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Sunscreening pigments shape the horizontal distribution of pendent hair lichens in the lower canopy of unmanaged coniferous forests

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Abstract

Hair lichens are distinctive for their capillary growth and typically arboreal occurrence, especially in temperate and boreal forests. They consist of two morphogroups based on cortical pigments: a brown-black group with fungal melanin and a pale yellow-green group with usnic acid. Here we test the hypothesis that these morphogroups are ecologically distinct and thus appropriately regarded as functional groups. We examine their respective horizontal occurrence in the lower canopy of 60-year-old conifer forests on a 250 m tall volcanic cone in south-central British Columbia. Trees on open south-facing slopes and near the summit were found to support mainly melanic hair lichens *(Bryoria* and *Nodobryoria)*, whereas more densely spaced trees on north-facing slopes and at the base had higher cover values of usnic lichens (especially *Alectoria sarmentosa* and *Ramalina thrausta*). The cover of melanic hair lichens was strongly correlated with canopy openness but not for their usnic counterparts. We suggest that investment in light-absorbing melanic pigments is an extreme form of specialization for high light, favouring persistence in dry, sun-exposed canopies of otherwise cool forests. By contrast, the cortex of pendent usnic hair lichens appears to facilitate optimum light transmission to underlying photobionts in shaded sites, though at the cost of sensitivity to light in open habitats, especially in rather dry regions.

Key words: *Alectoria*, boreal forest, *Bryoria*, canopy architecture, cortical pigments, photoprotection

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Introduction

Hair lichens constitute a dominant floristic element in boreal forests across the Northern Hemisphere (Ahti 1977; Esseen *et al.* 1996, 2016), extending southward to temperate latitudes along the Western Cordillera of North America (Brodo & Hawksworth 1977). Here we use the term hair lichen as a growth form category characterized by threadlike or narrowly cylindrical branches, the presence of a trebouxioid photobiont and, at boreal latitudes, a strong preference for conifers (Goward & Arsenault 2003). Throughout their range, hair lichens perform important ecosystem functions from nutrient and water cycling (Van Stan & Pypker 2015; Pypker *et al.* 2017) to habitat and/or food for various animals including invertebrates, birds and mammals (Pettersson *et al.* 1995; Rominger *et al.* 1996, 2000). These ecosystem services are now compromised in many regions by industrial forestry (Esseen *et al.* 2022). Interestingly, hair lichens can be sorted into two groups based on their colour. One group produces cortical melanic pigments which give the thallus a brownish or blackish colour, as in *Bryoria* and *Nodobryoria*, while another group is pale yellow-green owing to the presence of usnic acid in the cortex, as in *Alectoria*, *Ramalina thrausta* (Ach.) Nyl. and *Usnea*. All genera belong to the *Parmeliaceae*, apart from *Ramalina* (*thrausta*) (*Ramalinaceae*).

The two hair lichen morphogroups differ in their response to spatial gradients (Ahlner 1948). Usnic hair lichens are more dominant at southern latitudes than farther north, while melanic lichens show the opposite trend (Esseen *et al.* 2016). At the same time, usnic species are more common in the lower canopy of forest trees, while melanic species tend to dominate in the middle and upper canopy (Benson & Coxson 2002; Coxson & Coyle 2003; Goward 2003; Gauslaa *et al.* 2008). Finally, the annual growth rates of the usnic hair lichens *Alectoria sarmentosa* (Ach.) Ach. and *Usnea dasopoga* (Ach.) Nyl. have been shown to increase strongly with increasing rainfall, whereas growth in the melanic species *Bryoria fuscescens* (Gyelnik) Brodo & D. Hawksw. remained unchanged (Phinney *et al.* 2021). These observations are consistent with the importance of canopy ventilation in the distributional ecology of water-retentive species in the genus *Bryoria* (Goward 1998; Coxson & Coyle 2003). Ventilation facilitates rapid desiccation and may thus counter the damaging effects of much externally stored water (Esseen *et al.* 2017). By contrast, usnic hair lichens are less water-retentive (Eriksson *et al.* 2018) and should therefore be less dependent on ventilation. At the same time, an instantaneous photosynthetic activation of thin hair lichens upon exposure to humid air (Phinney *et al.* 2018) may explain their ability to inhabit sheltered canopies (Gauslaa *et al.* 1998) where rain is shed centrifugally (Beier *et al.* 1993).

Our purpose is to describe the horizontal distribution of melanic versus usnic hair lichens on the lower branches of trees in even-aged coniferous stands formed over a small volcanic cone (Fig. 1). More specifically, we aim to test the potential of the

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Fig. 1. The upper portions of Pyramid Mountain (British Columbia, Canada) as viewed from the east. The southern slope on the left had an open pine-dominated forest, whereas the northern slope on the right had denser forest with few pines. Note that dead and grey pine trees in this photograph were killed by the Mountain Pine Beetle (*Dendroctonus ponderosae*) a few years after fieldwork for this study was completed. In colour online.

canopy openness parameter, Angle-To-Canopy-Skyline measure (ATCS; see Goward *et al.* 2022), to predict spatial variation in the percent cover of usnic versus melanic hair lichens. Consistent with the 'similar gradient hypothesis' of McCune (1993), we predict that earlier findings concerning the vertical distributions of these two groups in the forest canopy (Benson & Coxson 2002) will be mirrored in their respective horizontal positions relative to canopy openness.

Material and Methods

Study area

Fieldwork was performed in 2004 on Pyramid Mountain (Fig. 1), a 250 m conical volcano rising from the Murtle Plateau (800 m; 51°N, 120°W) in the Clearwater Valley of south-central British Columbia (BC). Soils were shallow and well drained, and derived from per-alkaline basalts laid down in the volcanic eruptions that formed this mountain *c.* 12 000 years ago (Hickson 1986). This area of BC has cool, moist summers and cold, snowy winters (Goward & Ahti 1992). Forest cover was mostly *c.* 60 years old, dating from a wildfire that swept the area *c.* 1940. Common tree species were *Abies lasiocarpa*, *Betula papyrifera*, *Picea glauca* × *engelmannii*, *Pinus contorta*, *Populus tremuloides* and *Pseudotsuga menziesii*, with some *Populus trichocarpa*, *Thuja plicata* and *Tsuga heterophylla* in moister sites at its base. Henceforth these trees are referred to by genus name only. A detailed description of our study area appears in Goward *et al.* (2022).

