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ARE LICHEN GROWTH FORM CATEGORIES SUPPORTED BY CONTINUOUS FUNCTIONAL TRAITS: WATER-HOLDING CAPACITY AND SPECIFIC THALLUS MASS?

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The focus of community ecology has shifted from the description of taxonomic composition towards an understanding of community assembly based on species' 'functional traits'. The functional trait approach is well developed for vascular plants, utilising variability of continuous phenotypic characters that affect ecological fitness, such as specific leaf area, tissue nitrogen concentration or seed mass, to explain community structure. In contrast, community assembly studies for poikilohydric cryptogamic plants and fungi, such as lichens, remain focused on broad categorical traits such as growth form difference: fruticose, foliose or crustose. This study examined intra- and interspecific variability for two highly promising continuous phenotypic measurements that affect lichen physiology and ecological fitness: water-holding capacity (WHC) and specific thallus mass (STM). Values for WHC and STM were compared within and among species, and within and among key macrolichen growth forms (fruticose and green-algal and cyanolichen foliose species), asking whether these widely used categories adequately differentiate the continuous variables (WHC and STM). We show large intra- and interspecific variability that does not map satisfactorily onto growth form categories, and on this basis provide recommendations and caveats in the future use of lichen functional traits.

Keywords. Functional traits, growth form, hydration, lichen, thallus morphology.

Introduction

Developments in plant community ecology have shifted from the description of species taxonomic composition towards a more process-based understanding of community structure drawing on 'functional traits' (McGill *et al.*, 2006; Violle *et al.*, 2007), i.e. phenotypic variability that affects species ecological fitness (reproduction, establishment or growth, and survival) across different environmental circumstances. Classically, traits that increase species fitness in one environmental circumstance are traded off against those that increase fitness in a different set of circumstances, leading to the recognition of mutually exclusive life-history classes such as competitors–colonists (Ehrlén & van Groenendael, 1998; Cadotte *et al.*, 2006) or Grime's triangular classification of competitors–stress-tolerant-ruderals (Grime, 1974, 1977; Grime *et al.*, 1997). Non-random associations of functional traits among co-occurring species are used to infer the ecological processes of community assembly, such as interspecific competition or environmental filters (Weiher *et al.*, 1998; Ackerly & Cornwell, 2007). To test community assembly in this way, vascular

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plant ecology can draw on phenotypic measures, such as specific leaf area, that are quantified along a continuum of variation and integrate across important physiological responses to the environment (Hoffmann *et al.*, 2005), and are thus well supported as functional explanations for plant community assembly (Kraft *et al.*, 2008; Cornwell & Ackerly, 2009). On this basis, patterns across multiple functional traits have been used to show that their variability within plant species (among individuals of the same species) can be as important in community assembly as variability among species (Jung *et al.*, 2010; Siefert *et al.*, 2015), whereas co-occurring species tend to be more similar in their functional characteristics than would be expected at random, a sign of environmental filtering, although with these patterns depending on the successional stage of a plant community (cf. Li *et al.*, 2018; Marteinsdóttir *et al.*, 2018).

In contrast to vascular plants, work on cryptogamic groups such as lichens continues to use a more limited spectrum of discontinuous and broad morphological categories such as growth form – fruticose, foliose, crustose – when attempting a functional explanation of community structure (Ellis & Coppins, 2006; Lewis & Ellis, 2010; Prieto *et al.*, 2017) or more recently in understanding the response to global change (Matos *et al.*, 2015; Nascimbene & Marini, 2015). There is a difference, therefore, between the continuum of variation that can be applied across multiple functional traits recognised in vascular plant ecology (specific leaf area, nitrogen concentration, seed mass, etc.) and the broad categories applied to cryptogamic organisms such as lichens (growth form, photobiont type, reproductive mode, etc.). Despite the known importance of cryptogams in regulating planetary biogeochemical cycles such as nitrogen fixation (Elbert *et al.*, 2012; Porada *et al.*, 2014), we lack a detailed understanding of continuous functional traits affecting their community assembly.

