulate nutrients, lichens can in some ecosystems store a substantial proportion of the total nutrients present in the ecosystem. For example, in an open *Picea mariana* woodland in northern Québec, mat-forming terricolous lichens covering 97 % of the ground surface contained up to 20 % of the total biomass, 25 % of the N and 12 % of the P in the ecosystem (Rencz & Auclair, 1978; Auclair & Rencz, 1982).

Approximately 10% of all lichen species contain $N_2$-fixing cyanobacteria. Because lichens often grow in nutrient-poor ecosystems, those containing cyanobacteria can greatly increase the inputs of N to the ecosystem. For instance, *Pseudotsuga menzeisii* forests in Oregon support a high abundance of the N-fixing *Lobaria oregana* that contributes approximately 50 % of the total ecosystem N input (Denison, 1973). Further in a synthesis of 17 studies, Nash (2008) lists estimations of lichen $N_2$ fixation contributions to the N economy for various ecosystems.

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

These values vary from 0.04-0.21 kg N $ha^{-1}$ $y^{-1}$ in tundras and forests in subarctic Alaska in which *Peltigera* spp. is the dominant lichen (Gunther, 1989) to 16.5 kg N $ha^{-1}$ $y^{-1}$ in old growth *Pseudotsuga* forests in NW USA in which *Lobaria oregana* is dominant (Antoine, 2004). However, Nash (2008) also notes that most estimates (and particularly the highest ones) are somewhat inaccurate and may be unreliable due to various methodological flaws.

### *(2) Litter decomposition*

There is a substantial literature focused on understanding how vascular plant traits and litter quality govern variation in litter decomposition rates among plant species, and these show decomposition to be associated positively with nutrient concentrations and specific leaf area, and negatively with concentrations of lignin and secondary defence compounds and leaf dry mass content (Cornelissen *et al.*, 1999; Pérez-Harguindeguy *et al.*, 2000; Cornwell *et al.*, 2008; Makkonen *et al.*, 2012). However, although several studies have quantified rates of decomposition of lichen litter (Wetmore, 1982; Guzman, Quilhot, & Galloway, 1990; Knops *et al.*, 1996; Esseen & Renhorn, 1998; Coxson & Curteanu, 2002; Caldiz, Brunet, & Nihlgård, 2007; Campbell, Fredeen, & Prescott, 2010), these have each considered too few species to enable reliable evaluation of which lichen functional traits are important in regulating decomposition. However, two recent comparative studies have shown that lichen decomposition is related to a spectrum of thallus traits that are broadly analogous to leaf traits known to regulate vascular plant litter decomposition. Specifically, Lang *et al.* (2009) found lichen litter decomposition to be positively related to thallus metabolic carbohydrates, lipids, N, Ca, K, pH and amino acids, while Asplund and Wardle (2013) showed lichen decomposition to be related to thallus N, P and pH. Further, Asplund & Wardle (2013) showed through removing thallus CBSCs by means of acetone rinsing that CBSCs are powerful regulators of lichen decomposition, and that all CBSCs that reduced decomposition also deterred lichenivorous snails. They also found foliose lichens to decompose quicker than did fruticose ones, which probably is due to them having a higher N content.

The rate at which N is released from lichens during decomposition also varies between lichens with differing functional characteristics. For instance, Campbell et al. (2010) found N to quickly be released without initial N immobilization from the N-fixing lichens *Lobaria pulmonaria* and *Nephroma helveticum*. They argued that the relatively high N mineralization rates from these lichens may be due to the lack of lignin and the fact that their N occurs in labile proteins, chitin and nucleic acids (Dahlman *et al.*, 2003) which can be solubilized and rapidly leached during the early stages of the decay process (Rai, 1988). In contrast, rapid release of N during decomposition was not found to occur for two chlorolichens, i.e., *Alectoria sarmentosa* and *Platismatia glauca*, probably because of their low initial N concentration (Campbell *et al.*, 2010). Meanwhile, Asplund & Wardle (2013) did not find any difference in N release during decomposition between $N_2$-fixing and non $N_2$-fixing lichens. Lichen growth form also seems to play a role in the release of N. For example, Asplund et al. (2013) found that epiphytic fruticose lichens, which have a large surface area, release more N than do epiphytic foliose lichens during decomposition, despite the higher initial N concentration of foliose lichens. They also found that most foliose lichens growing on rocks rapidly lost N but this was probably due to many of them having a high initial N concentration. Further, P has been shown to be released quickly during decomposition from a variety of species of lichens, including cyano-, cephalo- and chlorolichens (Caldiz *et al.*, 2007; Campbell *et al.*, 2010; Asplund *et al.*, 2013), and most of the P in the thallus is frequently released within 5 months (Campbell *et al.*, 2010; Asplund *et al.*, 2013). In contrast, litter of *Cladonia* spp. growing on nutrient poor soils can retain or even accumulate P during decomposition (Moore, 1984; Asplund *et al.*, 2013). Other elements such as K which are present as dissolved monovalent ions can also be readily released early during the decomposition of lichen thalli (Caldiz *et al.*, 2007; Campbell *et al.*, 2010) in much the same manner as is often observed during plant litter decomposition (Lousier & Parkinson, 1978).

A vast body of literature has explored the impact of soil invertebrates on vascular plant litter decomposition (Petersen & Luxton, 1982; Kampichler & Bruckner, 2009), and has revealed that these effects are driven by invertebrates consuming and fragmenting litter, dispersing microbial propagules, and stimulating soil microbial activity (Parkinson, Visser, & Whittaker, 1979; Seastedt, 1984). In contrast, only a few studies have investigated whether lichenivorous invertebrates may play a role in lichen decomposition. For instance, McCune and Daly (1994) found half-lives of decomposing lichen litter to be two to nine times shorter in the presence of animals larger than 1 mm than when these were excluded. Similarly, *Hypogymnia physodes* thallus litter decomposed 1.9 times faster when animals sized 0.5 - 3 mm had access to it (Biazrov, 1995). Further, Asplund *et al.* (2013) showed that micro-arthropods can increase decomposition rates of lichens, but that their effects can be mitigated by high levels of CBSCs in the lichen thalli that deter lichen-feeding activity. Some lichen CBSCs degrade fairly quickly during thallus senescence, suggesting that they only impact micro-arthropods during early stages of decomposition (Asplund & Wardle, 2012). However, other compounds are more recalcitrant and thus increase in concentration relative to thallus litter mass, and are therefore likely to have longer term effects on micro-arthropod feeding activity (Bidussi, Solhaug, & Gauslaa, 2016).