Field investigations

To capture hair lichen cover on lower conifer branches on all aspects of Pyramid Mountain, we established five linear east-west transects running in parallel at a distance of 200 m. Each transect consisted of 30 plots spaced at 50 m intervals. The transects thus created a slope-corrected grid over the mountain and the adjacent plateau (see Goward *et al.* 2022). Candidate trees were situated within 25 m of the plot centre and measured ≥ 10 m tall. Only living or recently dead branches with intact bark were examined. Four branches per tree (1.5–2.5 m above the ground) were studied in each cardinal direction (N, E, S and W), though only 1–3 suitable branches were available in some cases. In total, 523 branches were examined on 145 trees.

Total hair lichen cover (in percent) was assessed over a 1 m length of the upper side of the main branch axis centered midway between the trunk of the tree and the tip of the branch. The percent cover of each hair lichen species was also visually estimated on this branch segment. Lichen cover was calculated as the sum of individual species for melanic genera (*Bryoria* and *Nodobryoria*) versus usnic genera (*Alectoria sarmentosa*, *Ramalina thrausta* and *Usnea* spp.).

Relative degree of canopy ventilation is influenced by three separate variables, namely canopy height, stand spacing, and Angle-To-Canopy-Skyline (ATCS). Average canopy height was assessed within a 20-m radius of the plot centre. For stand spacing, we recorded the number of trees taller than 3 m growing within 10 m of the focal tree. ATCS is defined as the lowest angle at which foliar cover in the forest canopy obscures > 50% of the sky as viewed through a 4.5 cm circular viewfinder held 30 cm from the observer's eye (Goward *et al.* 2022). Each branch was accorded a separate ATCS reading across a horizontal span of 180°. Also measured was the diameter of the focal tree at breast height (DBH). Slope and aspect were estimated within 20 m of each focal tree. Finally, macroslope position was recorded as plateau surface, lower slope, middle slope and upper slope.

Table 1. Functional lichen groups recorded on trees on Pyramid Mountain (British Columbia, Canada).

	Picea	*Pinus*	*Pseudotsuga*	*Thuja*	*Tsuga*	ANOVA	
Number of trees (n)	17	62	54	7	5	*P*-value	$R^2_{adj.}$
Usnic hair lichens (% cover)*	2.1 ± 0.7	1.6 ± 0.2	2.7 ± 0.3	3.8 ± 2.2	1.9 ± 0.9	0.089	0.029
Melanic hair lichens (% cover)*	5.6 ± 3.4^{C}	56.9 ± 2.8^{A}	12.6 ± 1.9^{B}	0.2 ± 0.2^{C}	0.0 ± 0.0^{C}	< 0.001	0.715
Total hair lichens (% cover)*	7.6 ± 3.4^{C}	58.5 ± 2.8^{A}	15.3 ± 2.0^{B}	4.0 ± 2.4^{C}	1.9 ± 0.9^{C}	< 0.001	0.642

Means ± 1 standard error of functional groups also include trees without the presence of a given functional group.
*: log-transformation required for the ANOVA. Data for trees sharing the same superscript letter do not significantly differ from each other.

Our fieldwork preceded important revisionary work on *Bryoria* and *Usnea* by Myllys *et al.* (2011) and Clerc (2016), respectively. Taxonomic innovations advanced in these studies bring into question some of the species concepts applied by us in the field. Accordingly, and for the purposes of this paper, we prefer to unite morphologically similar species under a single 'form name'. Hence the name *Bryoria pseudofuscescens* (Gyelnik) Brodo & D. Hawksw., as applied here, includes *B. pikei* Brodo & D. Hawksw. and *B. inactiva* Goward *et al.* (erroneously recorded in the field as *B. friabilis*), while *B. fuscescens* (Gyelnik) Brodo & D. Hawksw. includes *B. glabra* (Motyka) Brodo & D. Hawksw. and *B. lanestris* (Ach.) Brodo & D. Hawksw. For *Usnea*, we recognize two morphogroups: 1) 'shrubby *Usnea* species' in the case of *U. glabrescens* (Nyl. ex Vain.) Vain., *U. perplexans* Stirt. and *U. substerilis* Motyka; 2) 'pendent *Usnea* species' in the case of *U. barbata* (L.) F. H. Wigg and *U. dasopoga* (Ach.) Nyl.

Statistical analyses

All data recorded per branch were averaged for each tree. Normality was tested and data were treated in ways appropriate to their distributions and log-transformed when required. One-way ANOVAs for lichen functional group variables across host tree species were applied with level effects tested using the post-hoc Tukey-Kramer test. Significance cut-off values were $P = 0.05$ throughout. Means were reported ± one standard error. These statistics were analyzed using Jamovi 2.2.5 (https://www.jamovi.org/).

Best subsets multiple linear regression models for the cover of 1) usnic and 2) melanic hair lichens were searched for by including measured stand-related parameters. Regression models and correlation matrices were made in Minitab®, v. 21.1.1.

Results

Stand characteristics

Study plots had slopes between 0–37°, canopy height ranked 8–30 m, DBH was 10–65 cm, and ATCS varied from close to zero to 90° (see Supplementary Material Fig. S1, available online). *Pinus* was the most frequent tree recorded, followed by *Pseudotsuga*, *Picea*, *Thuja* and *Tsuga* (Table 1). *Pinus* was mostly situated on the steepest slopes (22 ± 1°) near the top and on open south-facing slopes, and had the lowest ATCS (11 ± 1°); *Pseudotsuga* (ATCS = 37 ± 2°) occurred on less steep slopes (10 ± 2°), whereas *Thuja* situated on level ground had the highest ATCS (60 ± 7°), consistent with its association with closed canopies.