Lichens are a good example of a cryptogamic group that is highly diverse and functionally important in ecosystems (Asplund & Wardle, 2017). Lichens are poikilohydric, so regulation of their hydration is determined by a passive interaction of their morphology with microclimate rather than being actively maintained (Gauslaa, 2014). There are promising morphological variables that are continuous and may reflect a species' ecological fitness (its adaptation and acclimation to different microclimates), building on the key observation that lichen physiology is fundamentally constrained by light availability during periods of thallus hydration (Palmqvist & Sundberg, 2000) as well as night-time physiological recovery and assimilation of carbohydrates into growth (Bidussi *et al.*, 2013; Alam *et al.*, 2015). The correlated relationship between water-holding capacity (WHC) and specific thallus mass (STM), a measure of photosynthetic area (PhA) per unit mass (Gauslaa & Coxson, 2011; Gauslaa, 2014), affects physiological response to wetting–drying cycles (Gauslaa *et al.*, 2017) and shows strong inter- and intraspecific variability (Merinero *et al.*, 2014; Longinotti *et al.*, 2017). These represent excellent characteristics in a putative functional trait.

Consideration of WHC and STM as potential continuous, functional traits, comparable to specific leaf area for vascular plants, raises the question as to whether the previously applied categorical traits such as growth form are defensible. Accordingly, in this study, we measured WHC and STM for different macrolichen species that represent contrasts within each of several categorical functional groups ≈ growth forms: fruticose, foliose green-algal, tripartite and cyanolichens. We asked whether WHC and STM were statistically different when considering variability within species (intraspecific) and among species (interspecific), and then among the growth form categories. Our hypothesis was that the majority of variation in WHC and STM would occur among growth forms, suggesting that these widely applied growth form categories might be interpreted as ecologically meaningful functional groups.

Materials and Methods

We sampled 10 specimens of 14 different lichen species from three field sites (Table 1). Nomenclature follows Smith *et al.* (2009): *Bryoria fuscescens* (Gyeln.) Brodo & D.Hawksw., *Bunodophoron melanocarpum* (Sw.) Wedin, *Evernia prunastri* (L.) Ach., *Hypogymnia physodes* (L.) Nyl., *Leptogium burgessii* (L.) Mont., *Lobaria pulmonaria* (L.) Hoffm., *Lobaria scrobiculata* (Scop.) DC., *Parmelia sulcata* Taylor, *Peltigera membranacea* (Ach.) Nyl., *Platismatia glauca* (L.) W.L.Culb. & C.F.Culb., *Pseudevernia furfuracea* (L.) Zopf, *Ramalina farinacea* (L.) Ach., *Sticta fuliginosa* (Hoffm.) Ach. and *Usnea subfloridana* Stirt. The field sites were climatically contrasting and corresponded to the preferred environmental habitat of each of the sampled species (Ellis *et al.*, 2015), either oceanic (Glen Nant National Nature Reserve) or relatively more continental (Dawyck Botanic Garden and the Royal Botanic Garden Edinburgh). However, within each of the sites, individual specimens were sampled from unique and contrasting microhabitats, from shaded to more open canopy conditions.

Thalli were cleaned of detritus under a dissecting microscope (× 10–50) and two functional traits measured: WHC and STM.

Measurement of water-holding capacity

The WHC was calculated as water storage at saturation per unit of PhA. First, specimens were immersed in a Petri dish of distilled water until fully saturated, after which excess surface water was gently blotted with absorbent tissue before weighing of the wet mass (Wm). Specimens were then dried at 30°C for 24 h and reweighed for dry mass (Dm). Water storage was calculated as Wm – Dm.

Second, fully saturated specimens were positioned on a tile of contrasting colour and digitally photographed using a Canon PowerShot SX220 HS camera (Canon, Tokyo, Japan), alongside a 1-cm^2 scale and a unique specimen label. Complex thallus forms were sectioned into individual lobes to avoid overlaps. The planar area (A) over the surface of a specimen was estimated using the automated procedures of ImageJ version 1.51h (Rasband, no date). This is equivalent to the PhA for heteromerous green-algal, tripartite and cyanobacterial foliose lichens. The homiomerous *Leptogium burgessii* often has a densely tomentose lower thallus and was treated similarly. The PhA for fruticose lichens with approximately cylindrical lobes (*Bryoria fuscescens* and *Usnea subfloridana*) was calculated by assuming the planar area as the longitudinal section for the diameter of a cylinder: $\mathrm{PhA} = \pi.A$. For the strap-shaped lobes of *Ramalina farinacea*: $\mathrm{PhA} = 2.A$. For *Bunodophoron melanocarpum*, with lobes part way between strap-shaped and cylindrical: $\mathrm{PhA} = (\pi.A + 2A)/2$. Thus, $\mathrm{WHC} = (\mathrm{Wm} - \mathrm{Dm})/\mathrm{PhA}$.