Some studies that have quantified decomposition rates of lichen and vascular plant litter in the same study have shown that lichen litter often decomposes more slowly (Moore, 1983, 1984; Wardle *et al.*, 2003). However, the lichen species that have been used in these comparisons (i.e., *Cladonia* spp.), have thalli that are very nutrient poor and generally decompose

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

considerably more slowly than do thalli from most other lichens species (Asplund & Wardle, 2013). In a litter-bed experiment comparing decomposition rates of 27 bryophytes, 17 lichens and five vascular plants, lichens overall had comparable decomposition rates to those of vascular plants, whereas bryophytes had the slowest decomposition (Lang *et al.*, 2009). Meanwhile, Vogt et al. (1983) found that the pendulous epiphytic lichen *Alectoria sarmentosa* decomposed much more quickly than associated vascular plant litter.

Like plant leaves, epiphytic lichen material falls to the ground before decomposing. A number of studies have quantified litter-fall of lichens, primarily in temperate and boreal forests (e.g. Esseen, 1985; Knops *et al.*, 1996; Stevenson & Coxson, 2003; Caldiz & Brunet, 2006). However, because lichen litter usually falls in clumps and is therefore very spatially scattered, lichen litter-fall is often underestimated (McShane, Carlile, & Hinds, 1983). In temperate and boreal regions the majority of lichen litter-fall occur during autumn and winter and especially during stormy events (Esseen, 1985). This litter-fall hugely varies between stands, and lichen litter deposition of between 13 and 320 kg ha$^{-1}$ year$^{-1}$ has been reported (Caldiz & Brunet, 2006; Campbell *et al.*, 2010; Rawat, Upreti, & Singh, 2011) . This variation mainly reflects the standing crop in the stand and especially that of pendulous lichens which tend to fragment more easily than do other fruticose and foliose lichens. As such, the annual turnover of pendulous lichen is commonly 10 % (and up to 30 %) of the standing crop, while the turnover of foliose lichens is usually a few percent (Stevenson & Coxson, 2003). However, because epiphytic lichen litter is generally more nutrient rich than is tree leaf litter, its role in nutrient cycling is disproportionate to the biomass of its litter-fall. For example, in an oak woodland, litter inputs from the dominant non N-fixing lichen *Ramalina menziesii* was found to contain twice as much N as did oak leaf litter (Knops *et al.*, 1996). The relatively high nutrient concentrations in lichen litter compared with vascular plant leaf litter are in part because plants remobilize and resorb their nutrients before leaf abscission, which lichens cannot. However, mat-forming lichens, continuously die-off at the bottom creating necromass which leads to nutrients in the senescing parts then being partially recycled internally, leading to less nutrients being released to the ecosystem (Crittenden, 1991).

The presence of lichens, either when alive or as litter, can also affect the decomposition of associated plant litter. For instance, oak leaf litter was found to lose mass less rapidly during decomposition when in the presence of lichen litter, despite the lichen litter decomposing quicker than the oak litter (Knops *et al.*, 1996). This was proposed as due to the dominant lichen *R. menziesii* having a poor water retention capacity, leading to the decomposer community being more impeded by moisture limitation (Matthes-Sears, Nash, & Larson, 1986a, 1986b). In contrast, *Vaccinium myrtillus* litter decomposed more quickly in *Cladonia* mats than when the lichens had been removed, likely because of a more favourable microclimate and moisture conditions in the mats (Stark *et al.*, 2000). Meanwhile Wardle *et al*. (2003) found that vascular plant litter decomposition was largely unaffected by whether or not it was mixed with litter from the lichen *Cladonia stellaris*, although the decomposition of the lichen litter was impeded by the vascular plant litter. However, too few studies have been performed to determine what types of lichens, or what lichen characteristics, exert the greatest positive or negative effects on other litters, or the role of environmental context on these effects.

## IV. How variation among lichens affects their interactions with consumers

### *(1) Lichen food webs*

Despite the antibacterial and antifungal properties often ascribed to their CBSCs, lichens provide microhabitats for numerous eukaryotic and prokaryotic microorganisms, (Lawrey & Diederich,

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

2003; Grube & Berg, 2009). Indeed, recent work has highlighted the role of lichen-associated bacteria as an important component of the lichen meta-organism, challenging the traditional view of lichens simply being a symbiosis between a fungus and one or two photobionts (Aschenbrenner *et al.*, 2016). Bacterial cell densities in lichens dramatically exceed those in or on vascular plant leaves (Cardinale *et al.*, 2008; Grube *et al.*, 2009; Saleem, 2015), and they likely play an important role in lichen-mediated food webs through serving as food for nematodes and protozoa. Bacteria varies hugely in numbers and diversity between lichen species, and this is largely driven by differences in lichen growth form and photobiont type (Hodkinson *et al.*, 2012). The variation with photobiont type is likely to be due to the green algal symbionts providing mainly sugar alcohols and the cyanobacterial symbionts providing glucose, and because only the cyanobacteria provide N through biological fixation (Elix & Stocker-Wörgötter, 2008). Bacterial symbionts can contribute functionally to the lichen by providing resistance to biotic and abiotic stresses, biosynthesis of vitamins, detoxification of inorganic substances (e.g. arsenic, copper and zinc) and nutrient supply including $N_2$-fixation (as reviewed by Grube, Cardinale, & Berg, 2012; Aschenbrenner *et al.*, 2016).

The lichen thallus hosts aquatic microfauna (i.e., those that live in water films), such as nematodes, protozoa, rotifers and tardigrades (Fig. 3) (Gerson & Seaward, 1977). As such, there are complex food webs inhabiting the lichen thallus. For instance, fungal-feeding nematodes likely feed on the lichen mycobiont while bacterial-feeding nematodes (which can be abundant in lichen thalli; Bokhorst *et al.*, 2015) feed on various bacterial symbionts. There is also a relatively high abundance of predacious nematodes at least in epiphytic foliose lichens (Bokhorst *et al.*, 2015), and these are likely to feed on various lichen-associated microfauna. The knowledge of how these aquatic faunal communities varies between lichens is limited, although densities of rotifers and tardigrades are greater on lichen species that have a higher biomass (Stubbs, 1989).