Hair lichen species distribution patterns

Nine hair lichen species (s. lat.) were recorded (Table 2). Among these, *Alectoria sarmentosa*, *Ramalina thrausta*, and shrubby and pendent *Usnea* morphogroups comprised the usnic species, whereas *Bryoria fremontii* (Tuck.) Brodo & D. Hawksw., *B. fuscescens* s. lat., *B. pseudofuscescens* s. lat., *Nodobryoria abbreviata* (Müll. Arg.) R. Howe and *N. oregana* (Tuck.) Common & Brodo made up the melanic species. Mean total hair lichen cover was 31.9 ± 2.4% but varied considerably according to tree

Table 2. Summary statistics given as means ± 1 standard error (SE), minimum (Min) and maximum (Max) value, median with lower (Q1) and upper quartiles (Q3), for hair lichen species frequency and percent cover on lower branches where these lichens are present on studied trees ($n = 145$) on Pyramid Mountain (British Columbia, Canada). Species are ranked by decreasing frequency in each pigment group.

Cortical pigment	Species	*n*	Mean ± SE	Min	Q1	Median	Q3	Max
Usnic acid	*Alectoria sarmentosa*	117	1.86 ± 0.18	0.05	0.50	1.14	2.94	10.00
Usnic acid	*Usnea*; shrubby species	83	0.52 ± 0.05	0.01	0.19	0.44	0.71	2.29
Usnic acid	*Ramalina thrausta*	38	1.42 ± 0.31	0.06	0.48	0.85	1.50	10.33
Usnic acid	*Usnea*; pendent species	5	0.49 ± 0.23	0.13	0.14	0.20	0.98	1.33
Melanin	*Bryoria fuscescens* s. lat.	121	20.46 ± 1.67	0.19	4.10	13.63	34.33	74.20
Melanin	*B. fremontii*	117	12.25 ± 1.26	0.13	1.28	6.31	20.77	51.79
Melanin	*B. pseudofuscescens* s. lat.	71	4.40 ± 0.79	0.06	1.00	2.19	3.88	32.40
Melanin	*Nodobryoria oregana*	54	0.98 ± 0.14	0.03	0.33	0.61	1.31	4.64
Melanin	*N. abbreviata*	28	1.16 ± 0.25	0.04	0.20	0.49	2.10	5.31

Shrubby *Usnea* species include *U. glabrescens*, *U. perplexans* (formerly *U. lapponica* Vain.) and *U. substerilis*; pendent *Usnea* species include *U. barbata* (formerly *U. scabrata* Nyl.) and *U. dasopoga* (formerly *U. filipendula* Stirt.); *Bryoria fuscescens* includes *B. glabra* and *B. lanestris; B. pseudofuscescens* includes *B. pikei* and *B. inactiva*.

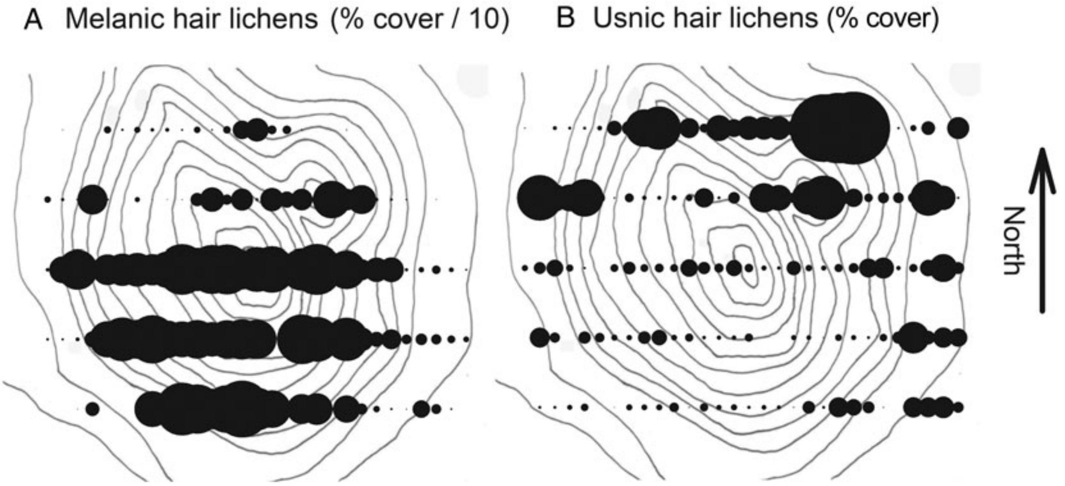

Fig. 2. The distribution of total cover (relative scale) of melanic (A) and usnic (B) hair lichens in the lower canopy on Pyramid Mountain (British Columbia, Canada). The symbol size for melanic hair lichens has been reduced to 1/10 compared to usnic hair lichens due to the former's much greater abundance.

(Table 1) and lichen species (Table 2). The most frequent hair lichens (growing on > 80% of the trees) were *B. fuscescens* s. lat., *B. fremontii* and *A. sarmentosa* (Table 2). The best host tree species for hair lichens in these young stands was *Pinus* (58.5% hair lichen cover), followed by *Pseudotsuga* (15.3% hair lichen cover).

Taken as a whole, the distribution of percent cover of usnic hair lichens on Pyramid Mountain was broadly mutually exclusive with that of the melanic hair lichens (Fig. 2), although the cover of the latter was *c.* 10 times higher (Table 2). Thus, while the melanic species (Fig. 2A) dominated on the south flanks of the mountain, usnic lichens (Fig. 2B) had their highest cover on its east, west,