TABLE 1. Study species classified by growth form category and including their collection localities

Growth form and species	Sample site	Oven-dry weight, mean ± 1 SD (g)
Fruticose		
Bryoria fuscescens[a]	Dawyck Botanic Garden	0.0147 ± 0.0135
Bunodophoron melanocarpum	Glen Nant National Nature Reserve	0.0682 ± 0.0449
Ramalina farinacea	Dawyck Botanic Garden	0.0689 ± 0.0404
Usnea subfloridana[a]	Dawyck Botanic Garden	0.1061 ± 0.0921
Alternatively classified as fruticose (model A) or green-algal foliose lichens (model B)		
Evernia prunastri	Royal Botanic Garden Edinburgh	0.0674 ± 0.09018
Pseudevernia furfuracea	Dawyck Botanic Garden	0.0365 ± 0.03899
Green-algal foliose		
Hypogymnia physodes	Dawyck Botanic Garden	0.0468 ± 0.03483
Parmelia sulcata	Dawyck Botanic Garden	0.0119 ± 0.00694
Platismatia glauca	Dawyck Botanic Garden	0.0351 ± 0.02272
Tripartite		
Lobaria pulmonaria	Glen Nant National Nature Reserve	0.1401 ± 0.14173
Cyanolichen foliose		
Leptogium burgessii	Glen Nant National Nature Reserve	0.0135 ± 0.01042
Lobaria scrobiculata	Glen Nant National Nature Reserve	0.1248 ± 0.04268
Peltigera membranacea	Dawyck Botanic Garden	0.0598 ± 0.04097
Sticta fuliginosa	Glen Nant National Nature Reserve	0.0460 ± 0.05922

[a] Alternatively classified within a distinct fruticose category of ‘alectorioid’ lichens (model C).

Calculation of specific thallus mass

The STM was calculated as the oven-dried mass (i.e. Dm) per unit of PhA: STM = Dm/PhA.

Morphological models

To explore discrepancies between alternative growth form classifications, the species were categorised into three different morphological models (see Table 1):

- model A, including a single category for fruticose lichens and with the heavily branched but internally anatomical ‘foliose’ lichens (having an upper cortex and lateral algal layer and a distinct lower cortex), *Evernia prunastri* and *Pseudevernia furfuracea*, categorised as foliose lichens
- model B, including *Evernia prunastri* and *Pseudevernia furfuracea* as fruticose lichens to reflect their external growth form (in contrast to their internal anatomy)

- model C, separating the fruticose lichens into robust fruticose species (*Bunodophoron melanocarpum* and *Ramalina farinacea*) distinct from the alectorioid ‘hair lichens’, *Bryoria fuscescens* and *Usnea subfloridana*.

Statistical analysis

The single tripartite foliose lichen (*Lobaria pulmonaria*) was dropped from statistical analysis to ensure a balanced data set for classic two-way analysis of variance (ANOVA) in R (R Development Core Team, 2013), including the factors growth form and species identity. ANOVA was separately applied to the traits WHC and STM.

RESULTS

There were statistically significant differences in WHC and STM among growth form categories (Table 2 and the Fig. 1), although the variance explained depended on the classification of species (model A, B or C) and the choice of trait for comparison (WHC and STM).

For WHC, the alternative classification of *Evernia prunastri* and *Pseudevernia furfuracea* as green-algal foliose (model A) or fruticose lichens (model B) made little overall difference. In both cases, WHC values had a marginally stronger separation among growth forms (38% variance explained) compared with among species (26% variance explained), decreasing in the order fruticose < green-algal foliose < cyanolichen foliose. However, STM values were better segregated among growth form categories when *Evernia prunastri* and *Pseudevernia furfuracea* were classified as green-algal foliose lichens (model A; 32% variance explained) as opposed to fruticose lichens (model B; 18% variance explained), although for both models there was stronger separation of STM among species than among growth forms. The classification of alectorioid lichens as a separate fruticose category (model C) was supported, because it strengthened the variance explained by growth form for both WHC and STM. The tripartite *Lobaria pulmonaria* had intermediate values for both WHC and STM, falling between those of the foliose green-algal lichens and the cyanolichens.

