Canopy throughfall links canopy epiphytes to terrestrial vegetation in pristine conifer forests

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ABSTRACT

To what extent does epiphytic community composition in boreal forests reflect soil nutrient status? To answer this question, we investigated potential links between terrestrial plants and lichen-dominated communities in *Picea glauca* × *engelmannii* canopies in south-central British Columbia. We combined original data on vegetation composition in the ground and tree layers with published data on elemental uptake in standardized transplants of the lichen *Lobaria pumonaria* affixed to the lower branches of studied trees. Procrustean association metrics revealed a significant concordance between community composition among the epiphytic and terrestrial vegetation, which was stronger in Mn-enriched conifer canopy settings, and weaker within the cation-enriched dripzones of adjacent *Populus* trees. We also found that the NMDS1-gradient for each vegetation layer was strongly correlated with base cations (and inversely with Mn) in canopy throughfall, as well as with soil and bark pH. We conclude that elemental composition in canopy throughfall forms a functional link between terrestrial and epiphytic vegetation.

1. Introduction

Chemical recycling, necessary for life on earth, occurs at a wide range of scales, from world-wide recycling mechanisms like plate tec-tonics and atmospheric photochemical processes (Falkowski et al., 2008) to local processes in e.g., forest ecosystems (Attiwill and Adams 1993), where nutrient cycling requires input from the lithosphere, a major source of elements needed for plant growth; the biosphere, prime agent of elemental uptake from the soil; the hydrosphere, source of rain; and the atmosphere, agent of water-mediated canopy throughfall which returns nutrients to the forest floor. Epiphytic lichens living at the atmosphere-biosphere interface participate in forest nutrient cycling (Knops et al. 1991, 1996), e.g., by affecting canopy throughfall chemistry (Lang et al., 1976; Van Stan and Pypker 2015). In areas impacted by air pollution, clear linkages between ion concentration and epiphytic lichen vegetation have often been demonstrated (e.g., Conti and Cecchetti 2001; Garty 2001; Richardson and Cameron 2004; Nash III 2008; Bargagli 2016), and epiphytic lichens have been used as a convenient proxy for assessing air pollution chemistry (e.g., Loppi and Pirintinos 2003; Yemets et al., 2014; Root et al., 2015).

The ongoing loss of primary forests to industrial forestry has two main outcomes for epiphytic lichens: first, a reduction in overall epiphytic abundance and diversity (Lesica et al., 1991; Dettki and Esseen 2003; Nascimbene et al., 2013; Boudreault et al., 2015; Bezzola and Coxson 2020); and second, a corresponding reduction in their performance of key ecological functions of primary forest ecosystems (Coxson and Nadkarni 1995; Asplund and Wardle 2017; Pypker et al., 2017; Porada et al., 2018). Any attempts to reverse these declines require a detailed understanding of the mechanisms and factors that shape epiphytic communities. While many studies have addressed knowledge gaps by investigating, for example, lichen diversity in relation to climate and stand setting (e.g., Esseen et al., 2016; Hurtado et al., 2019; Nascimbene et al., 2013; Boudreault et al., 2015), there have been few attempts to examine the relation of epiphytic lichen vegetation to spatial variation in throughfall chemistry (but see Campbell et al., 2010; 2013; Asplund et al., 2015).

It has long been known that tree species with nutrient-poor bark support lichen communities very different from those that predominate on nutrient-rich tree species (Du Rietz 1945), with bark pH often serving as a convenient proxy for the complex underlying chemical factors...
involved (Barkman, 1958). Yet bark pH on its own has lately been found to lose explanatory power in lichen growth models that include elemental concentrations as explanatory parameters (Gauslaa et al., 2020b), pointing to the need for further, more detailed work on the relation of epiphytic communities to the chemical factors that shape them.

In the most recent of an on-going series of ecological lichen studies (Goward and Arsenault 2000, 2018; Goward 2003; Goward and Campbell 2005; Gauslaa and Goward 2012; Bidussi et al., 2013; Bidussi and Gauslaa 2015; Arsenault and Gauslaa 2016) conducted in a region of high atmospheric purity in south-central British Columbia, Gauslaa et al. (2020a) transplanted thalli of the epiphytic lichen Lobaria pulmonaria to the lower living branches of hybrid spruce (Picea glauca x engelmannii) for 1 y. Because these transplants were affixed to plastic nets, they had no direct contact with tree bark and were thus exposed exclusively to airborne elements from wet and dry deposition, as well as to canopy throughfall. A key finding of this study was that 1-y lichen transplants can yield a clearer picture of canopy-specific elemental throughfall than rain gauges placed out for one season (Campbell et al., 2010).

In this study, we supplemented the chemical and other environmental data of Gauslaa et al. (2020a) with previously unpublished comprehensive data on the epiphytic macrolichens of the host trees, as well as on the vascular ground vegetation within 3 m of their trunks. By combining these data sets, we aim: (1) to quantify possible links between epiphytes in the lower tree canopies and vascular plants on the ground within the root zone of the respective trees, and (2) to identify environmental drivers that shape these vegetation components. More generally, our objective here is to test the hypothesis that throughfall elemental chemistry shapes epiphytic vegetation in ways consistent with soil chemistry and hence terrestrial vegetation.