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

Further, Bokhorst *et al.* (2015) showed that the diversity, but not the abundance, of lichen-associated nematodes increases with increasing thallus mineral nutrient concentration. They also showed large differences in nematode community composition between between lichens that occupy different growth substrates, and lichens that grow on rocks supported a much higher density of omnivorous nematodes than did epiphytic and terricolous lichens. Bokhorst et al. (2005) also found large differences in nematode community composition between lichens with and without $N_2$-fixation capability, due in part to higher abundances of bacterial-feeding nematodes in $N_2$-fixing lichens that are adapted for feeding on their cyanobacterial symbionts.

Further, a diverse group of terrestrial invertebrates feed on and seek shelter on or in lichens (Fig. 3). These include species of gastropods, springtails, mites, beetles, moth larvae and woodlice (Gerson & Seaward, 1977). For instance, springtails use lichens for both food and shelter, and the undersides of lichen thalli can be almost completely covered with springtails (Leinaas & Fjellberg, 1985). Further, lichenivorous psocids and mites are fed upon by both pseudoscorpions and true bugs that lives on the lichens (Gerson & Seaward, 1977). Among lichenivorous invertebrates, gastropods play a particularly important role, and Asplund (2010) lists 64 species of terrestrial gastropods known to feed on lichens. Lichenivorous gastropods are found worldwide and feed on calcicolous lichens in limestone grasslands (e.g. Fröberg, Baur, & Baur, 1993) or rocky deserts (Shachak, Jones, & Granot, 1987), and on epiphytic lichens in temperate broadleaved and boreal forests (Asplund *et al.*, 2010b). A few snail species are specialized lichen-feeders or feed predominantly on lichens (Kerney, 1999), and thus depend heavily on lichens as a food resource. Some snails even have specialized radulae that enable them to graze off epi- and endolithic lichens from rocks (Schmid, 1929; Breure & Gittenberger, 1981). Further, the foliose lichen *Xanthoria parietina* provides the snail *Balea perversa* with all essential elements and nutrients necessary for its growth and reproduction (Baur & Baur, 1997).

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

In addition to serving as a food source, lichens provide gastropods with shelter from predators and desiccation. For instance, *B. perversa* seeks protection under thalli of *X. parietina* that also serves as its food supply (Baur & Baur, 1997). Some snails may also use lichens to conceal themselves; for example the snail *Napaeus barquini* actively covers its shell with lichens (Allgaier, 2007).

Snails show clear preferences for different lichen species based on the functional characteristics of the lichens (Baur, Baur, & Fröberg, 1994; Asplund *et al.*, 2010b; Asplund & Wardle, 2013). Co-existing snail species may prefer different lichen species, and weight increase in juvenile snails varies greatly depending on which lichen species the snails are fed (Baur, Baur, & Fröberg, 1992; Baur *et al.*, 1994; Fröberg *et al.*, 1993). One major driver of lichen palatability is their secondary chemistry; The presence of CBSCs is an important determinant of lichen palatability and the removal CBSCs greatly increases the consumption of lichens by snails (Gauslaa, 2005; Pöykkö, Hyvärinen, & Bačkor, 2005; Černajová & Svoboda, 2014), as we discuss below. Furthermore, Asplund & Wardle (2013) found that generalist snails preferred fruticose to foliose lichens, and foliose chlorolichens over cephalo- and cyanolichens. Meanwhile, unlike what is often found for vascular plants (Mattson, 1980), Asplund & Wardle (2013) did not find any relationship between thallus consumption by snails and concentrations of thallus N or P across 28 forest lichen species. Further, Asplund *et al.* (2010a) found that lichens exposed to N fertilization (and which were more N-rich) were actually less preferred by lichenivorous gastropods. They attributed this to lower supply of energy in terms of mannitol in fertilized thalli. In contrast, Asplund, Gauslaa, & Merinero (2016) showed that snails prefer thalli from *L. pulmonaria* that had a lower C : N ratio as a consequence of infection by the parasitic fungus *Plectocarpon lichenum*.

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

Lichen traits also affect communities of other lichen-associated invertebrates. For instance, Bokhorst *et al.* (2015) found that thallus nutrient status (i.e., N concentration and N to P ratio) positively affected the diversity and abundance of both mites and springtails and also altered their community composition. Consequently, $N_2$-fixing lichens, which are richer in nutrients, tended to support more (and different species of) springtails and mites. Several studies have also shown that foliose lichens usually support more springtails and mites than do fruticose or crustose lichens (André, 1983, 1984, 1986; Colloff, 1988; Bokhorst *et al.*, 2015), although André (1984) found high numbers of the mite *Dometorina plantivaga* in crustose lichens only. Further, Søchting & Gjelstrup (1985) found that foliose lichens supported more springtails relative to mites than did fruticose lichens. These studies in combination point to lichen growth form as an important regulator of both the abundance and community composition of microarthropods (André, 1985). A possible explanation for the higher abundance of invertebrates on foliose compared with fruticose lichens is the favourable microclimatic conditions and shelter provided by the interface between the lichen thallus and its substrate (Søchting & Gjelstrup, 1985). In this light, springtails may completely cover the underside of those foliose lichens that provide them with both food and shelter (Leinaas & Fjellberg, 1985).

The importance of lichens in driving invertebrate communities is further demonstrated by the positive correlation often observed between arthropod density and biomass of lichens across communities (Stubbs, 1989; Pettersson *et al.*, 1995; Gunnarsson, Hake, & Hultengren, 2004). This is true both for arthropods that feed on lichens such as mites and springtails, and for higher trophic levels, such as spiders. The greater spider density in communities that support a higher biomass of epiphytic lichens has been explained in terms of lichens increasing the structural complexity of the habitat (Gunnarsson *et al.*, 2004). However, lichens with identical structural complexity can support different densities of spiders through supporting contrasting amounts of prey (i.e. lichenivorous springtails), due to variation in defense compounds (Asplund *et al.*, 2015). Likewise, passerine birds that feed on invertebrates are more abundant in forests that support a high lichen biomass due to increased abundance of prey (Pettersson *et al.*, 1995).

