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4 1 **Lichens as drivers of community and ecosystem properties in terrestrial**
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6 2 **ecosystems**
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18 **Abstract**

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

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3 42 mixtures of lichens affect the key community- and ecosystem-level processes that they drive, the
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5 43 extent to which lichens in early succession influence vascular plant succession and ecosystem
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7 44 development in the longer term, and how global change drivers may impact on ecosystem
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9 45 functioning through altering the functional composition of lichen communities.
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17 48 **Keywords (5-10):** Decomposition; Functional traits; Invertebrate food-webs; Lichenized fungi;
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19 49 Nutrient cycling; Trophic interactions
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7 51 **Contents**
8 52 I. Introduction..... 4
9
10 53 II. Characterizing the diversity of lichen growth forms and functional characteristics..... 6
11
12 54 III. How variation among lichens affect ecosystem nutrient and carbon flux..... 11
13 55 (1) Biogeochemical nutrient cycling 11
14 56 (2) Litter decomposition..... 13
15
16
17 57 IV. How variation among lichens affects their interactions with consumers..... 17
18 58 (1) Lichen food webs 17
19 59 (2) Defence 23
20
21
22 60 V. How variation among lichens affects their impacts on plants..... 26
23
24 61 VI. Conclusions and future directions 28
25
26 62 VII. Acknowledgements..... 30
27 63 VIII. References..... 30
28
29 64
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35 66 **I. Introduction**

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37 67 Lichens are symbiotic associations between a heterotrophic mycobiont (i.e., fungus) and one or
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39 68 more autotrophic photobionts (green algae and/or cyanobacteria). Lichens are generally slow-
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41 69 growing, long-lived and stress-tolerant, but they show a wide diversity of growth forms (Fig. 1).
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44 70 As such, some are prostrate and have leaf-like structures, while others have complex three-
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46 71 dimensional structures that resemble minute forests. Lichens occur in most terrestrial ecosystems;
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49 72 often they occur as minor contributors, but in some forest, grassland and tundra ecosystems they
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51 73 make up a large proportion of the ground layer biomass. Further, they frequently dominate in
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53 74 habitats that are too nutrient-poor, too dry, or too cold to support a complete or permanent cover
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56 75 of plants. As such, lichens dominate approximately 8% of the Earth’s land surface (Ahmadjian,
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3 76 1995), and most of the land surface in xeric high latitude and high elevation ecosystems. More
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6 77 than 18,000 species of lichens exist world-wide and at higher latitudes the number of lichen
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8 78 species exceeds the number of vascular plant species (Nash, 2008). As such, Norway host 1.5
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10 79 times more lichen than vascular plant species and there are 190 times more lichen than vascular
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13 80 plant species in Antarctica.

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15 81 Most literature about how autotrophs affect ecosystem processes has focused on vascular
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17 82 plants, and over the past 25 years an enormous literature has emerged on how plant species
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19 83 differences drive ecosystems (Hobbie, 1992; Grime, 2001; Wardle, 2002). As such, it is well
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21 84 recognized that vascular plant species identity influences biogeochemical processes through
22
23 85 determining the quantity and quality of litter that enters the soil, and inputs of nitrogen (N)
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25 86 through biological N₂ fixation. In contrast, despite their importance in many ecosystems
26
27 87 worldwide, the roles of lichens as drivers of community processes and ecosystem functioning
28
29 88 have attracted less attention and are often overlooked. This is despite their potential importance in
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31 89 driving ecosystem biogeochemistry. As such, most lichen species capture nutrients from the air
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33 90 and roughly 10% of them fix atmospheric N₂ through their association with cyanobacteria. These
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35 91 nutrients trapped by lichens reach other ecosystem components through leaching, decomposition
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37 92 and consumption by animals. Further, lichens also provide habitats for various invertebrates that
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39 93 may or may not use them as a food source.

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41 94 Many studies on vascular plants have shown that the effect of species on ecosystem
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43 95 processes depends on their functional traits (Cornelissen *et al.*, 1999; Díaz *et al.*, 2004;
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45 96 Kurokawa, Peltzer, & Wardle, 2010), and that variation in functional traits may have a more
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47 97 important direct role than macroclimate in driving ecosystem processes (Cornwell *et al.*, 2008).
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49 98 This has led to calls for a shift from species-centred to traits-centred approaches in understanding
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51 99 community and ecosystem processes (McGill *et al.*, 2006; Violle & Jiang, 2009). However, the
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3 100 importance of functional traits for driving ecological processes in other ecologically important
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6 101 autotrophs such as lichens has seldom been acknowledged (e.g. Lang *et al.*, 2009; Asplund &
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8 102 Wardle, 2013). Despite this, lichens have a distinct suite of functional traits that are analogous to
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10 103 the types of functional traits frequently studied for vascular plants (Cornelissen *et al.*, 2007), and
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12 104 that potentially provide a mechanistic framework for understanding their contribution to
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14 105 community and ecosystem processes.

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17 106 In this paper we will review the role of lichens in terrestrial communities and ecosystems.
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19 107 We will start by discussing the functional characteristics of lichens, with particular focus on their
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21 108 traits and functional groupings because of their potential importance in driving lichen species
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23 109 effects on community and ecosystem processes. We will then explore the role that variation
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25 110 among lichens has in determining ecosystem carbon (C) and nutrient fluxes, for instance by
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27 111 affecting the decomposition and nutrient loss from their residues. Following that, we will discuss
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29 112 how differences among lichens affect their interactions with animals and plants, and the
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31 113 ecological consequences of these effects. By addressing these topics in combination we will draw
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33 114 attention to the important but often overlooked role of lichens as community and ecosystem
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35 115 drivers, and will identify areas which are in need of further work for better understanding the role
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37 116 of lichens in terrestrial ecosystems.
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47 118 **II. Characterizing the diversity of lichen growth forms and functional** 48 49 50 119 **characteristics**

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53 120 How lichens drive communities and ecosystems are regulated by a number of ways in which
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55 121 lichens differ. These include their growth form, associations with symbionts, functional traits,
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3 122 capacity for water retention, colour and secondary chemistry (Fig. 2). We now explore each of
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5 123 these characteristics in turn.

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8 124 Lichenized fungi form vegetative structures that are much more complex than those of
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10 125 other fungi. There is a great variability in the physical structure of lichens and they are
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12 126 traditionally divided into three main morphological groups: crustose, foliose and fruticose.
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14 127 However, there is a high level of morphological diversity within these groups which results in
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16 128 contrasting functional characteristics. Crustose lichens are tightly adhered to their substrate (often
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18 129 tree bark or rock, but sometimes evergreen tree leaves in moist forests) from which they cannot
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20 130 be removed without destruction. Some are very thin and do not produce much biomass,
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22 131 suggesting that their direct role in biogeochemical cycling probably is limited. However, other
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24 132 crustose lichens, particularly those that are endolithic (i.e., growing inside rocks), may induce
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26 133 rock weathering through both physical processes (via hyphal penetration and
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28 134 expansion/contraction of lichen thalli) and chemical processes (via excretion of various organic
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30 135 acids) (Chen, Blume, & Beyer, 2000). Furthermore, many crustose lichens are grazed by
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32 136 invertebrates (Baur, Fröberg, & Baur, 1995). Meanwhile foliose (i.e., leaf-like) lichens are
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34 137 loosely or tightly attached to their substrate. The lobes of these lichens sometimes overlap like
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36 138 tiles, and the lower side often has a tomentum or anchoring rhizinae, which helps generate
37
38 139 favourable microclimate and microhabitat conditions for different invertebrates. Fruticose lichens
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40 140 always stand out from the surface of their substrate. These are hair-like, strap-shaped or shrubby,
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42 141 with considerable variation in branching pattern. Their size varies from minute species of 1-2 mm
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44 142 to species up to 10 m long. An extreme growth form of these fruticose lichens includes vagrant
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46 143 epiphytic lichens that lack holdfasts in mature specimens, and that occupy the air spaces between
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48 144 branches of trees. Such lichens (e.g. *Usnea longissima*) can be >1 m long and their hair-like
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50 145 tissues tend to degrade when in direct contact with the tree branch (Gauslaa, 1997).
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3 146 In addition to their growth form, lichenized fungi also vary in their associations with their
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6 147 photobionts, and this can have important ecosystem-level implications. Chlorolichens have green
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8 148 algae as their only photobiont, whereas cyanolichens have cyanobacteria as their only photobiont,
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10 149 while cephalolichens have green algae as their main photobiont but also contain cyanobacteria in
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12 150 localized internal or external structures (i.e., cephalodia). The most obvious difference between
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14
15 151 these groups is that those lichens which contain cyanobacterial symbionts commonly fix N₂ and
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17 152 thus have a higher N concentration. However, these groups also differ in their water relations,
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19 153 which in turn influence both their physical structure and water holding capacity. As such,
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22 154 chlorolichens and cephalolichens readily activate their photosynthesis in equilibrium with high
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24 155 ambient air humidity (Lange, Kilian, & Ziegler, 1986), and some of them even prefer habitats
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27 156 that are deficient in liquid water such as below overhanging rocks or on the leeward parts of lower
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29 157 old spruce trunks. Meanwhile, cyanolichens need liquid water to activate photosynthesis (Lange
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31 158 *et al.*, 1986), which explains why they are most abundant in rain forests and open sites with
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34 159 frequent heavy dewfall.