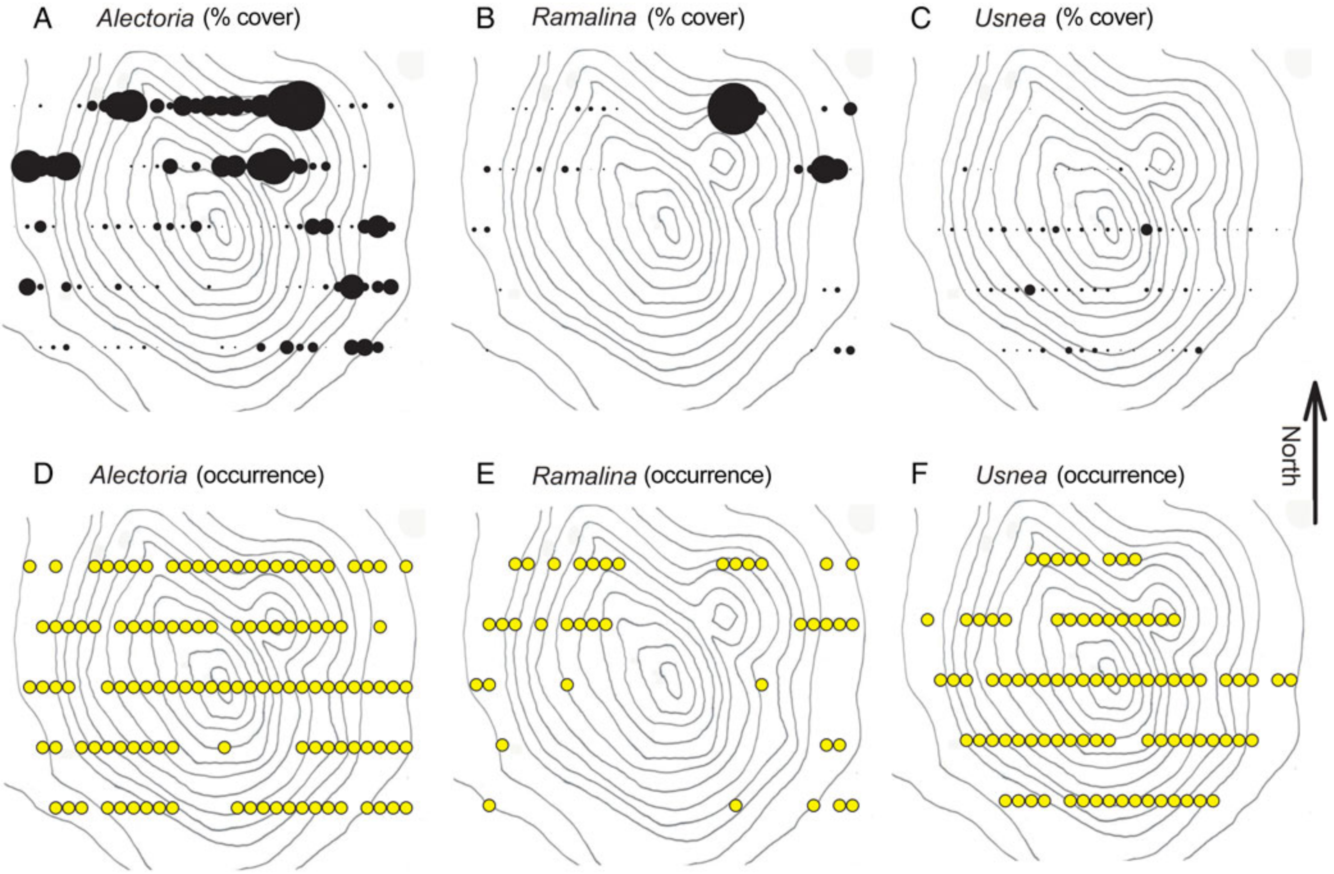

Fig. 3. The distribution of total cover (relative scale; A–C) and occurrence (D–F) of the usnic hair lichen genera *Alectoria* (A & D), *Ramalina* (B & E) and *Usnea* (C & F) in the lower canopy on Pyramid Mountain (British Columbia, Canada). In colour online.

and especially north flanks. Concerning the spatial distribution of percent cover of individual genera, *Alectoria* (Fig. 3A) and *Ramalina* (*R. thrausta*; Fig. 3B) had similar patterns and, as the two dominant genera, shaped the spatial distribution of the cover of usnic hair lichens as a group (Fig. 2B). *Alectoria* was present on most trees (Fig. 3D), excepting a small number of trees on the south flank of the mountain as well as at its base. Its cover was low, except on the north flank and again at the base (Fig. 3A). By comparison, *R. thrausta* occurred on the north, east and west flanks (Fig. 3E). The distribution of the genus *Usnea* (Fig. 3F), mainly represented by the shrubby *Usnea* morphogroup, resembled that of the melanic hair lichens (Fig. 2A), although *Usnea* contributed little to usnic hair lichen cover (Fig. 3C).

Regarding the two melanic hair lichen genera, *Bryoria* (Fig. 4A) was the more abundant genus, while *Nodobryoria* (Fig. 4B) was comparatively sparse. At the same time, both genera had their highest cover on the south flank of the mountain, and their lowest cover on the north flank and at the base. Only on south-facing slopes near the summit did *Nodobryoria* achieve moderate cover values.

Melanic hair lichens were more strongly correlated with ATCS ($r = -0.833$) than with any other measure including canopy height ($r = -0.638$), slope ($r = 0.596$), tree spacing ($r = -0.492$), and DBH ($r = -0.027$) (see Supplementary Material Table S1, available online). ATCS alone accounted for 69.2% of the variation in melanic hair lichen cover (Fig. 5A). The best subset regression model for melanic hair lichens (Supplementary Material Table S1), which included ATCS ($P < 0.001$) and canopy height ($P = 0.001$), accounted for slightly more variation ($R^2_{adj.} = 0.712$; Variation Inflation Factor, VIF < 1.65) than ATCS alone ($R^2_{adj.} = 0.692$). By contrast, usnic hair lichens did not correlate with ATCS (Fig. 5B) and increased significantly but weakly with canopy height ($r = 0.207$, $P = 0.012$) and DBH ($r = 0.195$, $P = 0.019$; Supplementary Material Table S2, available online). The best subset regression model for usnic hair lichens (Supplementary Material Table S2), which included canopy height and DBH, accounted for only a small part of the variation ($R^2_{adj.} = 0.073$, $P = 0.003$, VIF < 1.1).