Lichens are also utilized by vertebrate fauna (Fig. 3). A number of bird species use lichens as nesting material or as camouflage or decoration (Richardson & Young, 1977). In addition, flying squirrels make nests of lichens, predominately fruticose lichens of the genus *Bryoria*, on which they also feed. A number of mammals feed to varying extents on lichens in different regions of the world, including deer, elk, ibex, gazelle, musk ox, mountain goat, polar bear, lemming, vole, tree mouse, marmot, squirrel and monkeys (Seaward, 2008). Of these, reindeer and caribou (hereafter reindeer) that inhabit circumpolar northern latitudes are especially dependent on lichens. As such the winter diet of reindeer is more than 50 % lichen material, and these include mat-forming as well as epiphytic and saxicolous lichens (Scotter, 1967; Gaare & Skogland, 1975; Boertje, 1984). The vast majority of lichens consumed by reindeer are fruticose, and mainly of the genera *Cladonia*, *Bryoria*, *Alectoria* and *Stereocaulon* (Holleman & Luick, 1977; Danell *et al.*, 1994). These species are common in reindeer habitats and their growth form makes them easily accessible. Similar to reindeer, snob-nosed monkeys inhabiting north-western Yunnan, China depend on lichens as winter fall-back food; during seasons with low food availability, lichens can constitute up to 97% of their diet (Grueter *et al.*, 2009). These monkeys prefer fruticose lichens such as *U. longissimi* and *Bryoria* spp. which are easy to grab, and only occasionally feed on the smaller foliose lichens (Kirkpatrick, 1996; Grueter *et al.*, 2009). Because of their preference for *Usnea longissima*, these monkeys tend to occupy relatively high and cold elevations, where lichens are more abundant than in the milder lowland (Grueter *et al.*, 2012).

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

### *(2) Defence*

Already in the 19th century, Zukal (1895) suggested that CBSCs in lichens serve as defences against lichenivores. However, Zopf (1896) found that snails did not discriminate between potato slices smeared with lichen CBSCs and those without CBSCs. A few years later Stahl (1904) found that removal of CBSC by a sodium bicarbonate solution made the lichen more attractive to the snail *Cepaea hortensis.* In more recent times studies have utilized 100 % acetone to non-destructively remove CBSCs from living but air dry lichens; this enables comparisons between lichen material which does versus does not have CBSCs present (Solhaug & Gauslaa, 1996, 2001). This approach provides a unique way to test the role CBSCs play in lichen-invertebrate interactions while avoiding other confounding factors, and it has been used in several studies to show that lichen CBSCs do indeed deter invertebrates. (Reutimann & Scheidegger, 1987; Gauslaa, 2005; Pöykkö *et al.*, 2005; Asplund & Wardle, 2013; Černajová & Svoboda, 2014; Asplund *et al.*, 2015). For instance, Gauslaa (2005) offered the snail *C. hortensis* the choice between lichens with and without CBSC and found a significant preference for the acetone rinsed thalli in 14 out of the 17 tested lichen species. Meanwhile, Pöykkö *et al.*(2005) found higher survival rates of larvae of the moth *Eilema depressum* when reared on acetone-rinsed *Vulpicida pinastri* and *Hypogymnia physodes* than on control (non-rinsed) thalli, but found no effect of acetone rinsing on survival rates on *Parmelia sulcata* and *Xanthoria parietina.* The effect of acetone rinsing is highly variable between lichen species because CBSCs vary hugely both qualitatively and quantitatively among them. In general, CBSCs that are restricted to the cortical layer, such as atranorin, parietin and usnic acid and that protect the lichen from high solar radiation, are less effective against lichenivorous snails (Gauslaa, 2005, 2009; Asplund, Solhaug,

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

& Gauslaa, 2010c). In contrast, some medullary CBSCs are very effective against lichenivores, such as the yellow vulpinic acid (Gauslaa, 2005).

Lichen CBSCs not only deter lichenivores, but also control how they graze lichens, which affects lichen fitness. For instance, various lichen feeders, e.g. springtails, moth larvae and slugs and snails, preferentially attack the cortical layer and often also the photobionts of the lichen, but stop feeding when they reach the medulla (Hale, 1972; Baur *et al.*, 2000; Bačkor, Dvorský, & Fahselt, 2003; Asplund, 2011b) where the CBSCs are often mostly concentrated (Asplund, 2011b). However, lichens that are treated with acetone, and are therefore low in CBSCs, are instead grazed perpendicular to the lichen surface which leaves distinct holes through all the thallus layers. Further, the foliose lichen *Nephroma arcticum* has large cephalodia (containing colonies of N-fixing *Nostoc* spp.) which, unlike the surrounding medulla, lacks CBSCs (Renner, 1982). As such, slugs normally attack the cephalodia rather than the green-algal parts of the thallus, but when CBSCs are removed by acetone rinsing, slugs do not discriminate between the two parts (Asplund & Gauslaa, 2010). The high grazing susceptibility of cephalodia in this species may explain why it is restricted to northern and high elevation locations that support few gastropods. Several lichen species have higher concentrations or even other types of CBSCs in their reproductive structures such as soralia and ascocarps (Imshaug & Brodo, 1966; Brodo & Hawksworth, 1977; Tønsberg, 1992; Hyvärinen *et al.*, 2000; Asplund *et al.*, 2010c). As such, snails completely avoid the soralia of *Lobarina scrobiculata* which contains five times as much *m*-scrobiculin than does the rest of the thallus (Asplund *et al.*, 2010c). Meanwhile, in the absence of CBSCs, snails are instead more likely to attack the soralia than the somatic parts of the thallus. This is in line with the optimal defence theory which predicts that that the parts of an organism that are more likely to be attacked and are more important for species fitness (e.g. reproductive parts) are typically better defended against consumers (McKey, 1974; Rhoades, 1979).

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

Many lichen species are represented by different chemotypes, i.e. morphologically identical conspecifics containing different groups of CBSCs, and these chemotypes can be used for studying the ecological role of CBSCs. As such, thalli of one *Lobaria pulmonaria* chemotype contains high amounts of total CBSCs including stictic acid and small amounts of constictic, norstictic, peristictic and methyl norstictic acid, while another contains low total CBSCs and only norstictic acid (Asplund, 2011a). When growing on the same trees, the chemotype with the higher total CBSCs was not grazed by gastropods while the chemotype with only norstictic acid was heavily grazed. This pattern was later confirmed in a laboratory food choice experiment, and reveals that natural variation in CBSCs at the within-species level can serve as an important determinant of their susceptibility to their grazing by gastropods (Asplund, 2011a).