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36 160 Lichens have a high diversity of functional traits associated with resource uptake and
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38 161 retention (Cornelissen *et al.*, 2007; Asplund & Wardle, 2013), which may potentially play an
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40 162 important role in determining their effects on ecological processes (Lang *et al.*, 2009) and
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42 163 associated invertebrate communities (Bokhorst *et al.*, 2015). These traits include thallus nutrient
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44 164 content, defence compounds, specific thallus mass (STM; the equivalent of plant's specific leaf
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46 165 mass or the reciprocal of specific leaf area) and water-holding capacity, and are analogous to
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48 166 vascular plant leaf functional traits that are widely recognized as important ecological drivers
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51 167 (Table 1). However, very few studies have sought to characterize the variation of lichen
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53 168 functional traits that occur in natural communities, or whether lichens show trade-offs in traits
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56 169 between those that are characteristic of rapid resource acquisition versus resource conservation in
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3 170 the manner frequently shown for vascular plants (Grime *et al.* 1997; Díaz *et al.* 2004; Grime *et*
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5 171 *al.*, 1997; Wright *et al.*, 2004; Díaz *et al.*, 2004). Recently, it has been shown that within
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8 172 species variation in lichen functional traits can be more important than variation among species
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10 173 (and thus species turnover) in determining overall community-level measures of trait variation
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12 174 (Asplund & Wardle, 2014). This contrasts with what is usually found for vascular plants where
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15 175 across-species variation species turnover is usually more important (Kichenin *et al.*, 2013;
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17 176 Siefert *et al.*, 2015). For example, thallus nutrient concentration, a functional trait known to be
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20 177 important in driving thallus decomposability (Lang *et al.*, 2009; Asplund & Wardle, 2013), can
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22 178 show tremendous variation not only across but also within species (Palmqvist *et al.*, 2002;
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24 179 Asplund & Wardle, 2014). This high intraspecific variability is linked to the considerable ability
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27 180 of lichens to absorb and accumulate nutrients from atmospheric sources (Nash, 2008). Likewise,
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29 181 several studies have revealed that STM can show considerable variation within species (Snelgar
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31 182 & Green, 1981; Gauslaa *et al.*, 2009; Solhaug *et al.*, 2009; Asplund, Sandling, & Wardle,
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33 183 2012).

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35
36 184 Lichens vary greatly in their ability to retain moisture, and this has important ecological
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38 185 implications. Some lichens (e.g. those that are thin and pendulous) generally have a limited
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40 186 ability to retain water (Esseen *et al.*, 2015), even though they quickly take up water from humid
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42 187 air. Meanwhile, some other lichens (typically thick or gel-like foliose cyanobacterial lichens)
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44 188 have the ability to retain water for lengthy periods (Lange *et al.*, 1993; Lange, Belnap, &
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46 189 Reichenberger, 1998; Gauslaa & Solhaug, 1998; Lange, 2000). The water holding capacity of
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48 190 lichens is strongly positively correlated with their STM both within and across species (Gauslaa
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50 191 & Coxson, 2011; Merinero, Hilmo, & Gauslaa, 2014; Esseen *et al.*, 2015). There appears to be
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52 192 a trade-off between the flexible and rapid moisture uptake strategy characteristic of thin
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54 193 chlorolichens that utilize humid air every night, and the conservative water storage strategy of
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3 194 cyanolichens that limit their photosynthesis to rarer rainy periods (Gauslaa, Coxson, & Solhaug,
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6 195 2012). In lichen-dominated epiphytic communities, there is a need for frequent rain to sustain
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8 196 high cyanolichen and cephalolichen biomass and thus high N₂-fixation rates. In this light,
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10 197 epiphytic lichens may play an important role in the partitioning of moisture derived from
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12 198 precipitation and thus the humidity of the forest interior (Van Stan II & Pypker, 2015). In some
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14 199 sites with low rainfall, fruticose epiphytic lichens absorb moisture from fog and thereby supply
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16 200 underlying soils with water, in turn enhancing the availability of soil moisture for tree growth
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18 201 (Stanton & Horn, 2013; Stanton, Armesto, & Hedin, 2014).
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22 202 Lichens vary hugely in colour from almost white to black. This variation in spectral
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24 203 characteristics results in large differences in thallus surface temperatures (Kershaw, 1975;
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26 204 Gauslaa, 1984). As such, in cold environments dark pigmented lichens may elevate temperatures
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28 205 above 0 °C and induce melting of the surrounding snow, thereby enabling them to utilize snow-
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30 206 melt water (Kershaw, 1983). Variation in pigmentation among lichens may also affect
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32 207 microclimate at the soil surface (Kershaw, 1978). As such, the light-coloured, mat-forming
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34 208 lichens can increase the albedo of the land surface by around 1 % (Stoy *et al.*, 2012). Further, the
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36 209 surface and internal temperature of limestones are higher below the black-coloured *Verrucaria*
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38 210 *nigrescens* than below the light grey *V. baldensis*, and this contributes to increased rock
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40 211 weathering (Carter & Viles, 2003, 2004).
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44 212 There is considerable variation among lichens in their production of carbon based
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46 213 secondary compounds (CBSC), and in total more than 800 compounds have been described
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48 214 (Huneck & Yoshimura, 1996; Huneck, 2001). These are commonly weak phenolic acid
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50 215 derivatives and all are produced by the fungal partner. Most of them are unique to lichenized
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52 216 fungi with only a few also produced by non-lichenized fungi. These compounds have likely
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54 217 evolved to protect the lichens from a suite of physical and biotic stressors, such as light damage
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3 218 and attack by predators and pathogens (Lawrey, 2009; Solhaug & Gauslaa, 2012). Further, they
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5 219 likely play a key role in driving lichen-mediated ecosystem processes and community assembly
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7 220 (Asplund & Wardle, 2013; Asplund, Bokhorst, & Wardle, 2013; Asplund *et al.*, 2015). These
8
9 221 CBSCs are often present in concentrations ranging from 1 to 5 % of thallus dry mass, but in the
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11 222 widespread epiphyte *Hypogymnia physodes* can reach over 20% (Solhaug *et al.*, 2009).
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13 223 Considerable variation in CBSC concentration exists not only among but also within lichen
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15 224 species (Culberson & Culberson, 1958; McEvoy, Gauslaa, & Solhaug, 2007; Vatne, Asplund, &
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17 225 Gauslaa, 2011; Asplund & Wardle, 2014). For instance, concentrations of CBSCs in the lichen
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19 226 *Lobaria pulmonaria* varies from 0.7 to 13 % depending on thallus size, elevation and pH
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21 227 (Asplund & Gauslaa, 2007; Vatne *et al.*, 2011). In addition to phenolic compounds, some
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23 228 cyanobacteria (*Nostoc* sp.) in lichen symbioses produce microcystins which are a group of cyclic
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25 229 peptide hepatotoxins (Oksanen *et al.*, 2004; Kaasalainen *et al.*, 2012), although the ecological
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27 230 role of these toxins is not well established.
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35 231 **III. How variation among lichens affect ecosystem nutrient and carbon flux**