2. Material and methods

2.1. Study area

Our study area was located at 660–830 m in the Clearwater Valley of south-central British Columbia (51 N, 120 W), in a region characterized by cold, snowy winters and cool, moist summers. Average monthly temperatures ranges from −9.7 °C in January to 15.3 °C in July, while monthly precipitation varies between 24.1 mm in March and 71.1 mm in June (Environment Canada 1975a, b). Earlier work has shown that the Clearwater Valley experiences large diurnal temperature fluctuations, with strong nocturnal cooling conducive to high relative humidity and heavy dewfall (Bidussi and Gauslaa 2015). The resulting frequent hydration events promote lichen growth even in apparently dry habitats, subject mainly to the requisite chemical environment (Gauslaa and Goward 2012; Bidussi et al., 2013).

Soils are derived mostly from underlying peralkaline basalts dating from volcanic eruptions between one and two million years ago (Hickson 1986) and overlain by glacial till deposited during the most recent Pleistocene glaciation, which ended here about 11,000 years b.p. (Claude 1981). Soil fertility reflects localized, topography-dependent leaching or enrichment by glacial meltwaters and subsequent seasonal water movement. Vegetationally the study area belongs within the humid lower boreal subzone (sensu Tuhkanen 1984), as well as in the Interior Cedar-Hemlock Biogeoclimatic Zone (ICH) of Meidinger and Pojar (1991). See Hämäri-Ahti (1965) for a detailed description of the vegetation.

2.2. Canopy settings and habitat characteristics of studied localities

We selected nine coniferous forest localities along a 31-km north-south climatic gradient ranging from warmer and drier in the south to slightly cooler and moister in the north (see e.g., Arsenault and Goward 2016). The dominant tree species at each locality was Picea glauca x engelmannii (henceforth Picea), which we accordingly selected as the host tree for our transplant experiment. Subdominant or scattered trees included Abies lasiocarpa, Betula papyrifera, Pinus contorta, Populus tremuloides, P. trichocarpa, Pseudotsuga menziesii, Thuja plicata, and Tsuga heterophylla. Forests in the six southernmost localities dated from a stand-replacing wildfire in 1926 (Edwards 1954), while stands in the three northernmost ones dated from fire in the late 1890s (Trevor Goward, unpublished data). Our nine study localities were chosen so as to represent three major epiphytic community/forest settings characteristic of the study area, as follows: (1) Picea branches supporting only acidophytic chlorolichens (the Parmelion community: three localities); (2) Picea branches supporting a combination of cephalo-, cyano-, and chlorolichens within the dripzone of overarching Populus trees (the dripzzone Lobarion community: four localities); and (3) Picea branches supporting the Lobarion community outside of any Populus drizones (the non-dripzone Lobarion community: two localities).

At each locality, we chose ten Picea to receive transplants of L. pulmonaria collected from a small homogeneous source site and standardized for size and reproductive efforts. Transplant trees were selected on the following criteria: (1) they had living branches below 3 m; (2) they were positioned in rather open canopies (required by L. pulmonaria); (3) they were situated at least 100 m from the nearest forest edge; (4) they were spaced more than 30 m apart (to ensure non-overlapping root zones and drizones); and (5) they were representative of the dominant canopy setting for the respective locality (Parmelion, dripzone Lobarion, or non-dripzone Lobarion). For each of the 90 selected transplant trees, we recorded all macrolichens and bryophytes occurring on the lower branches (<3 m) as well as all vascular plants growing within the rooting zone of the tree, visualized as a circle drawn outward from the trunk to a distance of 3 m. Each tree then received one randomly selected transplant of L. pulmonaria on two separate branches; see Gauslaa et al. (2020a).

Environmental parameters recorded for each of the 90 selected trees were: tree height, trunk circumference at breast height, surrounding basal area (m2 ha−1), and percent open sky. Chemical factors included mean bark pH of two separate Picea branches, soil pH in a combined sample from the root zone of the selected tree, and elemental concentrations of a finely-ground combined sample of the two transplanted thalli pooled from each tree. Analyzed elements were Al, B, C, Ca, Cu, Fe, K, Mg, Mn, Mo, N, Na, P and Zn. See Gauslaa et al. (2020a) for details on environmental parameters.

2.3. Statistical analyses

We visualized the community composition of canopy epiphytes and ground vegetation separately using non-metric multidimensional scaling (NMDS) of Bray-Curtis distance matrices as well as the metaMDS function in the R package vegan (Oksanen et al., 2019). The envfit function in the vegan package was used to fit all measured environmental variables onto ordinations. Procrustean randomization tests (PROTEST; Peres-Neto and Jackson 2001) were used to evaluate the concordance between the epiphytic and terrestrial communities. We rotated the axes of the NMDS ordination of the ground vegetation to minimize the sum of squared deviation in relation to the epiphyte community NMDS axis scores and performed 9999 randomizations of procrustean associations. We then used the residuals from the procrustean solution (e.g., the procrustean association metrics; PAM) to assess the differences in the strength of epiphytic-terrestrial vegetation association among the three categories (i.e., dripzone Lobarion, non-dripzone Lobarion, and Parmelion) using ANOVA followed by a Tukey post-hoc test. To evaluate which environmental variables explained the Procrustean relationship between the two communities, we performed Pearson correlations between PAM and the environmental variables that correlated significantly with at least one of the ordinations. These analyses were performed in R version 4.0.2 (R Core Team, 2018).