There were statistically significant differences in WHC and STM among species for all models considered, for example: (i) *Bunodophoron melanocarpum* and *Hypogymnia physodes* had high WHC and STM values relative to their growth form (fruticose and green-algal foliose), approaching those of cyanolichens, whereas (ii) there were strong contrasts within the cyanolichen category, with *Leptogium burgessii* and *Peltigera membranacea* having higher and outlying values of WHC for their relatively lower STM.

DISCUSSION

Functional traits have become an important area of research in plant ecology (McGill *et al.*, 2006; Violle *et al.*, 2007), presenting the opportunity to link community assembly with ecosystem function (Lavorel & Garnier, 2002). Studies in lichen communities have started

TABLE 2. Results of ANOVA to decompose and test variability in thallus water-holding capacity (WHC) and specific thallus mass (STM) among lichen thallus growth forms and among species (cf. the Figure)[a]

	Degrees of freedom	Sum of squares × 1000	Mean square × 1000	Variance (%)	*F*	*P*
MODEL A						
WHC						
Growth form	2	5.027	2.514	38.33	62.94	< 0.0001
Species	10	3.412	0.341	26.02	8.54	< 0.0001
STM						
Growth form	2	0.732	0.366	32.66	59.81	< 0.0001
Species	10	0.794	0.079	35.40	12.97	< 0.0001
MODEL B						
WHC						
Growth form	2	5.070	2.535	38.67	63.48	< 0.0001
Species	10	3.368	0.337	25.69	8.43	< 0.0001
STM						
Growth form	2	0.400	0.200	17.86	32.71	< 0.0001
Species	10	1.126	0.113	50.20	18.39	< 0.0001
MODEL C						
WHC						
Growth form	3	6.219	2.073	47.43	51.91	< 0.0001
Species	9	2.220	0.247	16.93	6.175	< 0.0001
STM						
Growth form	3	1.077	0.359	48.04	58.65	< 0.0001
Species	9	0.449	0.499	20.02	8.15	< 0.0001
ALL MODELS						
WHC: residual	117	4.673	0.040			
STM: residual	117	0.716	0.006			

[a] Results are presented for alternative species categorisation (models A, B and C; cf. Table 1).

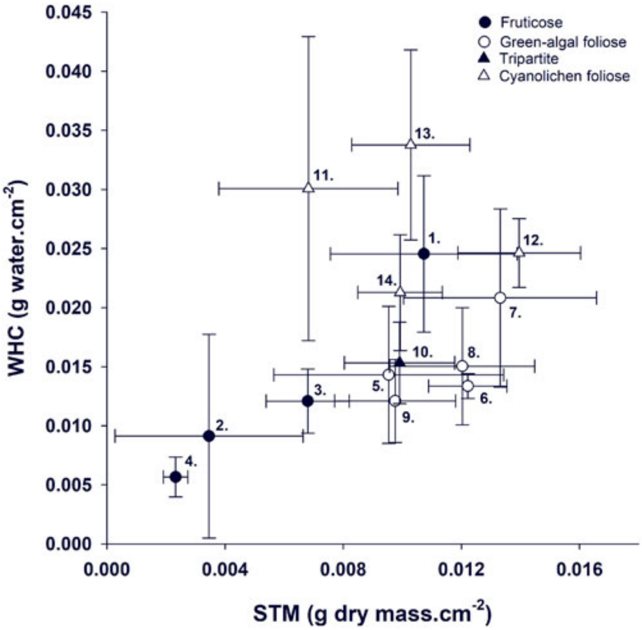

FIG. 1. Comparison of specific thallus mass (STM) and water-holding capacity (WHC) for the tested lichen species, with means and intraspecific variation as the standard deviation (error bars). 1, *Bunodophoron melanocarpum*; 2, *Bryoria fuscescens* ('alectorioid', model C); 3, *Ramalina farinacea*; 4, *Usnea subfloridana* ('alectorioid', model C); 5, *Evernia prunastri* (alternatively classified as fruticose, model B); 6, *Pseudevernia furfuracea* (alternatively classified as fruticose, model B); 7, *Hypogymnia physodes*; 8, *Parmelia sulcata*; 9, *Platismatia glauca*; 10, *Lobaria pulmonaria*; 11, *Leptogium burgessii*; 12, *Lobaria scrobiculata*; 13, *Peltigera membranacea*; 14, *Sticta fuliginosa*.

to apply functional traits to understand community structure (Ellis & Ellis, 2013; Nelson *et al.*, 2015), although many such studies continue to rely on broadly partitioned growth form categories (fruticose, foliose, crustose), standing in contrast to the experimentally-supported and continuous variables applied by vascular plant ecologists. This study explored two promising measures of lichen thallus morphology, which together link thallus hydration with PhA: WHC and STM.