36 37 38 232 39 40 233 *(1) Biogeochemical nutrient cycling*

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43 234 While plant dominated communities gets most of their nutrients from the soil or from nutrients
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45 235 cycled within the system, lichen-dominated ecosystems obtain a relatively larger part of their
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47 236 nutrients from outside the ecosystem. This is because lichens lack roots and instead take up
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49 237 significant nutrient pools from wet and dry depositions that originate primarily from outside the
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51 238 ecosystem. They do this efficiently because they have a large surface area relative to their
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53 239 biomass, and because their surfaces lack cuticles and stomata, which make them very effective at
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55 240 absorbing nutrients. In addition, lichens can accumulate concentrations of these captured
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3 241 nutrients that are vastly in excess of their physiological needs. However, lichens differ
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5 242 tremendously in their capacity to capture nutrients from outside the ecosystem and this depends
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7 243 on their characteristics. Some lichen growth forms, especially fruticose hair-like lichens, are
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9 244 particularly effective at capturing both dew and fog, which is often more rich in nutrients than is
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11 245 rain (Nash, 2008). For example, the epiphytic chlorolichen *Ramalina menziesii* in an oak
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13 246 woodland was shown to capture 2.85 and 0.15 kg ha⁻¹ y⁻¹ of N and phosphorus (P), respectively,
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15 247 from sources outside the ecosystem (Knops, Nash, & Schlesinger, 1996). Another study showed
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17 248 that this species alone was responsible for 13 % of the total annual canopy turnover of N, 4 % of
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19 249 P, 7 % of potassium (K), 1 % of calcium (Ca), 3 % of magnesium (Mg) and 8 % of sodium
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21 250 (Boucher & Nash, 1990). Further, fruticose lichens, which have a relative large surface area,
22
23 251 appear to be better at capturing elements than are foliose lichens (Yemets, Solhaug, & Gauslaa,
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25 252 2014). However, foliose lichens are generally richer in N, P and Ca than are fruticose lichens
26
27 253 (Mangelson *et al.*, 2002; Asplund & Wardle, 2013). Because of their capacity to take up and
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29 254 accumulate nutrients, lichens can in some ecosystems store a substantial proportion of the total
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31 255 nutrients present in the ecosystem. For example, in an open *Picea mariana* woodland in northern
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33 256 Québec, mat-forming terricolous lichens covering 97 % of the ground surface contained up to 20
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35 257 % of the total biomass, 25 % of the N and 12 % of the P in the ecosystem (Rencz & Auclair,
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37 258 1978; Auclair & Rencz, 1982).

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39 259 Approximately 10% of all lichen species contain N₂-fixing cyanobacteria. Because
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41 260 lichens often grow in nutrient-poor ecosystems, those containing cyanobacteria can greatly
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43 261 increase the inputs of N to the ecosystem. For instance, *Pseudotsuga menzeisii* forests in Oregon
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45 262 support a high abundance of the N-fixing *Lobaria oregana* that contributes approximately 50 %
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47 263 of the total ecosystem N input (Denison, 1973). Further in a synthesis of 17 studies, Nash (2008)
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49 264 lists estimations of lichen N₂ fixation contributions to the N economy for various ecosystems.
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3 265 These values vary from 0.04-0.21 kg N ha⁻¹ y⁻¹ in tundras and forests in subarctic Alaska in
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5 266 which *Peltigera* spp. is the dominant lichen (Gunther, 1989) to 16.5 kg N ha⁻¹ y⁻¹ in old growth
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7 267 *Pseudotsuga* forests in NW USA in which *Lobaria oregana* is dominant (Antoine, 2004).
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10 268 However, Nash (2008) also notes that most estimates (and particularly the highest ones) are
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13 269 somewhat inaccurate and may be unreliable due to various methodological flaws.
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17 271 *(2) Litter decomposition*

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20 272 There is a substantial literature focused on understanding how vascular plant traits and litter
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22 273 quality govern variation in litter decomposition rates among plant species, and these show
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25 274 decomposition to be associated positively with nutrient concentrations and specific leaf area, and
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27 275 negatively with concentrations of lignin and secondary defence compounds and leaf dry mass
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30 276 content (Cornelissen *et al.*, 1999; Pérez-Harguindeguy *et al.*, 2000; Cornwell *et al.*, 2008;
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32 277 Makkonen *et al.*, 2012). However, although several studies have quantified rates of
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34 278 decomposition of lichen litter (Wetmore, 1982; Guzman, Quilhot, & Galloway, 1990; Knops *et*
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36 279 *al.*, 1996; Esseen & Renhorn, 1998; Coxson & Curteanu, 2002; Caldiz, Brunet, & Nihlgård,
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38 280 2007; Campbell, Fredeen, & Prescott, 2010), these have each considered too few species to
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41 281 enable reliable evaluation of which lichen functional traits are important in regulating
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44 282 decomposition. However, two recent comparative studies have shown that lichen decomposition
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46 283 is related to a spectrum of thallus traits that are broadly analogous to leaf traits known to regulate
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48 284 vascular plant litter decomposition. Specifically, Lang *et al.* (2009) found lichen litter
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51 285 decomposition to be positively related to thallus metabolic carbohydrates, lipids, N, Ca, K, pH
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53 286 and amino acids, while Asplund and Wardle (2013) showed lichen decomposition to be related to
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55 287 thallus N, P and pH. Further, Asplund & Wardle (2013) showed through removing thallus CBSCs
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3 288 by means of acetone rinsing that CBSCs are powerful regulators of lichen decomposition, and
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5 289 that all CBSCs that reduced decomposition also deterred lichenivorous snails. They also found
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8 290 foliose lichens to decompose quicker than did fruticose ones, which probably is due to them
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10 291 having a higher N content.

11
12 292 The rate at which N is released from lichens during decomposition also varies between
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14 293 lichens with differing functional characteristics. For instance, Campbell et al. (2010) found N to
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16 294 quickly be released without initial N immobilization from the N-fixing lichens *Lobaria*
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18 295 *pulmonaria* and *Nephroma helveticum*. They argued that the relatively high N mineralization
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20 296 rates from these lichens may be due to the lack of lignin and the fact that their N occurs in labile
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22 297 proteins, chitin and nucleic acids (Dahlman *et al.*, 2003) which can be solubilized and rapidly
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24 298 leached during the early stages of the decay process (Rai, 1988). In contrast, rapid release of N
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26 299 during decomposition was not found to occur for two chlorolichens, i.e., *Alectoria sarmentosa*
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28 300 and *Platismatia glauca*, probably because of their low initial N concentration (Campbell *et al.*,
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30 301 2010). Meanwhile, Asplund & Wardle (2013) did not find any difference in N release during
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32 302 decomposition between N₂-fixing and non N₂-fixing lichens. Lichen growth form also seems to
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34 303 play a role in the release of N. For example, Asplund et al. (2013) found that epiphytic fruticose
35
36 304 lichens, which have a large surface area, release more N than do epiphytic foliose lichens during
37
38 305 decomposition, despite the higher initial N concentration of foliose lichens. They also found that
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40 306 most foliose lichens growing on rocks rapidly lost N but this was probably due to many of them
41
42 307 having a high initial N concentration. Further, P has been shown to be released quickly during
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44 308 decomposition from a variety of species of lichens, including cyano-, cephalo- and chlorolichens
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46 309 (Caldiz *et al.*, 2007; Campbell *et al.*, 2010; Asplund *et al.*, 2013), and most of the P in the
47
48 310 thallus is frequently released within 5 months (Campbell *et al.*, 2010; Asplund *et al.*, 2013). In
49
50 311 contrast, litter of *Cladonia* spp. growing on nutrient poor soils can retain or even accumulate P
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3 312 during decomposition (Moore, 1984; Asplund *et al.*, 2013). Other elements such as K which are
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5 313 present as dissolved monovalent ions can also be readily released early during the decomposition
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7 314 of lichen thalli (Caldiz *et al.*, 2007; Campbell *et al.*, 2010) in much the same manner as is often
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9 315 observed during plant litter decomposition (Lousier & Parkinson, 1978).