Discussion

Distribution patterns of functional hair lichen groups

In this study we recorded two measures of hair lichen occurrence in the lower canopy of conifer forests on Pyramid Mountain. The

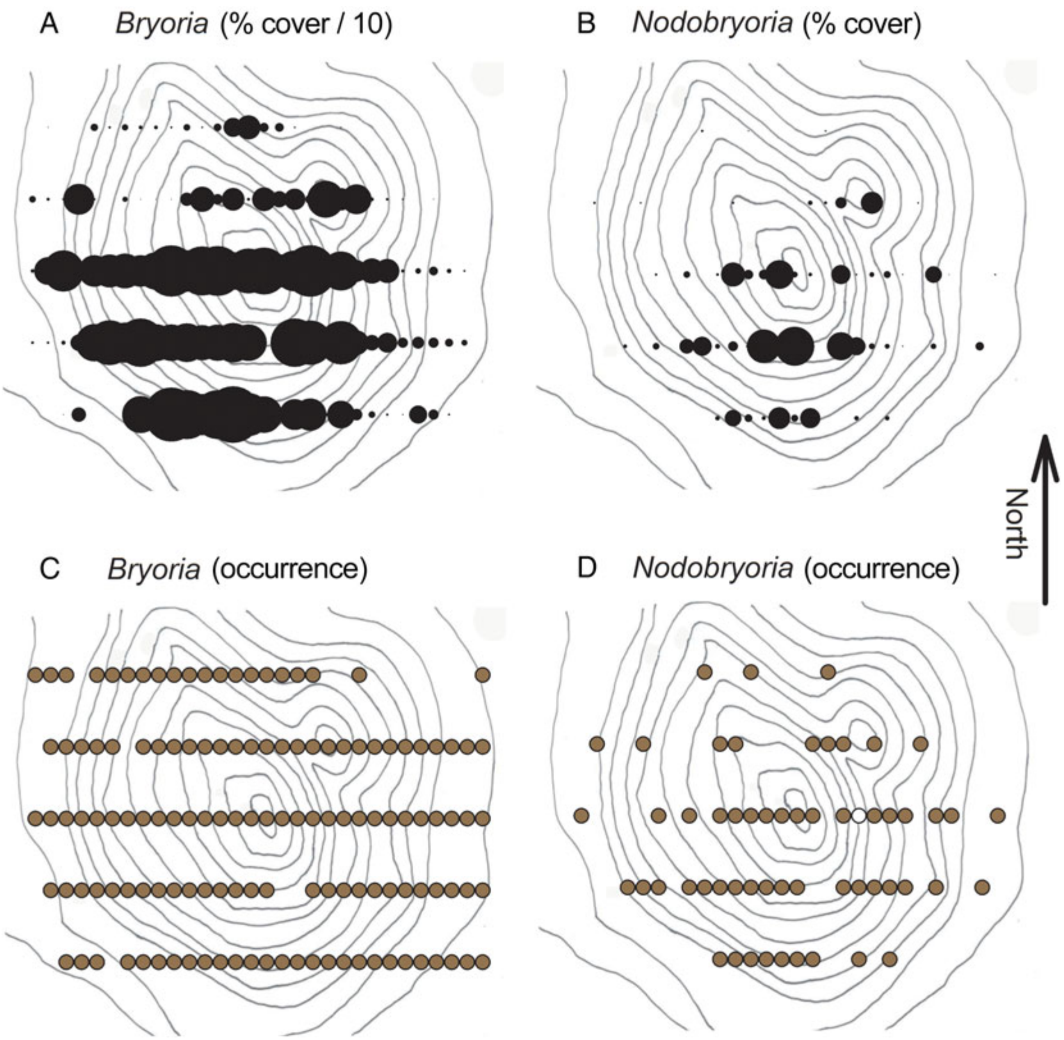

Fig. 4. The distribution of total cover (relative scale; A & B) and occurrence (C & D) of the melanic hair lichen genera *Bryoria* (A & C) and *Nodobryoria* (B & D) in the lower canopy on Pyramid Mountain (British Columbia, Canada). The symbol size for *Bryoria* has been reduced to 1/10 compared to *Nodobryoria* due to the former's much greater abundance. In colour online.

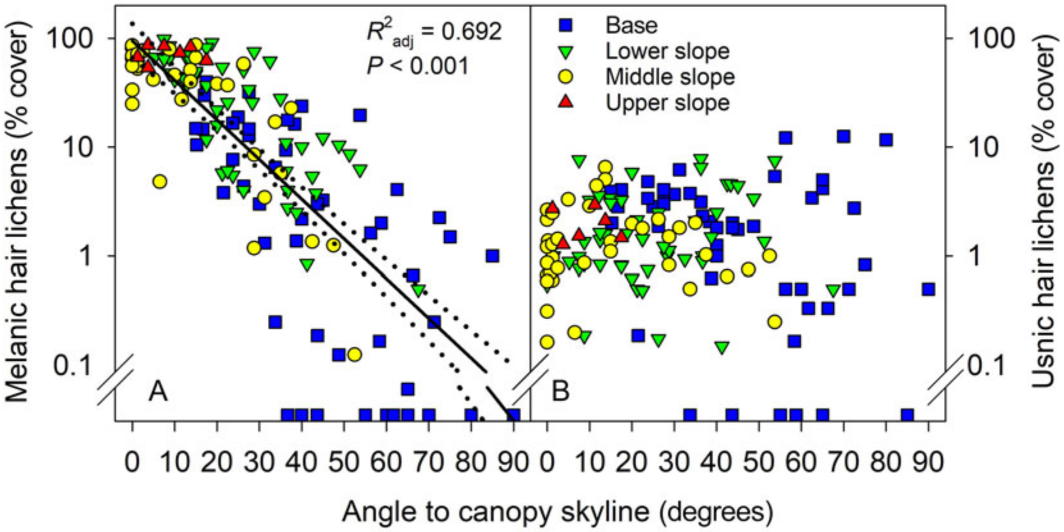

Fig. 5. The relationship between cover of melanic (A) and usnic (B) hair lichens versus angle to canopy skyline (solid line). Symbol shape and colour code for four macroslope positions: red upright triangles = upper slope and summit; yellow circles = middle slope; green down-facing triangles = lower slope; blue squares = base (plateau surface). The dotted lines show 95% confidence interval. In colour online.

first measure was presence/absence, which shows that melanic and usnic hair lichens were both widely distributed in these forests only six decades after stand initiation, a finding consistent with the inference that cortical chemistry per se has little relevance to the dispersal and establishment of *Alectoria*, *Bryoria*, *Nodobryoria*, *Ramalina* and *Usnea*. Even *A. sarmentosa* was well established here, though elsewhere it is often considered an associate of old-growth forests (e.g. Esseen *et al.* 2022). However, our second measure, percent cover, revealed a very different picture, in which the south flanks of Pyramid Mountain were dominated by melanic hair lichens while usnic hair lichens were most abundant on its north flanks, a strikingly complementary distributional pattern that probably has its basis in different pigment-specific responses (Färber *et al.* 2014).