Values of WHC and STM differ among species (Gauslaa & Coxson, 2011; Gauslaa, 2014) and may directly impact lichen physiology (Gauslaa *et al.*, 2017) and therefore ecological fitness for contrasting microclimates, making them excellent candidates as functional traits. Species-specific values of STM may also integrate with area- or mass-based competitive asymmetries (John, 1992) to reflect broader life-history strategies. However, previous studies have shown that intraspecific variability in WHC and STM is affected by thallus size, i.e. the area of the thallus (Merinero *et al.*, 2014; Longinotti *et al.*, 2017), and also by the environment from which a thallus has been sampled. Thus, WHC and/or STM may increase to support water retention in drier macroclimatic settings

(Gauslaa *et al.*, 2009), in more open gladed situations (Gauslaa *et al.*, 2006, 2009; Gauslaa & Coxson, 2011) or in canopy environments with a higher evaporative demand (MacDonald & Coxson, 2013; Merinero *et al.*, 2014), as well as longitudinally for the same microhabitat but during seasonally drier periods (Larsson *et al.*, 2012). This phenotypic plasticity raises the question as to whether variability for continuous functional trait variables such as WHC and STM, within and among species, is adequately summarised by or extends beyond the boundaries of traditional growth form categories.

The difference between cyanolichens and green-algal lichens is a commonly used trait category (Ellis, 2013), based on the observation that green-algal lichens can become photosynthetically reactivated at lower thallus moisture contents and in humid air, whereas cyanolichens require liquid water (Lange *et al.*, 1986, 1993). However, if thalli become supersaturated then gas exchange across the thallus is limited and photosynthesis can decline (Lange *et al.*, 1996). This may lead to an adaptive difference (Gauslaa & Coxson, 2011), supported here by the greater WHC of cyanolichens compared with green-algal foliose lichens with similar STM, and explained by internal structural differences such as photobiont-layer thickness. Thus, high WHC for a given STM in cyanolichens may be advantageous if it allows the uptake and retention of large amounts of available liquid water (typical of shadier and/or more moist conditions) to prolong photosynthesis, but with supersaturation avoided through carbon-concentrating mechanisms (Palmqvist, 1993; Máguas *et al.*, 1995). In contrast, lower WHC may facilitate rapid hydration for green-algal foliose lichens, which are able to reactivate in the absence of liquid water in higher light environments with a stronger evaporative demand (Gauslaa & Coxson, 2011; Phinney *et al.*, 2018). The low WHC values for alectorioid lichens may be further moderated by branching (not measured here), in addition to thallus STM (Esseen *et al.*, 2015).

Notwithstanding these key differences among growth forms, there was important variability among species in our study. This was most apparent for fruticose lichens, with more robust species (e.g. *Ramalina farinacea*) overlapping in their WHC with thin (*Platismatia glauca*) or highly branched (*Evernia prunastri* and *Pseudevernia furfuracea*) foliose lichens, whereas the alectorioid lichens *Bryoria fuscescens* and *Usnea subfloridana* formed a distinct fruticose category, supporting their separate recognition in studies of community assembly (McCune, 1993; McCune *et al.*, 1997). Furthermore, the extremely robust *Bunodophoron melanocarpum* overlapped in WHC and STM with cyanolichens, and the spread of trait values for lichens traditionally considered in the fruticose category was therefore very large.

Individual species also showed high intraspecific variation in their values of WHC and STM, reflecting differences in thallus size (see Table 1), and in terms of acclimation to their microclimatic habitat. This would support the trend towards individualistic functional trait values as a basis for community assembly in plant ecology (Jung *et al.*, 2010; Siefert *et al.*, 2015). Such an approach is feasible for lichens (Stanton, 2015).