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11
12 316 A vast body of literature has explored the impact of soil invertebrates on vascular plant
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14 317 litter decomposition (Petersen & Luxton, 1982; Kampichler & Bruckner, 2009), and has
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16 318 revealed that these effects are driven by invertebrates consuming and fragmenting litter,
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18 319 dispersing microbial propagules, and stimulating soil microbial activity (Parkinson, Visser, &
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20 320 Whittaker, 1979; Seastedt, 1984). In contrast, only a few studies have investigated whether
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22 321 lichenivorous invertebrates may play a role in lichen decomposition. For instance, McCune and
23
24 322 Daly (1994) found half-lives of decomposing lichen litter to be two to nine times shorter in the
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26 323 presence of animals larger than 1 mm than when these were excluded. Similarly, *Hypogymnia*
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28 324 *physodes* thallus litter decomposed 1.9 times faster when animals sized 0.5 - 3 mm had access to
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30 325 it (Biazrov, 1995). Further, Asplund *et al.* (2013) showed that micro-arthropods can increase
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32 326 decomposition rates of lichens, but that their effects can be mitigated by high levels of CBSCs in
33
34 327 the lichen thalli that deter lichen-feeding activity. Some lichen CBSCs degrade fairly quickly
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36 328 during thallus senescence, suggesting that they only impact micro-arthropods during early stages
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38 329 of decomposition (Asplund & Wardle, 2012). However, other compounds are more recalcitrant
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40 330 and thus increase in concentration relative to thallus litter mass, and are therefore likely to have
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42 331 longer term effects on micro-arthropod feeding activity (Bidussi, Solhaug, & Gauslaa, 2016).

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44 332 Some studies that have quantified decomposition rates of lichen and vascular plant litter
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46 333 in the same study have shown that lichen litter often decomposes more slowly (Moore, 1983,
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48 334 1984; Wardle *et al.*, 2003). However, the lichen species that have been used in these
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50 335 comparisons (i.e., *Cladonia* spp.), have thalli that are very nutrient poor and generally decompose

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3 336 considerably more slowly than do thalli from most other lichens species (Asplund & Wardle,
4
5 337 2013). In a litter-bed experiment comparing decomposition rates of 27 bryophytes, 17 lichens and
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7 338 five vascular plants, lichens overall had comparable decomposition rates to those of vascular
8
9 339 plants, whereas bryophytes had the slowest decomposition (Lang *et al.*, 2009). Meanwhile, Vogt
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11 340 *et al.* (1983) found that the pendulous epiphytic lichen *Alectoria sarmentosa* decomposed much
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13 341 more quickly than associated vascular plant litter.
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17 342 Like plant leaves, epiphytic lichen material falls to the ground before decomposing. A
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19 343 number of studies have quantified litter-fall of lichens, primarily in temperate and boreal forests
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21 344 (e.g. Esseen, 1985; Knops *et al.*, 1996; Stevenson & Coxson, 2003; Caldiz & Brunet, 2006).
22
23 345 However, because lichen litter usually falls in clumps and is therefore very spatially scattered,
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25 346 lichen litter-fall is often underestimated (McShane, Carlile, & Hinds, 1983). In temperate and
26
27 347 boreal regions the majority of lichen litter-fall occur during autumn and winter and especially
28
29 348 during stormy events (Esseen, 1985). This litter-fall hugely varies between stands, and lichen
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31 349 litter deposition of between 13 and 320 kg ha⁻¹ year⁻¹ has been reported (Caldiz & Brunet, 2006;
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33 350 Campbell *et al.*, 2010; Rawat, Upreti, & Singh, 2011). This variation mainly reflects the
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35 351 standing crop in the stand and especially that of pendulous lichens which tend to fragment more
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37 352 easily than do other fruticose and foliose lichens. As such, the annual turnover of pendulous
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39 353 lichen is commonly 10 % (and up to 30 %) of the standing crop, while the turnover of foliose
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41 354 lichens is usually a few percent (Stevenson & Coxson, 2003). However, because epiphytic lichen
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43 355 litter is generally more nutrient rich than is tree leaf litter, its role in nutrient cycling is
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45 356 disproportionate to the biomass of its litter-fall. For example, in an oak woodland, litter inputs
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47 357 from the dominant non N-fixing lichen *Ramalina menziesii* was found to contain twice as much
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49 358 N as did oak leaf litter (Knops *et al.*, 1996). The relatively high nutrient concentrations in lichen
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51 359 litter compared with vascular plant leaf litter are in part because plants remobilize and resorb
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3 360 their nutrients before leaf abscission, which lichens cannot. However, mat-forming lichens,
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5 361 continuously die-off at the bottom creating necromass which leads to nutrients in the senescing
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8 362 parts then being partially recycled internally, leading to less nutrients being released to the
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10 363 ecosystem (Crittenden, 1991).

11
12 364 The presence of lichens, either when alive or as litter, can also affect the decomposition of
13
14 365 associated plant litter. For instance, oak leaf litter was found to lose mass less rapidly during
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16 366 decomposition when in the presence of lichen litter, despite the lichen litter decomposing quicker
17
18 367 than the oak litter (Knops *et al.*, 1996). This was proposed as due to the dominant lichen *R.*
19
20 368 *menziesii* having a poor water retention capacity, leading to the decomposer community being
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22 369 more impeded by moisture limitation (Matthes-Sears, Nash, & Larson, 1986a, 1986b). In
23
24 370 contrast, *Vaccinium myrtillus* litter decomposed more quickly in *Cladonia* mats than when the
25
26 371 lichens had been removed, likely because of a more favourable microclimate and moisture
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28 372 conditions in the mats (Stark *et al.*, 2000). Meanwhile Wardle *et al.* (2003) found that vascular
29
30 373 plant litter decomposition was largely unaffected by whether or not it was mixed with litter from
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32 374 the lichen *Cladonia stellaris*, although the decomposition of the lichen litter was impeded by the
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34 375 vascular plant litter. However, too few studies have been performed to determine what types of
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36 376 lichens, or what lichen characteristics, exert the greatest positive or negative effects on other
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38 377 litters, or the role of environmental context on these effects.
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49 379 **IV. How variation among lichens affects their interactions with consumers**

50 380 *(1) Lichen food webs*

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52 381 Despite the antibacterial and antifungal properties often ascribed to their CBSCs, lichens provide
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54 382 microhabitats for numerous eukaryotic and prokaryotic microorganisms, (Lawrey & Diederich,
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3 383 2003; Grube & Berg, 2009). Indeed, recent work has highlighted the role of lichen-associated
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5 384 bacteria as an important component of the lichen meta-organism, challenging the traditional view
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8 385 of lichens simply being a symbiosis between a fungus and one or two photobionts
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10 386 (Aschenbrenner *et al.*, 2016). Bacterial cell densities in lichens dramatically exceed those in or
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12 387 on vascular plant leaves (Cardinale *et al.*, 2008; Grube *et al.*, 2009; Saleem, 2015), and they
13
14 388 likely play an important role in lichen-mediated food webs through serving as food for nematodes
15
16 389 and protozoa. Bacteria varies hugely in numbers and diversity between lichen species, and this is
17
18 390 largely driven by differences in lichen growth form and photobiont type (Hodkinson *et al.*,
19
20 391 2012). The variation with photobiont type is likely to be due to the green algal symbionts
21
22 392 providing mainly sugar alcohols and the cyanobacterial symbionts providing glucose, and
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24 393 because only the cyanobacteria provide N through biological fixation (Elix & Stocker-Wörgötter,
25
26 394 2008). Bacterial symbionts can contribute functionally to the lichen by providing resistance to
27
28 395 biotic and abiotic stresses, biosynthesis of vitamins, detoxification of inorganic substances (e.g.
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30 396 arsenic, copper and zinc) and nutrient supply including N₂-fixation (as reviewed by Grube,
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32 397 Cardinale, & Berg, 2012; Aschenbrenner *et al.*, 2016).