Despite the clear effect of experimentally reducing concentrations of CBSC on lichen palatability, variation in palatability among lichen species does not appear to be closely related to the total concentration of CBSCs (Asplund & Wardle, 2013; Bokhorst *et al.*, 2015). This lack of relationship is likely because of qualitative differences in CBSCs between species and because different compounds have different levels of biological effectiveness and contrasting roles. As such, a species with high concentrations of an ineffective defence compound is likely to be more palatable than a species with lower concentrations of a very effective defence (Gauslaa, 2008). In this light, an accidental experiment in which the coleopteran *Lasioderma serricorne* attacked 1440 lichen herbarium specimens showed that the level of consumption was strongly linked to the qualitative composition of CBSCs in the lichens (Nimis & Skert, 2006).

The CBSCs in lichens can also impact the consumption by mammals, but the literature on this is very limited. For instance, it is known that the bank vole, *Myodes glareolus*, prefers lichens with reduced concentrations of CBSCs (Nybakken *et al.*, 2010). Further, usnic acid, a common lichen CBSC, has been reported to kill elk (Cook *et al.*, 2007). However, reindeer in

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

contrast consume large amounts of usnic acid-containing lichens, because they have an usnic acid-degrading bacterium (*Eubacterium rangiferina*) in their rumen that detoxify the lichens (Sundset *et al.*, 2008, 2010). As such, the presence of usnic acid actually increases the digestibility of lichens by reindeer (Palo, 1993).

## V. How variation among lichens affects their impacts on plants

The numerous ways that communities of plants (mainly trees) impact on lichen community assemblies, for instance by competition or by providing substrates and modifying environmental conditions, have been very well studied (Favero-Longo & Piervittori, 2010), and are outside the scope of this review. Meanwhile, how lichens regulate plant communities have been given much less attention (Fig. 4).

At the beginning of terrestrial primary succession, N is often the main limiting nutrient, and pioneer $N_2$ fixing plants and lichens may play an important and well known role in driving initial N build-up of the ecosystem. For example the $N_2$-fixing fruticose lichen *Stereocaulon* spp. can dominate the ground cover early in succession in both lava flows and glacial forelands (Eggler, 1971; Mueller-Dornbois, 1987; Vetaas, 1994). The $N_2$-fixed by lichens, and other $N_2$-fixing organisms, leads to N build-up that then facilitates colonization by non $N_2$-fixing vascular plants. In this light, the vascular plants, *Festuca octoflora* and *Mentzelia multiflora*, when grown in desert soil together with the cyanolichen *Collema* sp., have been shown to grow quicker and contain higher tissue element concentrations of N, P, K, Ca, Mg and iron than those grown in soil without the lichen. This is both because the lichens concentrate essential elements in available forms at the soil surface and because the gelatinous sheaths often associated with the cyanobacterial symbiont (e.g., *Nostoc* cells in *Collema* spp.) contain chelating compounds.

The early colonization by lichens may also induce rock weathering that in turn releases mineral elements in forms that plants can utilize (Viles, 1995; Chen *et al.*, 2000; Adamo & Violante, 2000). Lichen growth form can potentially play a role in governing these rock-weathering processes. However, although crustose lichens are more strongly adhered to the rock (through their entire lower surface) than are foliose lichens, their ability to weather rock and release nutrients from it is not necessarily greater (Adamo, Marchetiello, & Violante, 1993). Instead, the freeze-thaw action can be larger on rock surfaces occupied by the bigger foliose lichens than those occupied by crustose lichens, which may compensate in part for their weaker connection with the rock (Adamo & Violante, 2000). Further, the chemical weathering of rock and release of nutrients from it may also be driven by the amount and types of CBSCs produced by the lichens which themselves vary tremendously both among and within lichen species (Adamo & Violante, 2000).

Lichens have been reported to both enhance (Zamfir, 2000; Houle & Filion, 2003) and reduce (Deines *et al.*, 2007) vascular plant seedling establishment, and these effects of lichens are dependent on the types of plant and lichen species present and on environmental context (e.g. Escudero *et al.*, 2007). As such, ground covered by *Cladonia* has been shown to stongly reduce emergence of seedlings of plant species that depend heavily on light for germination (i.e. *Arenaria serpyllifolia* and *Veronica spicata*) relative to those that do not (i.e., *Filipendula vulgaris* and *Festuca ovina*) (Zamfir, 2000). Further, the physical environment created by ground-dwelling lichens may inhibit seeds and seedling radicals from reaching the soil, thereby reducing seedling establishment (Deines *et al.*, 2007). In contrast, mat-forming lichens such as *Cladonia* spp. may conserve soil moisture and thus facilitate seedling establishment (Zackrisson *et al.*, 1995, 1997). However, these lichens accumulate little organic matter, and N mineralization rates below these mats are low, which leads to lower N availability under lichens compared with under plants and bryophytes (Sedia & Ehrenfeld, 2005). This results in a sparser vascular plant development and a more open forest, which leads to a feedback that in turn benefits mat-forming lichens (Sedia & Ehrenfeld, 2003).

Because of the rich secondary chemistry of lichens, their CBSCs are often claimed to have allelopathic effects on plants (Lawrey, 1986, 1995). However, studies finding an allelopathic effect of lichen CBSCs have often been made in the laboratory through bioassays that use unrealistically high concentrations of CBSCs or that use water extracts that also contain many (and often unknown) compounds other than CBSCs. Furthermore, many of these studies have evaluated the allelopathic effect of lichen CBSCs on crop plants species like tomato, lettuce, maize or sunflower, that are not naturally exposed to lichen CBSCs (Lascève & Gaugain, 1990; Romagni *et al.*, 2000; Lechowski, Mej, & Bialczyk, 2006; Latkowska *et al.*, 2006). However, in reality very low amounts of lichen CBSC are leached to the soil because of their low water-solubility (Stark, Kytöviita, & Neumann, 2007), and at ecological relevant conditions the common lichen CSBC usnic acid does not reach concentrations in the soil that are able to impair pine seedling growth or mycorrhizal-mediated nutrient uptake (Kytöviita & Stark, 2009). In this light, we currently do not have a good understanding of the role of allelopathic interactions involving lichens in natural ecosystems, or convincing and consistent evidence that allelopathic effects of lichens are actually important.

## VI. Conclusions and future directions

(1) In this review we have shown how lichens impact ecosystem processes, notably those that involve the fluxes of carbon and nutrients, and how this is in turn regulated by the considerable variation that exists for the functional characteristics of lichens (Fig. 2). We

have also outlined how this variation impacts on the interactions of lichens with other primary producers as well as with higher trophic levels, and the consequences of this for community and ecosystem properties.