We conclude that when WHC and STM values are unavailable at an inter- or intraspecific level, then broad growth form categories should be used cautiously and partitioned according to available evidence, for example treating *Evernia prunastri* and *Pseudevernia furfuracea* as foliose lichens and separating alectorioid lichen from other types of fruticose lichen. Furthermore, establishing the functional relationship of crustose lichens remains a major challenge. Contrasts in STM are harder to determine for microlichen crusts, simply because of the low absolute values in their weight measurement, whereas less easily characterised phenotypic traits such as cortical hydrophobicity (Lakatos *et al.*, 2006) may become relatively more important in regulating the water relations of dry-adapted crustose species existing within the boundary layer (Stanton & Horn, 2013).

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References

Ackerly, D. D. & Cornwell, W. K. (2007). A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecol. Letters* 10(2): 135–145.

Alam, M.A., Gauslaa, Y. & Solhaug, K. A. (2015). Soluble carbohydrates and relative growth rates in chloro-, cyano- and cephalolichens: effects of temperature and nocturnal hydration. *New Phytol.* 208(3): 750–762.

Asplund, J. & Wardle, D. A. (2017). How lichens impact on terrestrial community and ecosystem properties. *Biol. Rev.* 92(3): 1720–1738.

Bidussi, M., Gauslaa, Y. & Solhaug, K. A. (2013). Prolonging the hydration and active metabolism from light periods into nights substantially enhances lichen growth. *Planta* 237(5): 1359–1366.

Cadotte, M. W., Mai, D. V., Jantz, S., Collins, M. D., Keele, M. & Drake, J. A. (2006). On testing the competition–colonization trade-off in a multispecies assemblage. *Amer. Naturalist* 168(5): 704–709.

Cornwell, W. K. & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecol. Monogr.* 79(1): 109–126.

Ehrlén, J. & van Groenendael, J. M. (1998). The trade-off between dispersability and longevity – an important aspect of plant species diversity. *Appl. Veg. Sci.* 1(1): 29–36.

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O. & Pöschl, U. (2012). Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geosci.* 5: 459–462.

Ellis, C. J. (2013). A risk-based model of climate change threat: hazard, exposure, and vulnerability in the ecology of lichen epiphytes. *Botany* 91(1): 1–11.

Ellis, C. J. & Coppins, B. J. (2006). Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. *J. Biogeogr.* 33(9): 1643–1656.

Ellis, C. J. & Ellis, S. C. (2013). Signatures of autogenic succession for an aspen chronosequence. *J. Veg. Sci.* 24(4): 688–701.

Ellis, C. J., Eaton, S., Theodoropoulos, M. & Elliott, K. (2015). *Epiphyte Communities and Indicator Species. An Ecological Guide for Scotland's Woodlands*. Edinburgh: Royal Botanic Garden Edinburgh.

Esseen, P.-A., Olsson, T., Coxson, D. & Gauslaa, Y. (2015). Morphology influences water storage in hair lichens from boreal forest canopies. *Fungal Ecol.* 18: 26–35.

GAUSLAA, Y. (2014). Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *Lichenologist* 46(1): 1–16.

GAUSLAA, Y. & COXSON, D. (2011). Interspecific and intraspecific variations in water storage in epiphytic old forest lichens. *Botany* 89(11): 787–798.

GAUSLAA, Y., LIE, M., SOLHAUG, K. A. & OHLSON, M. (2006). Growth and ecophysiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. *Oecologia* 147: 406–416.

GAUSLAA, Y., PALMQVIST, K., SOLHAUG, K. A., HILMO, O., HOLIEN, H., NYBAKKEN, L. & OHLSON, M. (2009). Size-dependent growth of two old-growth associated macrolichen species. *New Phytol.* 181(3): 683–692.

GAUSLAA, Y., SOLHAUG, K. A. & LONGINOTTI, S. (2017). Functional traits prolonging photosynthetically active periods in epiphytic cephalolichens during desiccation. *Environm. Exp. Bot.* 141: 83–91.

GRIME, J. P. (1974). Vegetation classsification by reference to strategies. *Nature* 250, 26–31.

GRIME, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Amer. Naturalist* 111(982): 1169–1194.