38 398 The lichen thallus hosts aquatic microfauna (i.e., those that live in water films), such as
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40 399 nematodes, protozoa, rotifers and tardigrades (Fig. 3) (Gerson & Seaward, 1977). As such, there
41
42 400 are complex food webs inhabiting the lichen thallus. For instance, fungal-feeding nematodes
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44 401 likely feed on the lichen mycobiont while bacterial-feeding nematodes (which can be abundant in
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46 402 lichen thalli; Bokhorst *et al.*, 2015) feed on various bacterial symbionts. There is also a relatively
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48 403 high abundance of predacious nematodes at least in epiphytic foliose lichens (Bokhorst *et al.*,
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50 404 2015), and these are likely to feed on various lichen-associated microfauna. The knowledge of
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52 405 how these aquatic faunal communities varies between lichens is limited, although densities of
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54 406 rotifers and tardigrades are greater on lichen species that have a higher biomass (Stubbs, 1989).

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3 407 Further, Bokhorst *et al.* (2015) showed that the diversity, but not the abundance, of lichen-
4
5 408 associated nematodes increases with increasing thallus mineral nutrient concentration. They also
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7 409 showed large differences in nematode community composition between between lichens that
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9 410 occupy different growth substrates, and lichens that grow on rocks supported a much higher
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11 411 density of omnivorous nematodes than did epiphytic and terricolous lichens. Bokhorst *et al.*
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13 412 (2005) also found large differences in nematode community composition between lichens with
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15 413 and without N₂-fixation capability, due in part to higher abundances of bacterial-feeding
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17 414 nematodes in N₂-fixing lichens that are adapted for feeding on their cyanobacterial symbionts.
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22 415 Further, a diverse group of terrestrial invertebrates feed on and seek shelter on or in
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24 416 lichens (Fig. 3). These include species of gastropods, springtails, mites, beetles, moth larvae and
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26 417 woodlice (Gerson & Seaward, 1977). For instance, springtails use lichens for both food and
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28 418 shelter, and the undersides of lichen thalli can be almost completely covered with springtails
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30 419 (Leinaas & Fjellberg, 1985). Further, lichenivorous psocids and mites are fed upon by both
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32 420 pseudoscorpions and true bugs that lives on the lichens (Gerson & Seaward, 1977). Among
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34 421 lichenivorous invertebrates, gastropods play a particularly important role, and Asplund (2010)
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36 422 lists 64 species of terrestrial gastropods known to feed on lichens. Lichenivorous gastropods are
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38 423 found worldwide and feed on calcicolous lichens in limestone grasslands (e.g. Fröberg, Baur, &
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40 424 Baur, 1993) or rocky deserts (Shachak, Jones, & Granot, 1987), and on epiphytic lichens in
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42 425 temperate broadleaved and boreal forests (Asplund *et al.*, 2010b). A few snail species are
43
44 426 specialized lichen-feeders or feed predominantly on lichens (Kerney, 1999), and thus depend
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46 427 heavily on lichens as a food resource. Some snails even have specialized radulae that enable them
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48 428 to graze off epi- and endolithic lichens from rocks (Schmid, 1929; Breure & Gittenberger,
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50 429 1981). Further, the foliose lichen *Xanthoria parietina* provides the snail *Balea perversa* with all
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52 430 essential elements and nutrients necessary for its growth and reproduction (Baur & Baur, 1997).
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3 431 In addition to serving as a food source, lichens provide gastropods with shelter from predators
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5 432 and desiccation. For instance, *B. perversa* seeks protection under thalli of *X. parietina* that also
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7 433 serves as its food supply (Baur & Baur, 1997). Some snails may also use lichens to conceal
8
9 434 themselves; for example the snail *Napaeus barquini* actively covers its shell with lichens
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11 435 (Allgaier, 2007).
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15 436 Snails show clear preferences for different lichen species based on the functional
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17 437 characteristics of the lichens (Baur, Baur, & Fröberg, 1994; Asplund *et al.*, 2010b; Asplund &
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19 438 Wardle, 2013). Co-existing snail species may prefer different lichen species, and weight increase
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21 439 in juvenile snails varies greatly depending on which lichen species the snails are fed (Baur, Baur,
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23 440 & Fröberg, 1992; Baur *et al.*, 1994; Fröberg *et al.*, 1993). One major driver of lichen
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25 441 palatability is their secondary chemistry; The presence of CBSCs is an important determinant of
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27 442 lichen palatability and the removal CBSCs greatly increases the consumption of lichens by snails
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29 443 (Gauslaa, 2005; Pöykkö, Hyvärinen, & Bačkor, 2005; Černajová & Svoboda, 2014), as we
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31 444 discuss below. Furthermore, Asplund & Wardle (2013) found that generalist snails preferred
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33 445 fruticose to foliose lichens, and foliose chlorolichens over cephalo- and cyanolichens.
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35 446 Meanwhile, unlike what is often found for vascular plants (Mattson, 1980), Asplund & Wardle
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37 447 (2013) did not find any relationship between thallus consumption by snails and concentrations of
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39 448 thallus N or P across 28 forest lichen species. Further, Asplund *et al.* (2010a) found that lichens
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41 449 exposed to N fertilization (and which were more N-rich) were actually less preferred by
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43 450 lichenivorous gastropods. They attributed this to lower supply of energy in terms of mannitol in
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45 451 fertilized thalli. In contrast, Asplund, Gauslaa, & Merinero (2016) showed that snails prefer thalli
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47 452 from *L. pulmonaria* that had a lower C : N ratio as a consequence of infection by the parasitic
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49 453 fungus *Plectocarpon lichenum*.
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3 454 Lichen traits also affect communities of other lichen-associated invertebrates. For
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6 455 instance, Bokhorst *et al.* (2015) found that thallus nutrient status (i.e., N concentration and N to P
7
8 456 ratio) positively affected the diversity and abundance of both mites and springtails and also
9
10 457 altered their community composition. Consequently, N₂-fixing lichens, which are richer in
11
12 458 nutrients, tended to support more (and different species of) springtails and mites. Several studies
13
14 459 have also shown that foliose lichens usually support more springtails and mites than do fruticose
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16 460 or crustose lichens (André, 1983, 1984, 1986; Colloff, 1988; Bokhorst *et al.*, 2015), although
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18 461 André (1984) found high numbers of the mite *Dometorina plantivaga* in crustose lichens only.
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20 462 Further, Søchting & Gjelstrup (1985) found that foliose lichens supported more springtails
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22 463 relative to mites than did fruticose lichens. These studies in combination point to lichen growth
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24 464 form as an important regulator of both the abundance and community composition of
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26 465 microarthropods (André, 1985). A possible explanation for the higher abundance of invertebrates
27
28 466 on foliose compared with fruticose lichens is the favourable microclimatic conditions and shelter
29
30 467 provided by the interface between the lichen thallus and its substrate (Søchting & Gjelstrup,
31
32 468 1985). In this light, springtails may completely cover the underside of those foliose lichens that
33
34 469 provide them with both food and shelter (Leinaas & Fjellberg, 1985).

40
41 470 The importance of lichens in driving invertebrate communities is further demonstrated by
42
43 471 the positive correlation often observed between arthropod density and biomass of lichens across
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45 472 communities (Stubbs, 1989; Pettersson *et al.*, 1995; Gunnarsson, Hake, & Hultengren, 2004).
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47 473 This is true both for arthropods that feed on lichens such as mites and springtails, and for higher
48
49 474 trophic levels, such as spiders. The greater spider density in communities that support a higher
50
51 475 biomass of epiphytic lichens has been explained in terms of lichens increasing the structural
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53 476 complexity of the habitat (Gunnarsson *et al.*, 2004). However, lichens with identical structural
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55 477 complexity can support different densities of spiders through supporting contrasting amounts of
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3 478 prey (i.e. lichenivorous springtails), due to variation in defense compounds (Asplund *et al.*,
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5 479 2015). Likewise, passerine birds that feed on invertebrates are more abundant in forests that
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7 480 support a high lichen biomass due to increased abundance of prey (Pettersson *et al.*, 1995).