This aspect-mediated trade-off in the horizontal distribution of melanic and usnic hair lichens corresponds well with earlier reports of their respective vertical distribution in the forest canopy (i.e. with the first group increasing in abundance with increasing height and the second group decreasing) (Campbell & Coxson 2001; Coxson & Coyle 2003; Gauslaa *et al.* 2008). Importantly, this pattern recalls the 'similar gradient hypothesis' (McCune 1993), which posits that the horizontal and vertical distributions of epiphytic lichens run in parallel, as also concluded by Esseen (2019). In the present case, melanic hair lichens would therefore be expected to attain their optimum development in open, sun-exposed sites, while usnic hair lichens should be more common in more sun-sheltered sites, consistent with our results. We suggest that this occurrence justifies the separation of pendent hair lichens into two pigment-based functional groups, here referred to as usnic hair lichens and melanic hair lichens.

Light screening of cortical pigments

The dominance of dark-pigmented hair lichens in sun-exposed situations and pale-pigmented hair lichens in more shaded sites can be attributed to quantified differences in their respective tolerance for direct sunlight, with light tolerance in the melanic group being markedly higher than that in the usnic group (Färber *et al.* 2014). This is true especially for lichens in the desiccated state, which less efficiently handle excess excitation and lack an active repair mechanism (Beckett *et al.* 2021). An interesting corollary of this is that frequent hydration allows usnic hair lichens to thrive in light-exposed upper canopies in wet climates (Benson & Coxson 2002; Antoine & McCune 2004) and on scattered trees in humid open forests, a consequence of hydration-dependent improved repair of photoinhibitory damage formed during dry periods.

The light-screening function of cortical pigments optimizes lichen performance along gradients from shade to sun (Gauslaa & Solhaug 2001; Solhaug & Gauslaa 2012; Gauslaa & Goward 2020). Effects of hydration on light screening in hair lichens are schematically summarized in Fig. 6. Usnic hair lichens (Fig. 6A) have pale cortices that are slightly transparent even when dry, thereby exposing the desiccated underlying chlorophylls to some light and thus to oxidative stress. Their distinct yellowish green colour is attributable partly to chlorophyll and partly to the faintly yellow usnic acid. Such pale pigments screen solar radiation by reflectance (Solhaug *et al.* 2010), thereby reducing solar radiation-induced warming (Kershaw 1975) and prolonging photosynthesis after hydration (Phinney *et al.* 2022). By contrast, the dark cortex of the melanic genus *Bryoria* (Fig. 6B) absorbs most incident solar radiation with hardly any visible green reflectance. Thereby, photoinhibitory damage to the underlying photosynthetic algae is prevented (Färber *et al.* 2014). At the same time, desiccated *Bryoria* also tolerates solar heating up to 70 °C (Lange 1953), probably a necessary adaptation for blackish lichens growing in sun-exposed sites. During wetting, photobiont cells become turgid and thus larger, while water absorbed into the expanding cortical hyphae dilutes their pigments and fills empty air spaces. Particularly in usnic hair lichens, this results in greater cortical transparency, seen as a green tinge caused by reflectance from the underlying algal chlorophylls. Crucially, a transparent cortical window optimizes photosynthesis in thalli growing in shaded sites.

An interesting finding of our study is the strong association of short, shrubby species (*Usnea glabrescens*, *U. perplexans*,