Species sufficiently abundant to satisfy chi-square test requirements
were tested to search for significant patterns of species distribution across the three canopy settings. To compare species number in these canopy settings, we used Kruskal-Wallis one-way ANOVA (non-parametric) with Dwass-Steel-Critchlow-Fligner Pairwise comparisons. Means ± 1 standard error are reported in the text.

3. Results

3.1. Epiphytic vegetation

In total, 57 species of epiphytes were recorded in the lower canopy of the 90 trees, of which 55 were macrolichens, two were bryophytes (Table 1). Of the macrolichens found, 13 (23.6%) were cyano- and cephalolichens while the remainder were chlorolichens. The mean number of epiphytes per tree was 10.3 (total range: 2–22; n = 90); the mean number of cyano- and cephalolichens was 2.5 (0–8). All chlorolichens with a significant distribution profile among the three canopy settings were less frequent in dripzone and/or non-dripzone Lobarion canopies compared to Parmelion canopies (Table 1). Mean number of chlorolichens per tree significantly increased from dripzone Lobarion canopies (4.9 ± 0.7) to non-dripzone Lobarion canopies (8.1 ± 0.5) and again to Parmelion (10.9 ± 0.7; Table 2), while it declined with bark pH in a simple regression analysis ($r^2_{adj} = 0.251; P < 0.001; n = 90$). Cephalo- and cyanolichens were abundant only in the dripzone (3.5 ± 0.3 species) and non-dripzone Lobarion canopies (4.1 ± 0.3 species; Table 2) and their species number per tree increased with bark pH ($r^2_{adj} = 0.148; P < 0.001; n = 90$). The two bryophytes occurred exclusively on study trees situated in Populus dripzones, somewhat bolstering the epiphytic community with the lowest mean number of epiphytes per tree (9.0 ± 0.7 species; Table 2). The dripzone Picea trees were particularly poor in

Table 1

| Frequency of common lichen species or genera recorded on lower branches of 90 Picea trees in the following categories: (1) Parmelion trees lacking epiphytic cephalo- and cyanolichens; (2) Non-dripzone Lobarion trees supporting cephalo- and cyanolichens in the absence of Populus dripzones; (3) Dripzone Lobarion trees occurring in sites within the dripzone of Populus tremulaeoides or P. trichocarpa. |
|-----------------|------------------|------------------|------------------|------------------|------------------|
| Category       | Parmelion n = 30 | Non-DZ Lobarion n = 20 | DZ Lobarion n = 40 | Chi square | P level |
| Chlorolichens  |                  |                  |                  |            |        |
| Bryoria, all spp (n = 28) | 66.7 | 25.0 | 7.5 | 19.60 | <0.0001 |
| Ulena, all spp. (19) | 36.7 | 0.0 | 20.0 | 7.68 | 0.0214 |
| Melanelia subMargina (25) | 46.7 | 0.0 | 27.5 | 9.41 | 0.009 |
| Tuckermannopsis chlorophae (40) | 80.0 | 45.0 | 17.5 | 15.07 | 0.0005 |
| Ramalia thurra (55) | 56.7 | 50.0 | 7.00 | 1.02 | ns |
| Hypogymnia protea (24) | 40.0 | 10.0 | 25.0 | 4.13 | ns |
| Parmelia scabefa (74) | 90.0 | 90.0 | 72.8 | 0.83 | ns |
| Hypogymnia physidea (61) | 86.7 | 85.0 | 45.0 | 5.52 | ns |
| Hypogymnia occidenta (46) | 83.3 | 65.0 | 25.0 | 11.59 | 0.003 |
| Hypogymnia tubulosa (335) | 63.3 | 50.0 | 15.8 | 11.11 | 0.0039 |
| Alectoris sarmentosa (39) | 53.3 | 80.0 | 17.5 | 13.06 | 0.0014 |
| Parmelia hyphropha (25) | 10.0 | 55.0 | 27.5 | 8.75 | 0.0126 |
| Parmelopsis ambigae (22) | 36.7 | 55.0 | 0.0 | 19.25 | <0.0001 |
| Parmelias hyperocata (24) | 30.0 | 75.0 | 0.0 | 28.31 | <0.0001 |
| Platismatia glauca (42) | 66.7 | 15.0 | 15.93 | 0.0003 |
| Cyanolichens     |                  |                  |                  |            |        |
| Lobaria, all spp (60) | 0.0 | 100.0 | 100.0 | 30.00 | <0.0001 |
| Nephroma helveticum (48) | 0.0 | 95.0 | 72.5 | 25.29 | <0.0001 |
| Nephroma parlic (40) | 6.7 | 80.0 | 32.5 | 18.81 | <0.0001 |
| Nephroma resupinatua (20) | 0.0 | 10.0 | 45.0 | 17.35 | 0.0002 |
| Leptogium satutinum (19) | 0.0 | 0.0 | 47.5 | 23.75 | <0.0001 |
| Bryophytes       |                  |                  |                  |            |        |
| Orthocorbia spp | 0.0 | 95.0 | 47.5 | 23.75 | <0.0001 |