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10 481 Lichens are also utilized by vertebrate fauna (Fig. 3). A number of bird species use
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12 482 lichens as nesting material or as camouflage or decoration (Richardson & Young, 1977). In
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14 483 addition, flying squirrels make nests of lichens, predominately fruticose lichens of the genus
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16 484 *Bryoria*, on which they also feed. A number of mammals feed to varying extents on lichens in
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18 485 different regions of the world, including deer, elk, ibex, gazelle, musk ox, mountain goat, polar
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20 486 bear, lemming, vole, tree mouse, marmot, squirrel and monkeys (Seaward, 2008). Of these,
21
22 487 reindeer and caribou (hereafter reindeer) that inhabit circumpolar northern latitudes are especially
23
24 488 dependent on lichens. As such the winter diet of reindeer is more than 50 % lichen material, and
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26 489 these include mat-forming as well as epiphytic and saxicolous lichens (Scotter, 1967; Gaare &
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28 490 Skogland, 1975; Boertje, 1984). The vast majority of lichens consumed by reindeer are
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30 491 fruticose, and mainly of the genera *Cladonia*, *Bryoria*, *Alectoria* and *Stereocaulon* (Holleman &
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32 492 Luick, 1977; Danell *et al.*, 1994). These species are common in reindeer habitats and their
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34 493 growth form makes them easily accessible. Similar to reindeer, snob-nosed monkeys inhabiting
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36 494 north-western Yunnan, China depend on lichens as winter fall-back food; during seasons with
37
38 495 low food availability, lichens can constitute up to 97% of their diet (Grueter *et al.*, 2009). These
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40 496 monkeys prefer fruticose lichens such as *U. longissimi* and *Bryoria* spp. which are easy to grab,
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42 497 and only occasionally feed on the smaller foliose lichens (Kirkpatrick, 1996; Grueter *et al.*,
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44 498 2009). Because of their preference for *Usnea longissima*, these monkeys tend to occupy relatively
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46 499 high and cold elevations, where lichens are more abundant than in the milder lowland (Grueter *et*
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48 500 *al.*, 2012).

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502 (2) Defence

503 Already in the 19th century, Zukal (1895) suggested that CBSCs in lichens serve as defences
504 against lichenivores. However, Zopf (1896) found that snails did not discriminate between potato
505 slices smeared with lichen CBSCs and those without CBSCs. A few years later Stahl (1904)
506 found that removal of CBSC by a sodium bicarbonate solution made the lichen more attractive to
507 the snail *Cepaea hortensis*. In more recent times studies have utilized 100 % acetone to non-
508 destructively remove CBSCs from living but air dry lichens; this enables comparisons between
509 lichen material which does versus does not have CBSCs present (Solhaug & Gauslaa, 1996,
510 2001). This approach provides a unique way to test the role CBSCs play in lichen-invertebrate
511 interactions while avoiding other confounding factors, and it has been used in several studies to
512 show that lichen CBSCs do indeed deter invertebrates. (Reutimann & Scheidegger, 1987;
513 Gauslaa, 2005; Pöykkö *et al.*, 2005; Asplund & Wardle, 2013; Černajová & Svoboda, 2014;
514 Asplund *et al.*, 2015). For instance, Gauslaa (2005) offered the snail *C. hortensis* the choice
515 between lichens with and without CBSC and found a significant preference for the acetone rinsed
516 thalli in 14 out of the 17 tested lichen species. Meanwhile, Pöykkö *et al.*(2005) found higher
517 survival rates of larvae of the moth *Eilema depressum* when reared on acetone-rinsed *Vulpicida*
518 *pinastri* and *Hypogymnia physodes* than on control (non-rinsed) thalli, but found no effect of
519 acetone rinsing on survival rates on *Parmelia sulcata* and *Xanthoria parietina*. The effect of
520 acetone rinsing is highly variable between lichen species because CBSCs vary hugely both
521 qualitatively and quantitatively among them. In general, CBSCs that are restricted to the cortical
522 layer, such as atranorin, parietin and usnic acid and that protect the lichen from high solar
523 radiation, are less effective against lichenivorous snails (Gauslaa, 2005, 2009; Asplund, Solhaug,

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2
3 524 & Gauslaa, 2010c). In contrast, some medullary CBSCs are very effective against lichenivores,
4
5 525 such as the yellow vulpinic acid (Gauslaa, 2005).
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8 526 Lichen CBSCs not only deter lichenivores, but also control how they graze lichens, which
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10 527 affects lichen fitness. For instance, various lichen feeders, e.g. springtails, moth larvae and slugs
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12 528 and snails, preferentially attack the cortical layer and often also the photobionts of the lichen, but
13
14 529 stop feeding when they reach the medulla (Hale, 1972; Baur *et al.*, 2000; Bačkor, Dvorský, &
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16 530 Fahselt, 2003; Asplund, 2011b) where the CBSCs are often mostly concentrated (Asplund,
17
18 531 2011b). However, lichens that are treated with acetone, and are therefore low in CBSCs, are
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20 532 instead grazed perpendicular to the lichen surface which leaves distinct holes through all the
21
22 533 thallus layers. Further, the foliose lichen *Nephroma arcticum* has large cephalodia (containing
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24 534 colonies of N-fixing *Nostoc* spp.) which, unlike the surrounding medulla, lacks CBSCs (Renner,
25
26 535 1982). As such, slugs normally attack the cephalodia rather than the green-algal parts of the
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28 536 thallus, but when CBSCs are removed by acetone rinsing, slugs do not discriminate between the
29
30 537 two parts (Asplund & Gauslaa, 2010). The high grazing susceptibility of cephalodia in this
31
32 538 species may explain why it is restricted to northern and high elevation locations that support few
33
34 539 gastropods. Several lichen species have higher concentrations or even other types of CBSCs in
35
36 540 their reproductive structures such as soralia and ascocarps (Imshaug & Brodo, 1966; Brodo &
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38 541 Hawksworth, 1977; Tønsberg, 1992; Hyvärinen *et al.*, 2000; Asplund *et al.*, 2010c). As such,
39
40 542 snails completely avoid the soralia of *Lobarina scrobiculata* which contains five times as much
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42 543 *m*-scrobiculin than does the rest of the thallus (Asplund *et al.*, 2010c). Meanwhile, in the absence
43
44 544 of CBSCs, snails are instead more likely to attack the soralia than the somatic parts of the thallus.
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46 545 This is in line with the optimal defence theory which predicts that that the parts of an organism
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48 546 that are more likely to be attacked and are more important for species fitness (e.g. reproductive
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50 547 parts) are typically better defended against consumers (McKey, 1974; Rhoades, 1979).
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3 548 Many lichen species are represented by different chemotypes, i.e. morphologically
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6 549 identical conspecifics containing different groups of CBSCs, and these chemotypes can be used
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8 550 for studying the ecological role of CBSCs. As such, thalli of one *Lobaria pulmonaria* chemotype
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10 551 contains high amounts of total CBSCs including stictic acid and small amounts of constictic,
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12 552 norstictic, peristictic and methyl norstictic acid, while another contains low total CBSCs and only
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14 553 norstictic acid (Asplund, 2011a). When growing on the same trees, the chemotype with the
15
16 554 higher total CBSCs was not grazed by gastropods while the chemotype with only norstictic acid
17
18 555 was heavily grazed. This pattern was later confirmed in a laboratory food choice experiment, and
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20 556 reveals that natural variation in CBSCs at the within-species level can serve as an important
21
22 557 determinant of their susceptibility to their grazing by gastropods (Asplund, 2011a).

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27 558 Despite the clear effect of experimentally reducing concentrations of CBSC on lichen
28
29 559 palatability, variation in palatability among lichen species does not appear to be closely related to
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31 560 the total concentration of CBSCs (Asplund & Wardle, 2013; Bokhorst *et al.*, 2015). This lack of
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33 561 relationship is likely because of qualitative differences in CBSCs between species and because
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35 562 different compounds have different levels of biological effectiveness and contrasting roles. As
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37 563 such, a species with high concentrations of an ineffective defence compound is likely to be more
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39 564 palatable than a species with lower concentrations of a very effective defence (Gauslaa, 2008). In
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41 565 this light, an accidental experiment in which the coleopteran *Lasioderma serricorne* attacked
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43 566 1440 lichen herbarium specimens showed that the level of consumption was strongly linked to
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45 567 the qualitative composition of CBSCs in the lichens (Nimis & Skert, 2006).