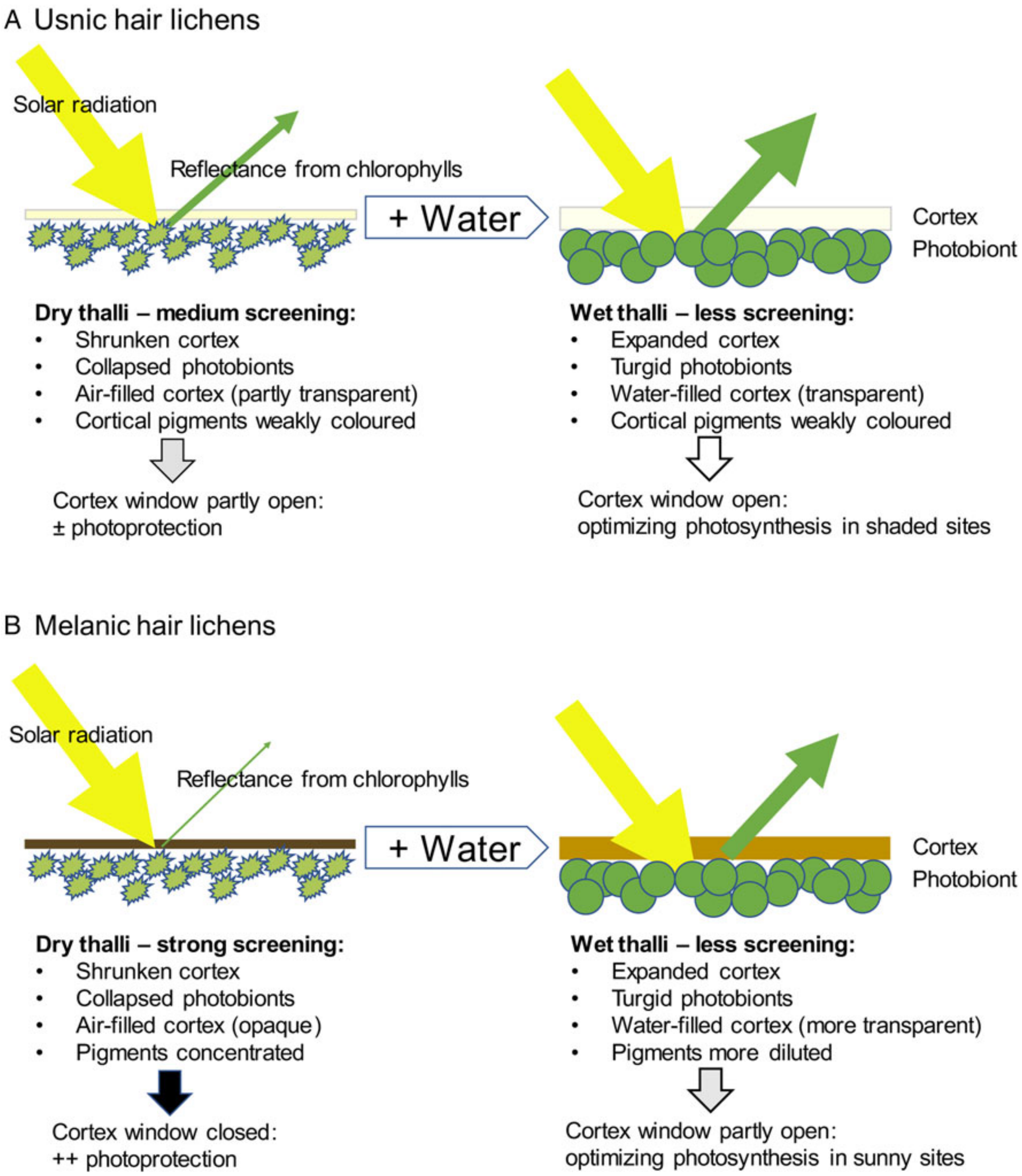

Fig. 6. Schematic interpretations of effects of hydration on light screening in hair lichen functional groups. A, usnic hair lichens (usnic acid in the cortex). B, melanic hair lichens (with cortical melanic pigments). The thickness of the green/darker shade arrows depicts the greenness in desiccated (left) and hydrated thalli (right) as seen from outside through the cortical window. The greenness is caused by reflectance from the algal chlorophylls and is thus a measure of cortical transmittance; see text for further explanation. Some lichen characteristics are summarized in the text below, emphasizing ways in which hydration state and pigments affect photoprotection in terms of cortical light screening and photosynthesis. In colour online.

U. substerilis) with south-facing, sun-exposed slopes (Fig. 3) versus the almost exclusive occurrence of long, pendent species such as *A. sarmentosa*, *Ramalina thrausta*, *U. barbata* and *U. dasopoga* (data for the two pendent *Usnea* species not shown) on more sun-sheltered aspects. It is worth noting that shrubby *Usnea* species have thick branches and high water storage capacity compared to the thin branches and low water storage of pendent species (Eriksson *et al.* 2018). Thallus morphology thus influences hydration traits in this genus. In addition, the thicker branches probably improve light screening efficiency, as suggested by their predominance on the south flanks of Pyramid Mountain. It is well known that thick foliose lichens containing usnic acid, such as *Arctoparmelia* and *Xanthoparmelia*, are well suited to fully sun-exposed arid environments, even in hot climates (e.g. Elix 1994; Hauck *et al.* 2007). By contrast, dry pendent usnic hair lichens have poor cortical screening (Färber *et al.* 2014), thereby hindering successful colonization in dry, sun-exposed habitats, a feature apparently unique among usnic lichens. We predict that usnic hair lichens will increase in the lower canopy of trees on Pyramid Mountain as the forests age and become shadier.

Conclusion

Considering the data summarized in this paper, the occurrence in pendent hair lichens of cortical melanin versus usnic acid justifies the recognition of two functional groups, consistent with our hypothesis. Investment in light-absorbing melanic pigments can be considered an extreme form of specialization for high light (one present in only a small number of hair lichen genera) that favours persistence in dry, sun-exposed canopies of otherwise cool forests. By contrast, an ability to synthesize light-reflecting usnic acid yields a more flexible solar radiation screen that has evolved across a wide array of lichen genera worldwide. Only in pendent usnic hair lichens is the cortex sufficiently thin to facilitate optimum light transmission in shaded sites, though this comes at the cost of high sensitivity to light in open habitats, especially in rather dry regions. By contrast, shrubby *Usnea* species characterized by thicker branches are less light-sensitive and hence better adapted to sun-exposed localities. Cortical pigments thus play important roles in shaping the ecological niches occupied by epiphytic hair lichens.

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Competing Interests. The authors declare none.

Supplementary Material. To view Supplementary Material for this article, please visit https://doi.org/10.1017/S0024282923000075.

References

Ahlner S (1948) Utbredningstyper bland Nordiska barrträdslavar. *Acta Phytogeographica Suecica* **22**, 1–257.

Ahti T (1977) Lichens of the boreal coniferous zone. In Seaward MRD (ed.), *Lichen Ecology*. London: Academic Press, pp. 145–181.

Antoine ME and McCune B (2004) Contrasting fundamental and realized ecological niches with epiphytic lichen transplants in an old-growth *Pseudotsuga* forest. *Bryologist* **107**, 163–172.

Beckett RP, Minibayeva F, Solhaug KA and Roach T (2021) Photoprotection in lichens: adaptations of photobionts to high light. *Lichenologist* **53**, 21–33.

Beier C, Hansen K and Gundersen P (1993) Spatial variability of throughfall fluxes in a spruce forest. *Environmental Pollution* **81**, 257–267.

Benson S and Coxson DS (2002) Lichen colonization and gap structure in wet-temperate rainforests of northern interior British Columbia. *Bryologist* **105**, 673–692.

Brodo IM and Hawksworth DL (1977) *Alectoria* and allied genera in North America. *Opera Botanica* **42**, 1–164.

Campbell J and Coxson DS (2001) Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forest. *Canadian Journal of Botany* **79**, 537–555.

Clerc P (2016) Notes on the genus *Usnea* (lichenized *Ascomycota*, *Parmeliaceae*) IV. *Herzogia* **29**, 403–411.

Coxson DS and Coyle M (2003) Niche partitioning and photosynthetic response of alectorioid lichens from subalpine spruce-fir forest in north-central British Columbia, Canada: the role of canopy microclimate gradients. *Lichenologist* **35**, 157–175.

Elix JA (1994) *Xanthoparmelia*. In Orchard AE (ed.), *Flora of Australia, Vol. 55.* Canberra: Australian Biological Resources Study, pp. 201–308.

Eriksson A, Gauslaa Y, Palmqvist K, Ekström M and Esseen P-A (2018) Morphology drives water storage traits in the globally widespread lichen genus *Usnea*. *Fungal Ecology* **35**, 51–61.