Chi-squares with corresponding P - levels were computed based on the number of trees with a given species satisfying the requirements. Bryoria included B. glabra (7), B. fremontii (4), B. fusceca (19), B. lance (5), B. pikei (13), B. pseudofusceca (3), B. vranjana (4). Ulena included U. barbara morph scabrusca (4), U. dasypog (7), U. glabrata (7), U. lapponica (15), U. subserilis (10). Lobaria included L. anomala (12), L. halli (11), L. palmonaria (60), L. scrobiculata (4). Other species present: Collema subflacide (2), Hypnum circinale (6), Hygrohypnia canadensis (2), H. dichromia (5), Nephroma bellum (6), P. isidiosum (1), Nothoforia aereana (2), Pelitoxa collina (1), Physcia eudacea (3), P. alnophila (4), Physconia perichiosa (2), Ramalina dilacera (9), R. farinacea (4), R. obtusa (5), R. pollinaria (2), Sticta fulgiforma (6), Tuckermannopsis americana (7), T. orbata (2), Vulpicida pinasi (14). Bold letters represent the code for the species abbreviations used in Fig. 1.

Table 2

| Number of species recorded on lower branches of 90 Picea trees in the following categories: (1) Parmelion trees lacking epiphytic cephalo- and cyanolichens; (2) Non-dripzone Lobarion trees supporting cephalo- and cyanolichens in the absence of Populus dripzones; (3) Dripzone Lobarion trees occurring in sites within the dripzone of Populus tremulaeoides or P. trichocarpa. |
|-----------------|------------------|------------------|------------------|------------------|------------------|
| Species groups  | Parmelion n = 30 | Non-dripzone Lobarion n = 20 | Dripzone Lobarion n = 40 | ANOVA on ranks: |      |
| Epiphytes       |                  |                  |                  | $F^2$ | $P$ |
| All epiphytes, no. of species | 10.9 ± 0.7 (10.5)$^{ab}$ | 12.1 ± 0.7 (12.5)$^a$ | 9.0 ± 0.7 (9.0)$^b$ | 10.5 | 0.005 |
| Chlorolichens, no. of species | 10.9 ± 0.7 (10.5)$^{ab}$ | 8.1 ± 0.5 (8.0)$^b$ | 4.9 ± 0.7 (4.5)$^a$ | 35.0 | <0.001 |
| Cyanolichens and cephalolichens, no. of species | 0.07 ± 0.05 (0.0)$^b$ | 4.1 ± 0.3 (4.0)$^a$ | 3.5 ± 0.3 (3.0)$^a$ | 61.9 | <0.001 |
| Bryophytes, no. of species | 0.0 ± 0.00 (0.0)$^b$ | 0.0 ± 0.00 (0.0)$^b$ | 0.0 ± 0.01 (0.0)$^a$ | 29.4 | <0.001 |
| Ratio (cyanol cephalolichens)/all lichens, % | 0.5 ± 0.4 (0.0)$^a$ | 33.3 ± 1.4 (34.3)$^a$ | 49.2 ± 4.1 (43.7)$^a$ | 63.4 | <0.001 |
| Plants on the ground |                  |                  |                  |      |      |
| All species, no. of species | 16.0 ± 0.7 (15.5)$^a$ | 16.6 ± 0.6 (60)$^a$ | 15.2 ± 0.6 (15.0)$^a$ | 2.09 | 0.353 |

Values are given as means ± standard errors and (medians). Similar superscript letters among species indicate no significant difference ($P ≥ 0.05$) in Kruskal-Wallis one-way ANOVA (non-parametric) with Dwass-Steel-Critchlow-Fligner Pairwise comparisons.
chlorolichens. Cyano- and cephalolichens represented nearly half of all lichen species in the dripzone Lobarian canopies versus one-third in the non-dripzone Lobarian canopies (Table 2).

In the NMDS-plot (based on the presence/absence of epiphytes in the lower canopy; Fig. 1A), the first NMDS axis represented a canopy throughfall chemistry gradient in which increasing NMDS1-scores reflected a decrease in concentration of base cations (Mg, K, Ca) and the macronutrient P. By contrast, Mn increased along the same gradient, whereas bark and soil pH decreased and thus followed the base cations. No significant correlation was noted between epiphytic vegetation and the elements N, Al, B, Cu, Fe, Mo, Na, S or Zn. The second NMDS-gradient related to stand and tree characteristics with increasing NMDS2-scores associated with increasing elevation and basal area and decreasing transplant tree size and percent open sky (Fig. 1).