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50 568 The CBSCs in lichens can also impact the consumption by mammals, but the literature on
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52 569 this is very limited. For instance, it is known that the bank vole, *Myodes glareolus*, prefers
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54 570 lichens with reduced concentrations of CBSCs (Nybakken *et al.*, 2010). Further, usnic acid, a
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56 571 common lichen CBSC, has been reported to kill elk (Cook *et al.*, 2007). However, reindeer in

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2
3 572 contrast consume large amounts of usnic acid-containing lichens, because they have an usnic
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5 573 acid-degrading bacterium (*Eubacterium rangiferina*) in their rumen that detoxify the lichens
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7
8 574 (Sundset *et al.*, 2008, 2010). As such, the presence of usnic acid actually increases the
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10 575 digestibility of lichens by reindeer (Palo, 1993).
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14 576 **V. How variation among lichens affects their impacts on plants**

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16 577 The numerous ways that communities of plants (mainly trees) impact on lichen community
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18 578 assemblies, for instance by competition or by providing substrates and modifying environmental
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20 579 conditions, have been very well studied (Favero-Longo & Piervittori, 2010), and are outside the
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22 580 scope of this review. Meanwhile, how lichens regulate plant communities have been given much
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24
25 581 less attention (Fig. 4).
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28 582 At the beginning of terrestrial primary succession, N is often the main limiting nutrient,
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30 583 and pioneer N₂ fixing plants and lichens may play an important and well known role in driving
31
32 584 initial N build-up of the ecosystem. For example the N₂-fixing fruticose lichen *Stereocaulon* spp.
33
34 585 can dominate the ground cover early in succession in both lava flows and glacial forelands
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36 586 (Eggler, 1971; Mueller-Dornbois, 1987; Vetaas, 1994). The N₂-fixed by lichens, and other N₂-
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38 587 fixing organisms, leads to N build-up that then facilitates colonization by non N₂-fixing vascular
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40 588 plants. In this light, the vascular plants, *Festuca octoflora* and *Mentzelia multiflora*, when grown
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42 589 in desert soil together with the cyanolichen *Collema* sp., have been shown to grow quicker and
43
44 590 contain higher tissue element concentrations of N, P, K, Ca, Mg and iron than those grown in soil
45
46 591 without the lichen. This is both because the lichens concentrate essential elements in available
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48 592 forms at the soil surface and because the gelatinous sheaths often associated with the
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50 593 cyanobacterial symbiont (e.g., *Nostoc* cells in *Collema* spp.) contain chelating compounds.
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3 594 The early colonization by lichens may also induce rock weathering that in turn releases
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6 595 mineral elements in forms that plants can utilize (Viles, 1995; Chen *et al.*, 2000; Adamo &
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8 596 Violante, 2000). Lichen growth form can potentially play a role in governing these rock-
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10 597 weathering processes. However, although crustose lichens are more strongly adhered to the rock
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12 598 (through their entire lower surface) than are foliose lichens, their ability to weather rock and
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14 599 release nutrients from it is not necessarily greater (Adamo, Marchettiello, & Violante, 1993).
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17 600 Instead, the freeze-thaw action can be larger on rock surfaces occupied by the bigger foliose
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19 601 lichens than those occupied by crustose lichens, which may compensate in part for their weaker
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21 602 connection with the rock (Adamo & Violante, 2000). Further, the chemical weathering of rock
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23 603 and release of nutrients from it may also be driven by the amount and types of CBSCs produced
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25 604 by the lichens which themselves vary tremendously both among and within lichen species
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27 605 (Adamo & Violante, 2000).

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31 606 Lichens have been reported to both enhance (Zamfir, 2000; Houle & Filion, 2003) and
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33 607 reduce (Deines *et al.*, 2007) vascular plant seedling establishment, and these effects of lichens
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35 608 are dependent on the types of plant and lichen species present and on environmental context (e.g.
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37 609 Escudero *et al.*, 2007). As such, ground covered by *Cladonia* has been shown to strongly reduce
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39 610 emergence of seedlings of plant species that depend heavily on light for germination (i.e.
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41 611 *Arenaria serpyllifolia* and *Veronica spicata*) relative to those that do not (i.e., *Filipendula*
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43 612 *vulgaris* and *Festuca ovina*) (Zamfir, 2000). Further, the physical environment created by
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45 613 ground-dwelling lichens may inhibit seeds and seedling radicals from reaching the soil, thereby
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47 614 reducing seedling establishment (Deines *et al.*, 2007). In contrast, mat-forming lichens such as
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49 615 *Cladonia* spp. may conserve soil moisture and thus facilitate seedling establishment (Zackrisson
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51 616 *et al.*, 1995, 1997). However, these lichens accumulate little organic matter, and N
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53 617 mineralization rates below these mats are low, which leads to lower N availability under lichens
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3 618 compared with under plants and bryophytes (Sedia & Ehrenfeld, 2005). This results in a sparser
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5 619 vascular plant development and a more open forest, which leads to a feedback that in turn
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7 620 benefits mat-forming lichens (Sedia & Ehrenfeld, 2003).

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9 621 Because of the rich secondary chemistry of lichens, their CBSCs are often claimed to
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11 622 have allelopathic effects on plants (Lawrey, 1986, 1995). However, studies finding an
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13 623 allelopathic effect of lichen CBSCs have often been made in the laboratory through bioassays
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15 624 that use unrealistically high concentrations of CBSCs or that use water extracts that also contain
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17 625 many (and often unknown) compounds other than CBSCs. Furthermore, many of these studies
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19 626 have evaluated the allelopathic effect of lichen CBSCs on crop plants species like tomato, lettuce,
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21 627 maize or sunflower, that are not naturally exposed to lichen CBSCs (Lascève & Gaugain, 1990;
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23 628 Romagni *et al.*, 2000; Lechowski, Mej, & Bialczyk, 2006; Latkowska *et al.*, 2006). However,
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25 629 in reality very low amounts of lichen CBSC are leached to the soil because of their low water-
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27 630 solubility (Stark, Kytöviita, & Neumann, 2007), and at ecological relevant conditions the
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29 631 common lichen CSBC usnic acid does not reach concentrations in the soil that are able to impair
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31 632 pine seedling growth or mycorrhizal-mediated nutrient uptake (Kytöviita & Stark, 2009). In this
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33 633 light, we currently do not have a good understanding of the role of allelopathic interactions
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35 634 involving lichens in natural ecosystems, or convincing and consistent evidence that allelopathic
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37 635 effects of lichens are actually important.
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47 636 **VI. Conclusions and future directions**

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51 638 (1) In this review we have shown how lichens impact ecosystem processes, notably those that
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53 639 involve the fluxes of carbon and nutrients, and how this is in turn regulated by the
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55 640 considerable variation that exists for the functional characteristics of lichens (Fig. 2). We
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3 641 have also outlined how this variation impacts on the interactions of lichens with other
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6 642 primary producers as well as with higher trophic levels, and the consequences of this for
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8 643 community and ecosystem properties.
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10 644 (2) Our knowledge about how lichen functional traits (both within and between species) vary
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12
13 645 among ecosystems or across environmental gradients is limited, and this topic requires
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15 646 further attention. Recent studies suggest that lichens show massive within-species
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17 647 (relative to across-species) variation, especially in comparison with vascular plants
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19 648 (Asplund & Wardle, 2014). There is a need for studies on how this high intraspecific
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21
22 649 variation impacts on lichen community assembly processes and ecosystem functioning, in
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24 650 the same manner that has recently been done for vascular plants (e.g., Jackson, Peltzer, &
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26 651 Wardle, 2013; Kumordzi *et al.*, 2015).
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29 652 (3) Lichens often occur in multispecies mixtures, yet studies to date have almost entirely
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31 653 considered only the effects of single lichen species. As such, little is known about how
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33 654 lichen species mixtures, and their functional and taxonomic diversity, affects the key
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35 655 community- and ecosystem-level processes that they drive. A large number of
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37 656 experimental studies have addressed how vascular plant biodiversity impacts ecosystem
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39 657 functioning (and, potentially, ecosystem services) (Cardinale *et al.*, 2012), but this issue
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41 658 remains unexplored for lichens, despite the relative ease by which they can be
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43 659 experimentally manipulated, and their importance as ecosystem drivers.
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46 660 (4) Future studies should also focus on the extent to which lichens, especially early in
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49 661 succession, influence vascular plant succession and ecosystem development in the longer
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51 662 term perspective. We show in this review that there are important short term effects, but
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53 663 how they are manifested in longer term time scales, through for example by influencing
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55 664 longer term vegetation successional trajectories and soil development, remain unknown.
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3 665 (5) Drivers of global change can potentially have important impacts on lichen communities.
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5 666 As such, both increased temperature and N-deposition are expected to have adverse
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7 667 effects on many lichen species and induce large shifts in their functional composition
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9 668 (Bobbink *et al.*, 2010; Elmendorf *et al.*, 2012a, 2012b). Further, land-use intensification
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11 669 may cause replacements of lichens that have fruticose growth by foliose species (Stofer *et*
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13 670 *al.*, 2006). Our review makes the case that functional differences between lichens are
14
15 671 powerful drivers of how they affect communities and ecosystems (Fig. 2), and there is a
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17 672 need to better understand how global change-driven shifts in the composition of lichen
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19 673 communities will mediate their impact on ecosystem functioning.
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44 681 **VIII. References**

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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, & Klunderud, 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 ₂ O 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 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 analogous. 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).