Esseen P-A (2019) Strong influence of landscape structure on hair lichens in boreal forest canopies. *Canadian Journal of Forest Research* **49**, 994–1003.

Esseen P-A, Renhorn K-E and Pettersson RB (1996) Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecological Applications* **6**, 228–238.

Esseen P-A, Ekström M, Westerlund B, Palmqvist K, Jonsson BG, Grafström A and Ståhl G (2016) Broad-scale distribution of epiphytic hair lichens correlates more with climate and nitrogen deposition than with forest structure. *Canadian Journal of Forest Research* **40**, 1348–1358.

Esseen P-A, Rönnqvist M, Gauslaa Y and Coxson DS (2017) Externally held water – a key factor for hair lichens in boreal forest canopies. *Fungal Ecology* **30**, 29–38.

Esseen P-A, Ekström M, Grafström A, Jonsson BG, Palmqvist K, Westerlund B and Ståhl G (2022) Multiple drivers of large-scale lichen decline in boreal forest canopies. *Global Change Biology* **28**, 3293–3309.

Färber L, Solhaug KA, Esseen P-A, Bilger W and Gauslaa Y (2014) Sunscreening fungal pigments influence the vertical gradient of pendulous lichens in boreal forest canopies. *Ecology* **95**, 1464–1471.

Gauslaa Y and Goward T (2020) Melanic pigments and canopy-specific elemental concentration shape growth rates of the lichen *Lobaria pulmonaria* in unmanaged mixed forest. *Fungal Ecology* **47**, 100984.

Gauslaa Y and Solhaug KA (2001) Fungal melanins as a sun screen for symbiotic green algae in the lichen *Lobaria pulmonaria*. *Oecologia* **126**, 462–471.

Gauslaa Y, Ohlson M and Rolstad J (1998) Fine-scale distribution of the epiphytic lichen *Usnea longissima* on two even-aged neighbouring *Picea abies* trees. *Journal of Vegetation Science* **9**, 95–102.

Gauslaa Y, Lie M and Ohlson M (2008) Epiphytic lichen biomass in a boreal Norway spruce forest. *Lichenologist* **40**, 257–266.

Goward T (1998) Observations on the ecology of the lichen genus *Bryoria* in high elevation conifer forests. *Canadian Field-Naturalist* **112**, 496–501.

Goward T (2003) On the vertical zonation of hair lichens (*Bryoria*) in the canopies of high-elevation oldgrowth conifer forests. *Canadian Field-Naturalist* **117**, 39–43.

Goward T and Ahti T (1992) Macrolichens and their zonal distribution in Wells Gray Provincial Park and its vicinity, British Columbia, Canada. *Acta Botanica Fennica* **147**, 1–60.

Goward T and Arsenault A (2003) Notes on the *Populus* 'dripzone effect' on lichens in well-ventilated stands in east-central British Columbia. *Canadian Field-Naturalist* **117**, 61–65.

Goward T, Gauslaa Y, Björk CR, Woods D and Wright KG (2022) Stand openness predicts hair lichen (*Bryoria*) abundance in the lower canopy, with implications for the conservation of Canada's critically imperiled Deep-Snow Mountain Caribou (*Rangifer tarandus caribou*). *Forest Ecology and Management* **520**, 120416.

Hauck M, Dulamsuren C and Mühlenberg M (2007) Lichen diversity on steppe slopes in the northern Mongolian mountain taiga and its dependence on microclimate. *Flora* **202**, 530–546.

Hickson CJ (1986) *Quaternary volcanism in the Wells Gray – Clearwater area, east central British Columbia*. Ph.D. thesis, University of British Columbia.

Kershaw KA (1975) Studies on lichen-dominated systems. XII. The ecological significance of thallus color. *Canadian Journal of Botany* **53**, 660–667.

Lange OL (1953) Hitze- und Trockenresistenz der Flechten in Beziehung zu ihrer Verbreitung. *Flora* **140**, 39–97.

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

Myllys L, Velmala S, Holien H, Halonen P, Wang LS and Goward T (2011) Phylogeny of the genus *Bryoria*. *Lichenologist* **43**, 617–638.

Pettersson RB, Ball JP, Renhorn K-E, Esseen P-A and Sjöberg K (1995) Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biological Conservation* **74**, 57–63.

Phinney NH, Solhaug KA and Gauslaa Y (2018) Rapid resurrection of chlorolichens in humid air: specific thallus mass drives rehydration and reactivation kinetics. *Environmental and Experimental Botany* **148**, 184–191.

Phinney NH, Gauslaa Y, Palmqvist K and Esseen P-A (2021) Macroclimate drives growth of hair lichens in boreal forest canopies. *Journal of Ecology* **109**, 478–490.

Phinney NH, Asplund J and Gauslaa Y (2022) The lichen cushion: a functional perspective of color and size of a dominant growth form on glacier forelands. *Fungal Biology* **126**, 375–384.

Pypker TG, Unsworth MH, Van Stan JT, II, and Bond BJ (2017) The absorption and evaporation of water vapor by epiphytes in an old-growth Douglas-fir forest during the seasonal summer dry season: implications for the canopy energy budget. *Ecohydrology* **10**, e1801.

Rominger EM, Robbins CT and Evans MA (1996) Winter foraging ecology of woodland caribou in northeastern Washington. *Journal of Wildlife Management* **60**, 719–728.

Rominger EM, Robbins CT, Evans MA and Pierce DJ (2000) Autumn foraging dynamics of woodland caribou in experimentally manipulated habitats, northeastern Washington, USA. *Journal of Wildlife Management* **64**, 160–167.

Solhaug KA and Gauslaa Y (2012) Secondary lichen compounds as protection against excess solar radiation and herbivores. *Progress in Botany* **73**, 283–304.

Solhaug KA, Larsson P and Gauslaa Y (2010) Light screening in lichen cortices can be quantified by chlorophyll fluorescence techniques for both reflecting and absorbing pigments. *Planta* **231**, 1003–1011.

Van Stan JT, II, and Pypker TG (2015) A review and evaluation of forest canopy epiphyte roles in the partitioning and chemical alteration of precipitation. *Science of the Total Environment* **536**, 813–824.