GRIME, J. P., THOMPSON, K., HUNT, R., HODGSON, J. G., CORNELISSEN, J. H. C., RORISON, I. H., HENDRY, G. A. F., ASHENDEN, T. W., ASKEW, A. P., BAND, S. R., BOOTH, R. E., BOSSARD, C. C., CAMPBELL, B. D., COOPER, J. E. L., DAVISON, A. W., GUPTA, P. L., HALL, W., HAND, D. W., HANNAH, M. A., HILLIER, S. H., HODKINSON, D. J., JALILI, A., LIU, Z., MACKEY, J. M. L., MATTHEWS, N., MOWFORTH, M. A., NEAL, A. M., READER, R. J., REILING, K., ROSS-FRASER, W., SPENCER, R. E., SUTTON, F., TASKER, D. E., THORPE, P. C. & WHITEHOUSE, J. (1997). Integrated screening validates primary axes of specialisation in plants. *Oikos* 79(2): 259–281.

HOFFMANN, L., FRANCO, A. C., MOREIRA, M. Z. & HARIDASAN, M. (2005). Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. *Funct. Ecol.* 19(6): 932–940.

JOHN, E. (1992). Distribution patterns and interthalline interactions of epiphytic foliose lichens. *Canad. J. Bot.* 70(4): 818–823.

JUNG, V., VIOLLE, C., MONDY, C., HOFFMANN, L. & MULLER, S. (2010). Intraspecific variability and trait-based community assembly. *J. Ecol.* 98(5): 1134–1140.

KRAFT, N. J. B., VALENCIA, R. & ACKERLY, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322(5901): 580–582.

LAKATOS, M., RASCHER, U. & BŰDEL, B. (2006). Functional characteristics of corticolous lichens in the understory of a tropical lowland rain forest. *New Phytol.* 172: 679–695.

LANGE, O. L., KILIAN, E. & ZIEGLER, H. (1986). Water vapor uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. *Oecologia* 71(1): 104–110.

LANGE, O. L., BŰDEL, B., MEYER, A. & KILIAN, E. (1993). Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. *Lichenologist* 25(2): 175–189.

LANGE, O. L., GREEN, T. G. A., REICHENBERGER, H. & MEYER, A. (1996). Photosynthetic depression at high thallus water contents in lichens: concurrent use of gas exchange and flourescence techniques with a cyanobacterial and a green algal *Peltigera* species. *Bot. Acta* 109(1): 43–50.

LARSSON, P., SOLHAUG, K. A. & GAUSLAA, Y. (2012). Seasonal partitioning of growth into biomass and area expansion in a cephalolichen and a cyanolichen of the old forest genus *Lobaria*. *New Phytol.* 194(4): 991–1000.

Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16: 545–556.

Lewis, J. E. J. & Ellis, C. J. (2010). Taxon- compared with trait-based analysis of epiphytes, and the role of tree species and tree age in community composition. *Plant Ecol. Divers.* 3(2): 203–210.

Li, Y., Shipley, B., Price, J. N., Dantas, V. de L.,Tamme, R., Westoby, M., Siefert, A., Schamp, B. S., Spasojevic, M. J., Jung, V., Laughlin, D. C., Richardson, S. J., Bagousse-Pinguet, Y. L. le, Schöb, C., Gazol, A., Prentice, H. C., Gross, N., Overton, J., Cianciaruso, M. V., Louault, F., Kamiyama, C., Nakashizuka, T., Hikosaka, K., Sasaki, T., Katabuchi, M., Dussault, C. F., Gaucherand, S., Chen, N., Vandewalle, M. & Batalha, M. A. (2018). Habitat filtering determines the functional niche occupancy of plant communities worldwide. *J. Ecol.* 106(3): 1001–1009.

Longinotti, S., Solhaug, K. A. & Gauslaa, Y. (2017). Hydration traits in cephalolichen members of the epiphytic old forest genus *Lobaria* (s. lat). *Lichenologist* 49(5): 493–506.

MacDonald, A. & Coxson, D. (2013). A comparison of *Lobaria pulmonaria* population structure between subalpine fir (*Abies lasiocarpa*) and mountain alder (*Alnus incana*) host-tree species in British Columbia's inland temperate rainforest. *Botany* 91(8): 535–544.

Máguas, C., Griffiths, H. & Broadmeadow, M. S. J. (1995). Gas exchange and carbon isotope discrimination in lichens: evidence for interactions between CO_2-concentrating mechanisms and diffusion limitation. *Planta* 196(1): 95–102.

Marteinsdóttir, B., Svavarsdóttir, K. & Thórhallsdóttir, T. E. (2018). Multiple mechanisms of early plant community assembly with stochasticity driving the process. *Ecology* 99(1): 91–102.