(2) Our knowledge about how lichen functional traits (both within and between species) vary among ecosystems or across environmental gradients is limited, and this topic requires further attention. Recent studies suggest that lichens show massive within-species (relative to across-species) variation, especially in comparison with vascular plants (Asplund & Wardle, 2014). There is a need for studies on how this high intraspecific variation impacts on lichen community assembly processes and ecosystem functioning, in the same manner that has recently been done for vascular plants (e.g., Jackson, Peltzer, & Wardle, 2013; Kumordzi *et al.*, 2015).

(3) Lichens often occur in multispecies mixtures, yet studies to date have almost entirely considered only the effects of single lichen species. As such, little is known about how lichen species mixtures, and their functional and taxonomic diversity, affects the key community- and ecosystem-level processes that they drive. A large number of experimental studies have addressed how vascular plant biodiversity impacts ecosystem functioning (and, potentially, ecosystem services) (Cardinale *et al.*, 2012), but this issue remains unexplored for lichens, despite the relative ease by which they can be experimentally manipulated, and their importance as ecosystem drivers.

(4) Future studies should also focus on the extent to which lichens, especially early in succession, influence vascular plant succession and ecosystem development in the longer term perspective. We show in this review that there are important short term effects, but how they are manifested in longer term time scales, through for example by influencing longer term vegetation successional trajectories and soil development, remain unknown.

Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

(5) Drivers of global change can potentially have important impacts on lichen communities. As such, both increased temperature and N-deposition are expected to have adverse effects on many lichen species and induce large shifts in their functional composition (Bobbink *et al.*, 2010; Elmendorf *et al.*, 2012a, 2012b). Further, land-use intensification may cause replacements of lichens that have fruticose growth by foliose species (Stofer *et al.*, 2006). Our review makes the case that functional differences between lichens are powerful drivers of how they affect communities and ecosystems (Fig. 2), and there is a need to better understand how global change-driven shifts in the composition of lichen communities will mediate their impact on ecosystem functioning.

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Asplund, J. & Wardle, D.A. (2017) How lichens impact on terrestrial community and ecosystem properties. Biological Reviews, 92, 1720–1738.

**Table 1** Range of trait values (2.5% and 97.5% quantiles) observed globally for a range of functional traits, for vascular plants (from the TRY database; Kattge *et al.*, 2011) and lichens (data from Demmig-Adams *et al.*, 1990; Gauslaa & Solhaug, 1998; Smith & Griffiths, 1998; Palmqvist *et al.*, 2002; Lange *et al.*, 2004; Gauslaa, 2005; Nybakken, Johansson, & Palmqvist, 2009; Nybakken *et al.*, 2010; Nybakken, Sandvik, & Klanderud, 2011; Solhaug *et al.*, 2009; Gauslaa & Coxson, 2011; Raggio *et al.*, 2012; Asplund & Wardle, 2013, 2014; Asplund, Ohlson, & Gauslaa, 2015b; Esseen *et al.*, 2015; Gauslaa *et al.*, 2016).

| Plant trait | n | 2.5% quantile | Median | 97.5% quantile | Equivalent lichen trait | n | 2.5% quantile | Median | 97.5% quantile |
|---|---|---|---|---|---|---|---|---|---|
| Leaf tissue N (%) | 33880 | 0.8 | 1.7 | 3.9 | Tissue N (%) | 98 | 0.3 | 1.3 | 4.5 |
| Leaf tissue P (%) | 17057 | 0.04 | 0.13 | 0.35 | Tissue P (%) | 34 | 0.02 | 0.11 | 0.31 |
| Leaf tissue C (%) | 7 856 | 40.5 | 47.6 | 54.1 | Tissue C (%) | 21 | 37.6 | 44.7 | 49.0 |
| Specific leaf mass (mg $cm^{-2}$; reciprocal of specific leaf area) | 45733 | 2.1 | 5.7 | 22.2 | Specific thallus mass (STM; mg $cm^{-2}$) | 54 | 6.4 | 12.3 | 40.3 |
| Phenolic compounds (%) | 454 | 2.4 | 11.9 | 25.1 | Phenolic compounds (%) | 28 | 0 | 2.7 | 23.7 |
| Leaf dry matter content (LDMC; g $g^{-1}$) | 16185 | 0.1 | 0.2 | 0.4 | Water holding capacity (WHC; mg $H_2O$ $cm^{-2}$)* | 27 | 5.4 | 12.9 | 60.2 |
| Maximum photosynthetic rate per leaf dry mass ($A_{max}$; µmol $g^{-1}$ $s^{-1}$) | 2384 | 0.02 | 0.12 | 0.49 | Maximum photosynthetic rate per per thallus dry mass (µmol $g^{-1}$ $s^{-1}$) | 58 | 0.002 | 0.014 | 0.042 |

* Lichens are poikilohydric and their water content is heavily dependent on water availability (liquid or air humidity). As such, LDMC and WHC are not functionally analagous. The maximum water holding capacity is highly variable and mostly driven by STM and growth form, and WHC within species are strongly related to thallus size (Gauslaa & Solhaug, 1998).

**Figure 1.** Lichens show tremendous variation both in terms of their growth form and colour. Upper three panels (left to right) are the crustose lichens *Caloplaca epithallina*, *Carbonea vitellinaria* and *Icmadophila ericetorum*. The middle panels (left to right) are the foliose lichens *Lobaria pulmonaria*, *Arctoparmelia centrifuga* and *Leptogium saturninum*. The lower three panels (left to right) are the fruticose lichens *Cladonia stellaris*, *Ramalina calicaris* and *Bryoria tenuis.* Photos are © Einar Timdal.

**Figure 2.** Lichens vary greatly in terms of growth form, type of photobiont, functional traits, water holding capacity, colour and secondary chemistry. This variation results in species-specific differences in the effect lichens have on community and ecosystem properties. Photos are © Einar Timdal.

**Figure 3.** A wide range of consumer organisms depend on lichens, and these range in size from microorganisms to large mammals. As such, lichen-consumer interactions operate at a wide range of spatial scales. For smaller organisms the primary role of lichens is in providing a habitat, while for larger organisms their primary role is as a food source.

**Figure 4.** Contrasting mechanisms by which lichens can affect the establishment and growth of plants, notably during early stages of primary succession. Red (–) and blue (+) = negative and positive effects of lichens on plants respectively. Illustration by Lennart Asplund.