Turning to the three community/canopy settings, the dripzone Lobarian, the non-dripzone Lobarian and the Parmelion were displayed along the first axis in that order (Fig. 1B), the first being characterized as base cation-rich, the second as a mix of base cations and Mn, and the

Fig. 1. Non-metric multidimensional scaling (NMDS) ordination plots of the epiphytic community composition on the branches of *Picea glauca* x *engelmannii*. (A) Species plot divided into cyano- and cephalolichens, green algal lichens and bryophytes. (B) Tree plot divided into three categories: dripzone Lobarian – those within dripzones of *Populus*; non-dripzone Lobarian – those with Lobarian not associated with *Populus* dripzones; Parmelion – those exclusively supporting acidophytic chlorolichens. The arrows show the direction of increasing environmental variables, their length being proportional to the correlation between the variable and the ordination (only significant \( P < 0.05 \) vectors are included). Species abbreviations appear in bold in Table 1.
third as Mn-rich. Along the NMDS2-gradient, the non-dripzone Lobaria tended to replace the Parmelion in more shaded stands at slightly higher elevations, although the dripzone Lobaria was distributed across the entire NMDS2-gradient (Fig. 1B).

Viewed at higher resolution, the lowest NMDS1-scores were achieved by the bryophytes and the chlorophylochrogena Phaeophycophyta, Physcia, and Physcomitrella, all characteristic of base-cation-rich, high pH dripzones. Along the first axis, they were followed by the cephalolichens together with the cyanolichens and the chlorophylochrogenus Ramalina (Fig. 1a), all with negative scores. With the exception of Ramalina obtusa, chlorophylochrenas with positive NMDS1-scores were Parmelioid lichens, characteristic of Mn-rich, low pH environments. They had no overlap with lichens characteristic of negative scores. Within the Parmelioid lichens, Bryoria (including Nodobryoria) and Tuckermannopsis stood out as having the highest NMDS1-scores (Fig. 1a). Lichen growth form changed along the NMDS2 axis representing a canopy openness gradient ($t = 7.45; P < 0.001; df = 51; t$-test). Fruticose genera (Alectoria, Bryoria, Ramalina, Usnea) had low NMDS2-scores (average $-0.61 \pm 0.10$) associated with open forest stands and larger trees, whereas foliose lichens had higher scores ($0.27 \pm 0.07$) characteristic of denser forest stands and smaller trees.

### 3.2. Ground vegetation

Altogether, 107 species of vascular plants occurred in the rooting zone (radius 3 m) of the transplant trees (Table 3). The mean number of plants around each tree was 15.8 (total range: 6–27 species), with no significant variation in number of species among the three community/canopy settings (Table 2).

In the plant ordination plot, the NMDS1-gradient was again associated with base cations in the canopy throughfall and with soil and bark pH, whereas the NMDS2-gradient mainly tracked canopy openness (Fig. 2). Factors that correlated significantly with the terrestrial vegetation were the throughfall elements Ca, Mg, K, Mn, Zn, S and C, as well as soil and bark pH, basal area, percent open sky and trunk diameter (Fig. 2). These gradients were rather similar to those of the epiphyte ordination (Fig. 1).

The plant ordination distinguished three groups (Fig. 2A), i.e., one group with negative scores indicative of elevated pH and cation-rich canopy throughfall, and two with positive NMDS1-scores associated with low-pH and cation-poor canopy throughfall. The first group consisted of species characteristic of rich mineral soils, e.g., Actaea rubra, Asarum caudatum, Athyrium felix-femina, Cornus sericea, Equisetum arvense, Gymnocarpium dryopteris s. lat., Hieracium alboferrum, Juniperus communis var. depressa, Kalmia polifolia, Lathyrus ochroleucus, Ledum groenlandicum, Lilium columbianum, Lysichiton americanus, Maleanthemum racemosum, M. stellatum, Melampyrum lineare, Menyanthes trifoliata, Menziesia ferruginea, Mitella nuda, Monotropa uniflora, Ophiopanax horridus, Orchis secunda, Osorhorhiza bertonii, Petales palustris s. lat., Picea glauca x engelmannii, Pinus contorta, Platanthera dilatata, P. orbiculata, Populus tremuloides, P. trichocarpa, Proseras hooker s. lat., Pseudotsuga menziesii, Pteridium aquilinum, Pyrola asarifolia, P. chlorantha, P. minor, Ribes lacustre, Rosa gymnocarpa, Rubus arcticus, R. idaeus, Salix alpina, Salix arctica, S. prostrata, S. scouleri, Salix sp., Sannica marilandica, Sorbus scopulina, Spigalum annuum, Strobilanthes ciliatus, Thalictrum occidentale, Thujopsis dolabrata, Thujopsis dolabrata, Thuya plicata, Tiarella trifoliata, Tragopogon pratensis, Vaccinium ovalifolium, V. ocellatus, Viburnum edule, Viola sp., Bold letters represent the code for the species abbreviations used in Fig. 2. Species without any bold letters were not printed on the ordination diagram (n ≤ 3).