Matos, P., Pinho, P., Aragón, G., Martínez, I., Nunes, A., Soares, A. M. V. M. & Branquinho, C. (2015). Lichen traits responding to aridity. *J. Ecol.* 103(2): 451–458.

McCune, B. (1993). Gradients in epiphyte biomass in three *Pseudotsuga–Tsuga* forests of different ages in western Oregon and Washington. *Bryologist* 96(3): 405–411.

McCune, B., Amsberry, K. A., Camacho, F. J., Clery, S., Cole, C., Emerson, C., Felder, G., French, P., Greene, D., Harris, R., Hutten, M., Larson, B., Lesko, M., Majors, S., Markwell, T., Parker, G. G., Pendergrass, K., Peterson, E. B., Peterson, E. T., Platt, J., Proctor, J., Rambo, T. R., Rosso, A., Shaw, D., Turner, R. & Widmer, M. (1997). Vertical profile of epiphytes in a Pacific Northwest old-growth forest. *N. W. Sci.* 71(2): 145–152.

McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21(4): 178–185.

Merinero, S., Hilmo, O. & Gauslaa, Y. (2014). Size is a main driver for hydration traits in cyano- and cephalolichens of boreal rainforest canopies. *Fungal Ecol.* 7: 59–66.

Nascimbene, J. & Marini, L. (2015). Epiphytic lichen diversity along elevational gradients: biological traits reveal a complex response to water and energy. *J. Biogeogr.* 42(7): 1222–1232.

Nelson, P. R., McCune, B., Roland, C. & Stehn, S. (2015). Non-parametric methods reveal non-linear functional trait variation of lichens along environmental and fire age gradients. *J. Veg. Sci.* 26: 848–865.

Palmqvist, K. (1993). Photosynthetic CO_2-use efficiency in lichens and their isolated photobionts: the possible role of a CO_2-concentrating mechanism. *Planta* 191(1): 48–56.

Palmqvist, K. & Sundberg, B. (2000). Light use efficiency of dry matter gain in five macro-lichens: relative impact of microclimate conditions and species-specific traits. *Pl. Cell Environm.* 23(1): 1–14.

Phinney, N. H., Solhaug, K. A. & Gauslaa, Y. (2018). Rapid resurrection of chlorolichens in humid air: specific thallus mass drives rehydration and reactivation kinetics. *Environm. Exp. Bot.* 148: 184–191.

Porada, P., Weber, B., Elbert, W., Pöschl, U. & Kleidon, A. (2014). Estimating impacts of lichens and bryophytes on global biogeochemical cycles. *Global Biogeochem. Cycles* 28(2): 71–85.

Prieto, M., Martínez, I., Aragón, G. & Verdú, M. (2017). Phylogenetic and functional structure of lichen communities under contrasting environmental conditions. *J. Veg. Sci.* 28(4): 871–881.

R Development Core Team (2013). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Downloadable from www.R-project.org

Rasband, W. (no date). *ImageJ: Image Processing and Analysis in Java*. Online. Available: https://imagej.nih.gov/ij/

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., Dantas, V. de L., de Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., Kamiyama, C., Katabuchi, M., Kembel, S. W., Kichenin, E., Kraft, N. J. B., Lagerström, A., Bagousse-Pinguet, Y. L. le, Li, Y., Mason, N., Messier, J., Nakashizuka, T., Overton, J.M., Peltzer, D.A., Pérez-Ramos, I. M., Pillar, V. D., Prentice, H. C., Richardson, S., Sasaki, T., Schamp, B. S., Schöb, C., Shipley, B., Sundqvist, M., Sykes, M. T., Vandewalle, M. & Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Letters* 18(12): 1406–1419.

Smith, C. W., Aptroot, A., Coppins, B. J., Fletcher, A., Gilbert, O. L., James, P. W., Wolseley, P. A. (2009). *The Lichens of Britain and Ireland*. London: British Lichen Society.

Stanton, D. E. (2015). Small scale fog-gradients change epiphytic lichen shape and distribution. *Bryologist* 118(3): 241–244.

Stanton, D. E. & Horn, H. S. (2013). Epiphytes as "filter-drinkers": life-form changes across a fog desert. *Bryologist* 116(1): 34–42.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007). Let the concept of trait be functional! *Oikos* 116(5): 882–892.

Weiher, E., Clarke, G. D. P. & Keddy, P. A. (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81(2): 309–322.

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