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Figure 1
215x155mm (300 x 300 DPI)

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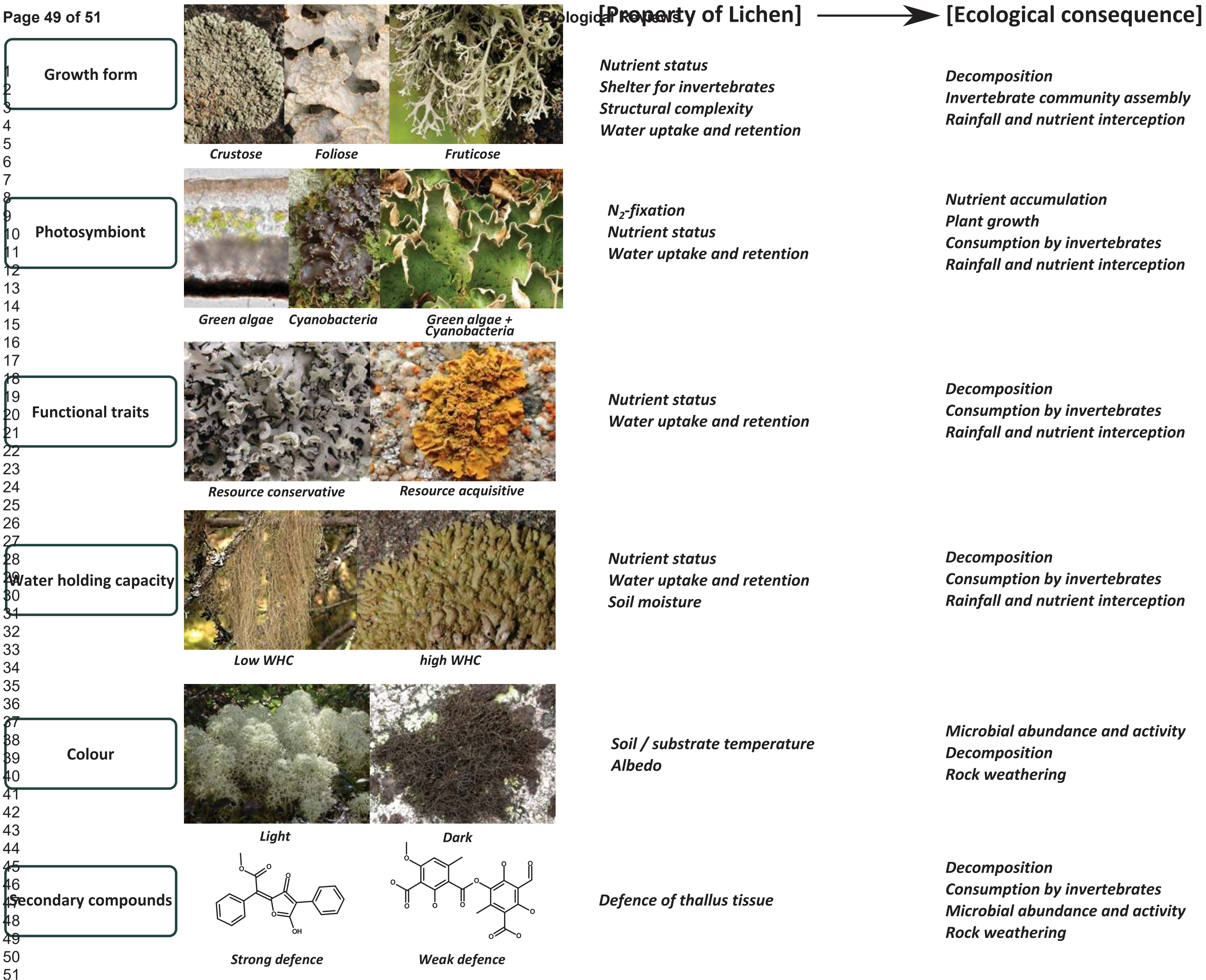

[Property of Lichen] → [Ecological consequence]

**Growth form**

*Nutrient status*
*Shelter for invertebrates*
*Structural complexity*
*Water uptake and retention*

*Decomposition*
*Invertebrate community assembly*
*Rainfall and nutrient interception*

**Photosymbiont**

*$N_2$-fixation*
*Nutrient status*
*Water uptake and retention*

*Nutrient accumulation*
*Plant growth*
*Consumption by invertebrates*
*Rainfall and nutrient interception*

**Functional traits**

*Nutrient status*
*Water uptake and retention*

*Decomposition*
*Consumption by invertebrates*
*Rainfall and nutrient interception*

**Water holding capacity**

*Nutrient status*
*Water uptake and retention*
*Soil moisture*

*Decomposition*
*Consumption by invertebrates*
*Rainfall and nutrient interception*

**Colour**

*Soil / substrate temperature*
*Albedo*

*Microbial abundance and activity*
*Decomposition*
*Rock weathering*

**Secondary compounds**

*Defence of thallus tissue*

*Decomposition*
*Consumption by invertebrates*
*Microbial abundance and activity*
*Rock weathering*