### 3.3. Relationships between epiphyte and ground vegetation

The two ordinations – one epiphyte-based (Fig. 1), the other vascular plant-based (Fig. 2) – showed a marked correspondence with respect to the clustering of the three canopy settings (represented by colored symbols for the host trees) and to the relation of environmental factors to the two first axes. Consistent with this, there was a significant
A concordance between community composition among the epiphytes on the one hand and the terrestrial vegetation on the other ($\phi^2 = 0.616; r = 0.619; P < 0.001$). The procrustean association metrics revealed that this latter concordance was strongest in the non-dripzone Lobarion canopy setting, less strong in the Parmelion setting, and weakest in the dripzone Lobarion setting (Fig. 3). Thus, relatively low-pH environments (Parmelion and non-dripzone Lobarion) – those exclusively supporting acidophytic chlorolichens. The arrows show the direction of increasing environmental variables, their length being proportional to the correlation between the variable and the ordination (only significant $[P < 0.05]$ vectors are printed). Species abbreviations appear in bold in Table 3.

We note that ten of the non-Lobarion trees used in the transplant experiment grew on peaty fen soils. While the terrestrial vegetation around these trees deviated strongly from the vegetation associated with non-Lobarion trees elsewhere (Fig. 2B), the canopy epiphytes did not discriminate well between peat and mineral soils (Fig. 1B).
Fig. 3. Mean effect of different canopy settings on the Procrustean relationship between the epiphytic community composition and the ground vegetation. A higher value indicates a lower concordance between the two communities. Bars topped by different letters are significantly different (*P < 0.05); error bars refer to 1 standard error.

Table 4
Pearson correlations between different environmental factors and the Procrustean relationship between communities of epiphytes and ground layer vegetation. *: P < 0.01; **: P < 0.001.

| Parameter          | $r^2$ |
|--------------------|-------|
| Bark pH (+)        | 0.197*** |
| Basal area         | 0.007 |
| C                  | 0.017 |
| Ca (+)             | 0.129*** |
| Circumference      | 0.038 |
| Elevation          | 0.015 |
| K (+)              | 0.091**  |
| Mg (+)             | 0.139*** |
| Mn (-)             | 0.224*** |
| Open sky           | 0.006 |
| P                  | 0.015 |
| S                  | 0.337*** |
| Soil PH (+)        | 0.003 |

The Procrustean relationship between the two vegetation layers was best explained by variables related to soil pH, bark pH and elemental composition (Ca, Mg, K, Mn) of the canopy throughfall (Table 4). Meanwhile, the concordance between terrestrial vegetation and epiphyte community composition was not explained by variables related to stand structure or tree size (Table 4).

4. Discussion

4.1. Epiphytic vegetation and throughfall chemistry

A key finding of Gauslaa et al. (2020a) was that judicial use of standardized lichen transplants (collected from a single homogeneous donor site) can broadly capture variation in throughfall elemental concentration at the scale of the individual tree. Consistent with this, we infer that a substantial part of the variation in epiphytic vegetation along the NMDS1-axis (Fig. 1) reflects the differential availability of readily leachable elements like Mn and the base cations K, Ca and Mg in different forest settings (Gauslaa et al., 2020a) – an inference consistent with earlier studies that identified bark pH as having a major role in structuring epiphytic communities (Gauslaa 1985, 1995; Rose 1988; Gauslaa and Holien 1998; Hauck and Sprübill 2002, 2005; Hauck 2003). This is further concordant with the recent finding that elemental composition shapes the growth rate of a locally dominant lichen (Gauslaa and Goward 2020), and also with the known adverse effects of e.g., Mn on some lichens (Hauck et al., 2002; Hauck and Zoller 2003; Hauck and Paul 2005). Here it is worth mentioning that some lichen compounds, e.g., physisodal acid in the Parmelion lichen Hypogymnia physodes, can inhibit intracellular uptake of Mn$^{2+}$ and Cu$^{2+}$ (Hauck and Huneck 2007) and thereby contributing to metal homeostasis (Hauck et al., 2013).

Throughfall chemistry in forest canopies (Parker 1983) is controlled by many factors. While forest canopies trap airborne wet and dry deposition (Weathers et al., 2001; Adriaenssens et al., 2012; Fenn et al., 2013; Root et al., 2015), they can also modify atmospheric deposition (Gandois et al., 2014) e.g., through addition of leached K, Ca, Mg, and Mn (Tukey 1970) as well as by leaching acidic organic substances (Nihlgård 1971; Gauslaa and Holien 1998). It has also been shown that deciduous canopies can neutralize acidic inputs (Cronan and Reiners 1983; Neary and Gizyn 1994). These and other similar processes result in tree species-specific stemflow and throughfall chemistry (Neary and Gizyn 1994; Asplund et al., 2015). At the same time, lichens are known to absorb some elements more efficiently than others (e.g., Paoli et al., 2018), so that the elemental profiles of our lichen transplants are not necessarily equivalent with canopy throughfall per se. Nevertheless, Asplund et al. (2015) found that the acidophytic lichen Hypogymnia physodes transplanted on pairs of neighboring trunks of Fagus sylvatica and Picea abies accumulated more Ca, Mg, and K in Fagus dripzones and more Mn in Picea dripzones, consistent with the nutrient accumulation in L. pulmonaria in our dripzone versus “non-dripzone” sites. Consistent with this, we note that PCA-ordination of our transplant host trees based on elemental composition of the lichen transplants (Gauslaa et al., 2020a) resulted in a gradient similar to that of trees based on their epiphyte vegetation (Fig. 1B).