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2
3 1201 **Figure 1.** Lichens show tremendous variation both in terms of their growth form and colour.

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5 1202 Upper three panels (left to right) are the crustose lichens *Caloplaca epithallina*, *Carbonea*

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7 1203 *vitellinaria* and *Icmadophila ericetorum*. The middle panels (left to right) are the foliose lichens

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9 1204 *Lobaria pulmonaria*, *Arctoparmelia centrifuga* and *Leptogium saturninum*. The lower three

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11 1205 panels (left to right) are the fruticose lichens *Cladonia stellaris*, *Ramalina calicaris* and *Bryoria*

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13 1206 *tenuis*. Photos are © Einar Timdal.

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18 1207 **Figure 2.** Lichens vary greatly in terms of growth form, type of photobiont, functional traits,

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20 1208 water holding capacity, colour and secondary chemistry. This variation results in species-specific

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22 1209 differences in the effect lichens have on community and ecosystem properties. Photos are ©

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24 1210 Einar Timdal.

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28 1211 **Figure 3.** A wide range of consumer organisms depend on lichens, and these range in size from

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30 1212 microorganisms to large mammals. As such, lichen-consumer interactions operate at a wide range

31
32 1213 of spatial scales. For smaller organisms the primary role of lichens is in providing a habitat, while

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34 1214 for larger organisms their primary role is as a food source.

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38 1215 **Figure 4.** Contrasting mechanisms by which lichens can affect the establishment and growth of

39
40 1216 plants, notably during early stages of primary succession. Red (–) and blue (+) = negative and

41
42 1217 positive effects of lichens on plants respectively. Illustration by Lennart Asplund.

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44 1218



Figure 1
215x155mm (300 x 300 DPI)

Growth form



Crustose

Foliose

Fruticose

Photosymbiont



Green algae + Cyanobacteria

Green algae + Cyanobacteria

Functional traits



Resource conservative

Resource acquisitive

Water holding capacity



Low WHC

high WHC

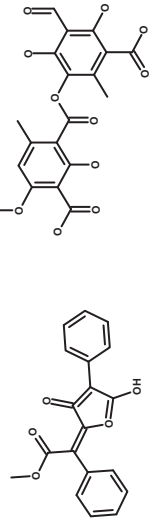
Colour



Light

Dark

Secondary compounds



Strong defence

Weak defence

Biological Property of Lichen

Nutrient status
 Shelter for invertebrates
 Structural complexity
 Water uptake and retention

N₂ fixation
 Nutrient status
 Water uptake and retention

Nutrient status
 Water uptake and retention

Nutrient status
 Water uptake and retention
 Soil moisture

Soil / substrate temperature
 Albedo

Defence of thallus tissue

[Ecological consequence]

Decomposition
 Invertebrate community assembly
 Rainfall and nutrient interception

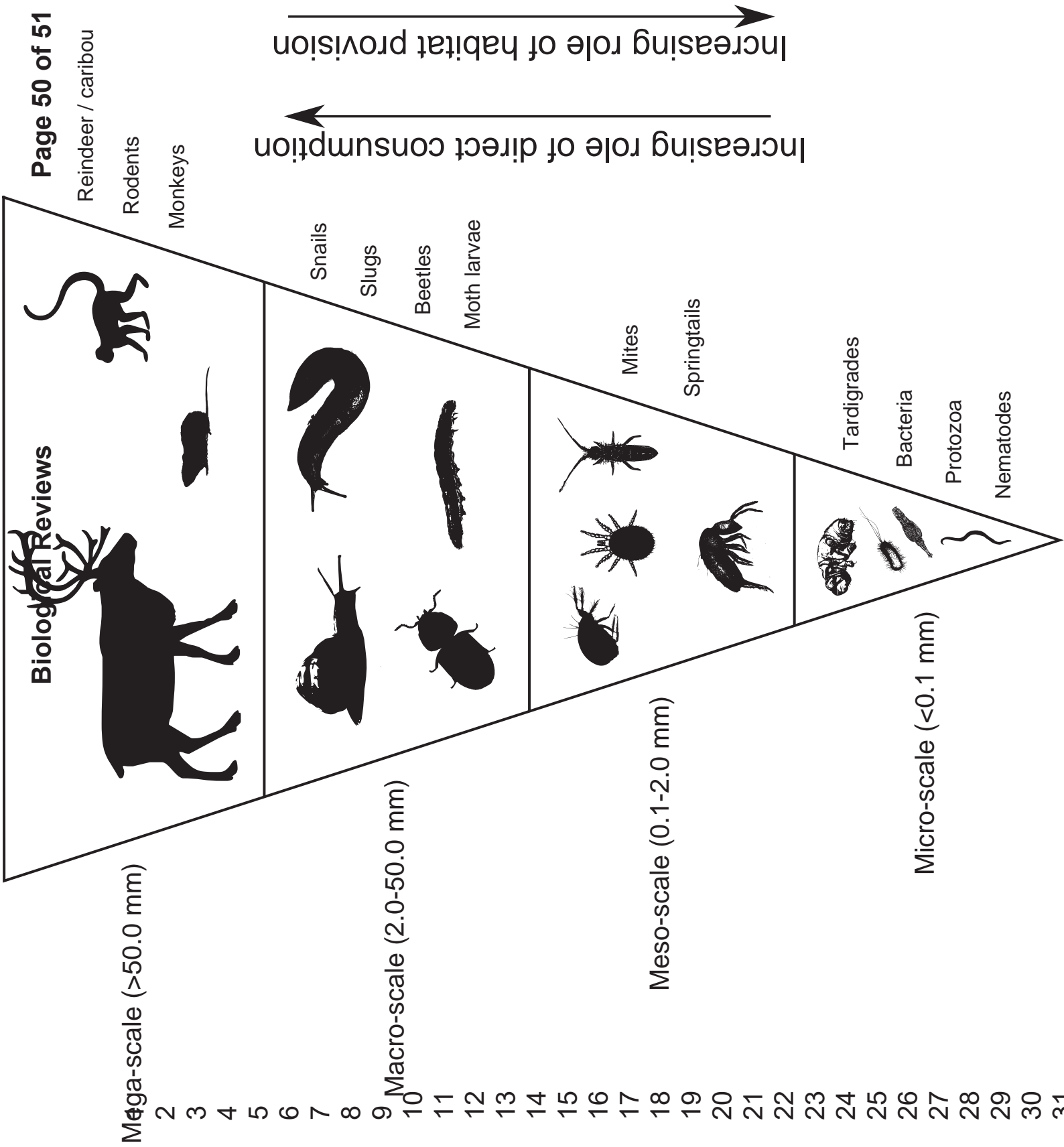
Nutrient accumulation
 Plant growth
 Consumption by invertebrates
 Rainfall and nutrient interception

Decomposition
 Consumption by invertebrates
 Rainfall and nutrient interception

Decomposition
 Consumption by invertebrates
 Rainfall and nutrient interception

Microbial abundance and activity
 Decomposition
 Rock weathering

Decomposition
 Consumption by invertebrates
 Microbial abundance and activity
 Rock weathering





LENN ART

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