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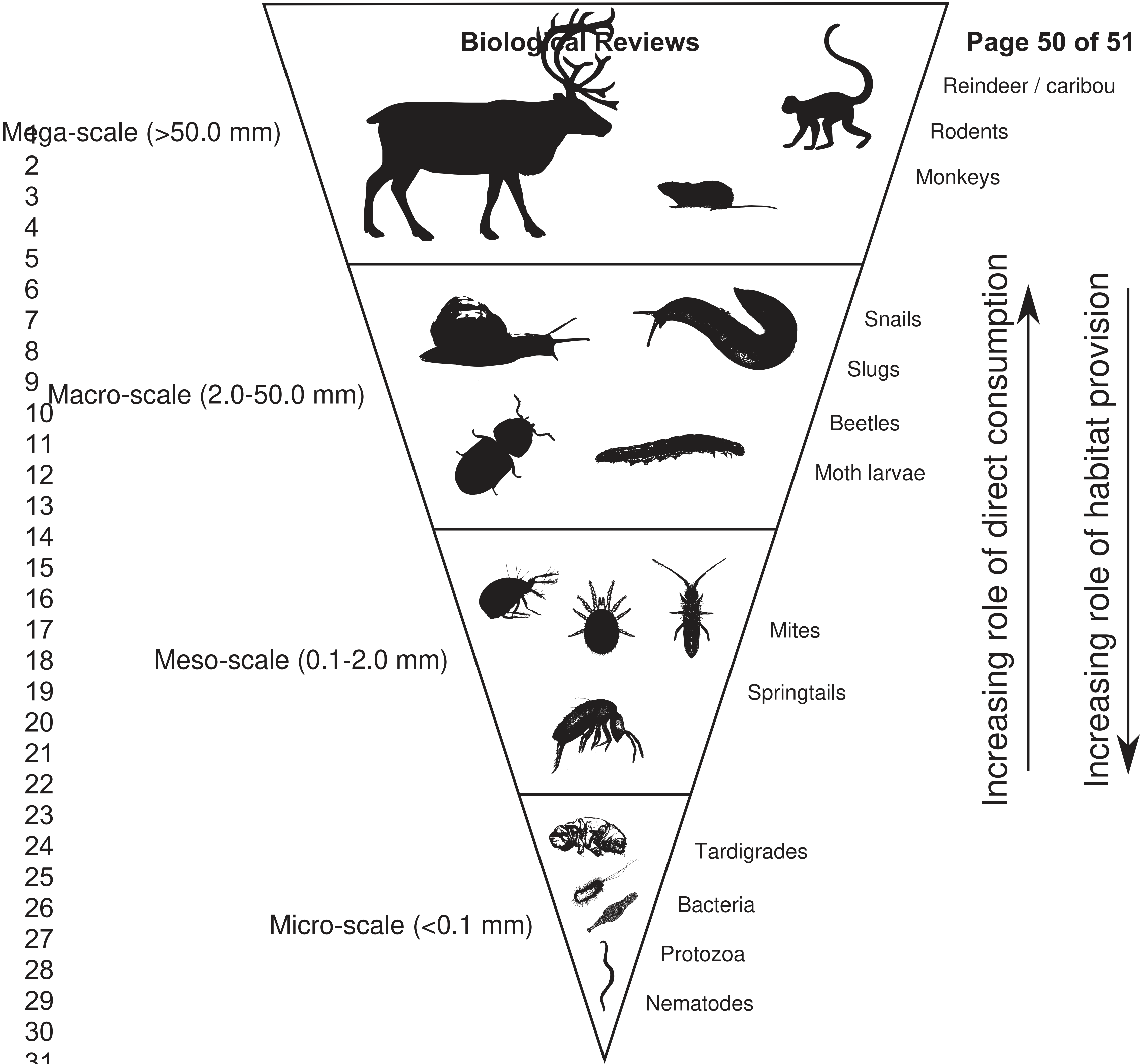

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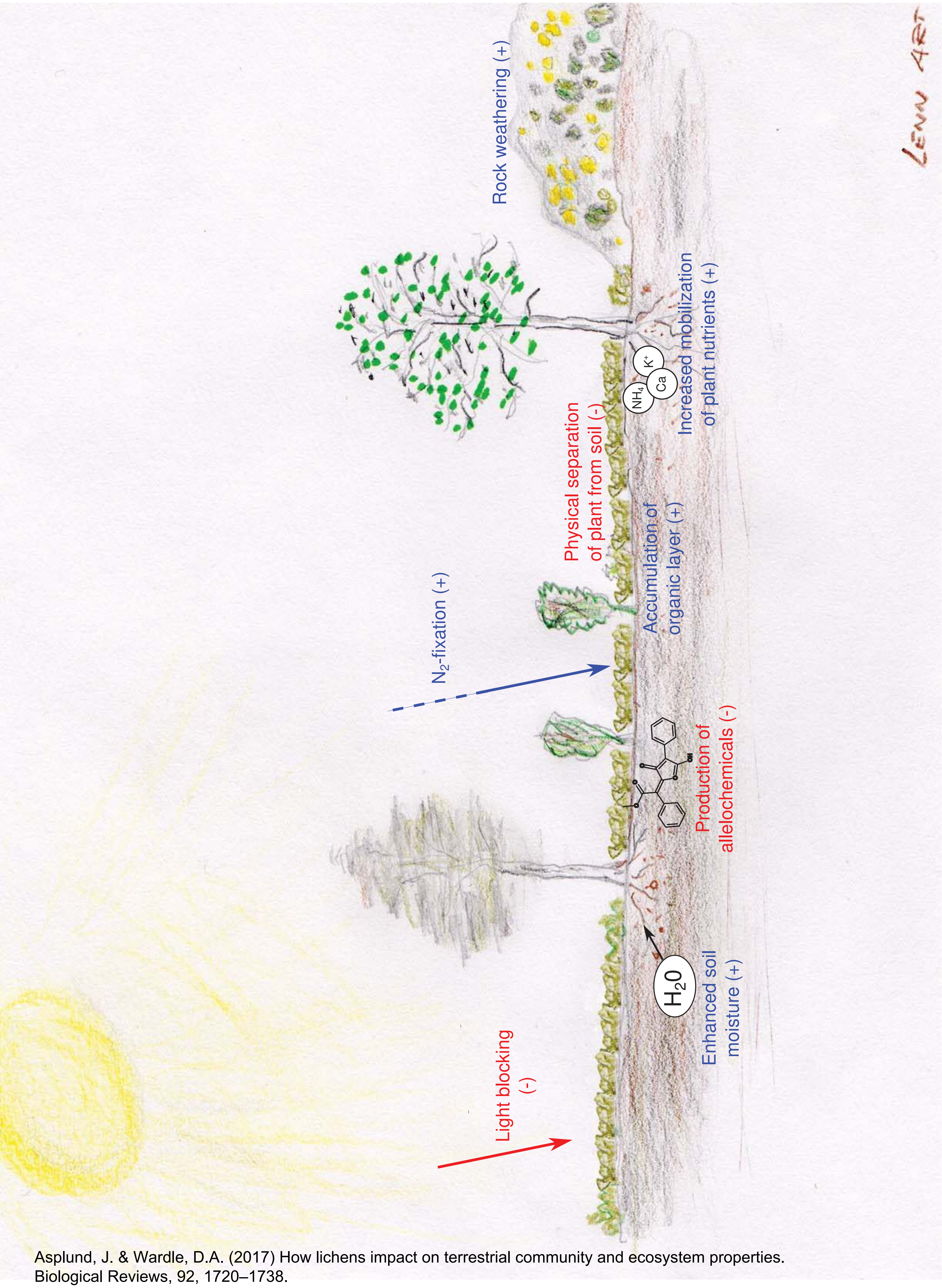

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