The question may be asked whether the occurrence of cyanobacterial and sometimes even nutrient-demanding chlorolichens in Populus dripzones may be caused by canopy setting-specific differences in humidity or light. This seems unlikely for two reasons: first, the presence of these lichens on Picea branches occurred primarily within the dripzones of Populus species (Goward and Arsenault 2000), not within dripzones of structurally similar Betula crowns; and second, the Populus dripzones studied by us were mainly restricted to solitary trees in a conifer forest matrix (Goward and Arsenault 2003).

4.2. Terrestrial vegetation and throughfall chemistry

In common with epiphytic communities in our study, throughfall elemental uptake in our lichen transplants aligned also with the ground vegetation (Fig. 2A). This finding is perhaps not surprising in a study area far removed from major sources of atmospheric pollution, where throughfall chemistry can be expected to broadly reflect the elements present in the rooting zones of trees, that is, allowing for tree species-specific selective mineral uptake and subsequent processes in the canopy (Nihlgård 1971; Cronan and Reiners 1983; Neary and Gizyn 1994; Beck and St. Clair, 2012). Thus, following the nutrient requirements given by Lausi and Nimis (1991) as well as in the plant indicator guide of Beaudry et al. (1999), the terrestrial vegetation associated with Picea within our Populus dripzones had a higher incidence of nutrient-demanding plants, whereas plants growing with Picea outside the Populus dripzone (hence often within the dripzones of conifers) had a higher incidence of less demanding plants.
Fig. 2. In both cases the canopy throughfall gradient spanned a continuum from base cation-rich (low scores) to base cation-poor (high scores). Notably, this elemental gradient corresponds to pH gradients observed both for *Picea* bark and for soils, both of which were mutually correlated across the three community/canopy settings (Gauslaa et al., 2020a). Not only does the similarity in these respective gradients point to a link between the two vegetation layers, it also suggests that soil chemistry is a primary driver of species composition in both layers, that is, operating on the terrestrial vegetation directly through root contact, and on the epiphytic vegetation indirectly, first through uptake by the roots of the host trees, and then by canopy throughfall (see Fig. 4 for a visual depiction of this hypothesis). In support of such a functional link, it is important to note that the transplants used in our assessment of throughfall chemistry were placed on nets without direct contact with tree bark.

We suggest that the significant concordance between the terrestrial and epiphytic vegetation in our study area can be explained by cycling of local elements from soils through trees to branch epiphytes (Fig. 4), with an ultimate return of elements to the soil when epiphytes detach and fall to the ground. Here it should be noted that this finding is somewhat at variance with an earlier study in the Swan Valley of Montana by McCune and Antos (1981), in which the herb and epiphyte layers did not align along ordination axes, leading these authors to conclude that these two vegetation layers are “uncoupled.” It is difficult to account for this discrepancy between the two studies, though it may be important to note that McCune and Antos reporting stand characteristics reached their conclusion in the absence of any direct measure of elemental composition or soil chemistry. In our study, we found that while throughfall chemistry (NMDS1-axis) was important, factors related to stand structure or tree size (NMDS2-axis; Figs. 1–2) did not explain the concordance between the two communities (Table 4), probably due to confounded openness-moisture factors that influence lichens and plants differently (see below).

The level of coupling between epiphyte and ground was strongest in the non-dripzone Lobarian setting and weakest in dripzone Lobarian setting (Fig. 3). The intermediate status of the Parmelian setting likely reflects our inclusion of 10 *Picea* trees growing in wet peaty soils of a fen – an anomaly in a study otherwise restricted to trees growing in mesic sites on well-drained mineral soils, yet consistent with our desire to capture a full range of the epiphytic vegetation on *Picea*. Clearly, the higher moisture content of the soils supporting the fen trees strongly impacted the ground vegetation without at the same time noticeably affecting the epiphytic vegetation, an inference consistent with McCune and Antos (1981) who likewise suggested that moisture levels controlling ground vegetation has little direct effect on epiphytic species composition. Similarly, it is worth noting that the effect of *Populus* in our dripzone Lobarian seems to be more pronounced on the epiphyte layer than on the terrestrial layer, perhaps in part explaining the somewhat weaker association between the two vegetation layers here than in our other community/canopy setting. Nonetheless, it is important to emphasize that even here our findings point clearly to a general alignment between canopy epiphytes and terrestrial vegetation on the one hand, and bark pH and soil pH on the other hand.

### 4.3. Links between epiphytic vegetation and plants in the ground layer

An important finding of this study is that the NMDS1-scores displayed environmental space in ways consistent with the elemental profiles of our lichen transplants, and that this is true regardless whether our ordination was based on epiphytic (Fig. 1) or terrestrial vegetation (Fig. 2). In both cases the canopy throughfall gradient spanned a continuum from base cation-rich (low scores) to base cation-poor (high scores). Notably, this elemental gradient corresponds to pH gradients observed both for *Picea* bark and for soils, both of which were mutually correlated across the three community/canopy settings (Gauslaa et al., 2020a). Not only does the similarity in these respective gradients point to a link between the two vegetation layers, it also suggests that soil chemistry is a primary driver of species composition in both layers, that is, operating on the terrestrial vegetation directly through root contact, and on the epiphytic vegetation indirectly, first through uptake by the roots of the host trees, and then by canopy throughfall (see Fig. 4 for a visual depiction of this hypothesis). In support of such a functional link, it is important to note that the transplants used in our assessment of throughfall chemistry were placed on nets without direct contact with tree bark.

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### 5. Conclusion

Our study area, the Clearwater Valley, is not only far removed from pollution sources and active agriculture, it is also subject to frequent pronounced hydration events from dewfall and other non-rain sources. In such a situation, it seems reasonable to expect that exogenous elemental deposition plays at most a minor role in shaping vegetation composition in forest ecosystems, while local soil chemistry plays the foundational role. This line of reasoning lends support to the main conclusions of this study: first, that vascular plants in the rooting zone of forest trees and epiphyte communities in the canopies of the same trees are strongly linked by canopy throughfall; and second, that differential uptake of Mn and base cations by different tree species shapes this link at the level of individual trees.

### References

Adriaenssens, S., Staelens, J., Wuyts, K., Samson, R., Verheyen, K., Boeckx, P., 2012. Retention of dissolved inorganic nitrogen by foliage and twigs of four temperate tree species. Ecosystems 15 (7), 1093–1107. https://doi.org/10.1007/s10021-012-9568-5.

Arsenault, A., Goward, T., 2016. Macrolichen diversity as an indicator of stand age and ecosystem resilience along a precipitation gradient in humid forests of inland British Columbia, Canada. Ecol. Indicat. 69, 730–738. https://doi.org/10.1016/j.ecolind.2016.04.015.

Asplund, J., Ohlson, M., Gauslaa, Y., 2015. Tree species shape the elemental composition in the lichen *Hypogymnia physodes* transplanted to pairs of spruce and beech trunks. Fungal Ecol. 16, 1–8. https://doi.org/10.1016/j.funeco.2015.03.006.

Asplund, J., Wardle, D.A., 2017. How lichens impact on terrestrial community and ecosystem properties. Biol. Rev. 92 (3), 1720–1738. https://doi.org/10.1111/brv.12305.

Attwill, P.M., Adams, M.A., 1993. Tansley review No. 50 nutrient cycling in forests. New Phytol. 124, 561–582.

Bargagli, R., 2016. Moss and lichen biomonitoring of atmospheric mercury: a review. Sci. Total Environ. 572, 216–231. https://doi.org/10.1016/j.scitotenv.2016.07.202.

Beaudry, L., Coupé, R., Delong, C., Pojar, J., 1999. Plant indicator guide for northern British Columbia: boreal, sub-boreal, and subalpine biogeoclimatic zones (BWBS,
Phinney, N.H., Gauslaa, Y., Palmqvist, K., Esseen, P.-A., 2021. Macroclimate drives growth of hair lichens in boreal forest canopies. J. Ecol. 109, 478–490. https://doi.org/10.1111/1365-2745.13532.

Porada, F., Van Stan, J.T., Kleidon, A., 2018. Significant contribution of non-vascular vegetation to global rainfall interception. Nat. Geosci. 11 (8), 563–567. https://doi.org/10.1038/s41561-018-0176-7.

Pypker, T.G., Unsworth, M.H., Van Stan, J.T., Bond, B.J., 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 (3). https://doi.org/10.1002/eco.1801.

Richardson, D.H.S., Cameron, R.P., 2004. Cyanolichens: their response to pollution and possible management strategies for their conservation in northeastern North America. Northeast. Nat. 11 (1), 1–22.

Root, H.T., Geiser, L.H., Jovan, S., Neitlich, P., 2015. Epiphytic macrolichen indication of air quality and climate in interior forested mountains of the Pacific Northwest, USA. Ecol. Indicat. 53, 95–105. https://doi.org/10.1016/j.ecolind.2015.01.029.

Rose, F., 1988. Phytogeographical and ecological aspects of Lobarion communities in Europe. Bot. J. Lim. Soc. 96, 69–79.

Tukey, H.B., 1970. Leaching of substances from plants. Annu. Rev. Plant Physiol. 21, 305–324. https://doi.org/10.1146/annurev.pp.21.060170.001513.

Van Stan II, J.T., Pypker, T.G., 2015. A review and evaluation of forest canopy epiphyte roles in the partitioning and chemical alteration of precipitation. Sci. Total Environ. 536, 813–824. https://doi.org/10.1016/j.scitotenv.2015.07.134.

Weathers, K.C., Cadenasso, M.L., Pickett, S.T.A., 2001. Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. Conserv. Biol. 15 (6), 1506–1514.

Yemets, O.A., Solhaug, K.A., Gauslaa, Y., 2014. Spatial distribution of airborne pollutants and their effects on growth and viability of lichen transplants along a rural highway in Norway. Lichenologist 46 (6), 809–823.