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Structural heterogeneity of trees influences epiphyte distributions in a northern temperate rainforest

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Abstract

Questions: Large trees provide structural heterogeneity that may influence the distribution and diversity of epiphytes, yet this has not been fully examined in northern temperate rainforest trees. How does epiphyte diversity, percent cover and composition vary among trunk and branch zones within northern temperate rainforest trees? Are there steep gradients in environmental conditions or resources within northern temperate rainforest trees? To what degree do species show specialization to particular zones within northern temperate rainforest trees?

Location: Temperate rainforest on the Olympic Peninsula in Washington State, USA.

Methods: We recorded epiphyte richness, percent cover, and composition in 78 plots from six tree zones (three trunk zones and three branch zones) in six large bigleaf maple (*Acer macrophyllum*) trees. At each survey point, we measured temperature, relative humidity, canopy cover, moss depth, height in tree, and branch diameter to examine the degree of habitat specialization along measured environmental and resource gradients and the importance of structural heterogeneity for epiphyte species diversity in entire trees.

Results: Rarefied epiphyte richness was 25% higher on the trunk than in the branches, and there was little overlap in species composition between trunk and branch zones. Species composition changed with height as well as decreasing canopy cover along the trunk. Within the branches, epiphyte composition was related to branch diameter and moss depth; while the inner and mid-branch zone communities were similar, the outer branch community differed. Microclimate variables did not vary significantly among tree zones and were not related to epiphyte distributions.

Conclusions: The structural heterogeneity of large *A. macrophyllum* trees created gradients in canopy cover and substrate characteristics that enabled up to 13 different epiphyte species to coexist. Thus, these trees are critical structures for the maintenance of forest diversity.

KEYWORDS

Acer macrophyllum, bryophytes, microclimate, microhabitat heterogeneity, niche differentiation, Olympic peninsula, structural diversity, temperate rainforest

1 | INTRODUCTION

A central goal in ecology is to understand the factors that establish and maintain patterns of biodiversity. Positive correlations between habitat heterogeneity and species diversity have been found in many habitats from terrestrial mammals (Tews et al., 2004) to tropical plants (DeWalt, Ickes, Nilus, Harms, & Burslem, 2006; Woods, Cardelús, & Dewalt, 2015). Theory suggests that habitats that are structurally complex with a diversity of resources provide more niches for species with specific habitat and resource requirements to partition the habitat and coexist (Hutchinson, 1959; Tews et al., 2004). Thus, habitats that are structurally complex should theoretically have a higher proportion of species that are specialized to particular niches than homogeneous habitats.

One habitat that is structurally complex is the rainforest canopy. In both temperate and tropical rainforests, steep environmental and resource gradients exist both vertically (from the base of the trunk to the crown) and horizontally within trees (Hofstede, Dickinson, & Mark, 2002; Johansson, 1974; Kenkel & Bradfield, 1986; Woods et al., 2015), and the epiphytic plants within their crowns exhibit remarkable levels of diversity with distinct colonization patterns. These steep gradients in light, relative humidity, temperature, and the availability of humus substrate (Hofstede et al, 2002; Johansson, 1974; Woods et al., 2015) create particular microhabitats within which different epiphyte species specialize. While research on colonization patterns of epiphytes in tropical rainforests has a long and rich history (e.g., Schimper, 1888), epiphytes in temperate rainforests have received less attention despite being an important and integral component of these forests (Hofstede et al, 2002; Nadkarni, 1981).

Temperate rainforests are found near coastal regions in both the northern and southern hemisphere (Alaback, 1991; Zotz, 2005); non-vascular epiphytes are abundant in most temperate rainforests but vascular epiphytes are more abundant and species rich in the temperate rainforests of the southern hemisphere. For example, vascular epiphytes can represent up to 20% of the regional floral diversity in temperate rainforests in the Maungataniwha Ranges in New Zealand (Dawson & Sneddon, 1969) and up to 10% in Valdivian temperate rainforests in Chile (Arroyo, Cavieres, Peñaloza, Riveros, & Faggi, 1996). On the contrary, vascular epiphytes in northern temperate rainforests are quite rare with only three predominantly epiphytic species found (Sillett, 1999). In northern temperate rainforests on the Olympic Peninsula in Washington State, large broad-leaved trees such as *Acer macrophyllum* (Aceraceae; bigleaf maple) support many non-vascular epiphytes including mosses, liverworts, and lichens, whose biomass can be four times that of the foliage of their host trees (Nadkarni, 1984). These epiphytes contribute to forest biodiversity, provide habitat and even food for a diversity of organisms (Nadkarni Nalini & Longino, 1990; Peck & Moldenke, 2011), provide a nutrient source for their host trees, and buffer their host trees from nutrient pulses (Nadkarni, 1984, 1986). In fact, *A. macrophyllum* trees even grow aerial canopy roots to directly absorb water and nutrients from the moss mats they host (Nadkarni, 1981). The majority of epiphyte research in these northern temperate rainforests has been through an ecosystem ecology lens focused on examining the contribution of epiphytes to total foliar biomass and nutrient pools (Nadkarni, 1984, 1986), and the few studies that have examined epiphyte distribution patterns within trees have found species turnover with distance along the trunk or height in tree as indirect measures of water and light availability (Kenkel & Bradfield, 1986; McCune, 1993). However, these studies were either restricted to a small area on the trunk (up to 5 m, Kenkel & Bradfield, 1986) or were restricted to felled trees (McCune, 1993). No study has yet surveyed epiphyte communities within entire, live trees in Pacific Northwest rainforests; thus little is known about what factors directly influence patterns of diversity in these epiphyte communities.

In southern temperate rainforests in New Zealand, tree structural variables including height and the abundance of varying branch sizes influenced the distribution of non-vascular epiphytes (Hofstede et al, 2002); branch epiphyte communities were dominated by pendent moss species and differed from trunk epiphyte communities. Height in tree also influenced species composition of epiphytic bryophytes in a montane *Nothofagus* forest in the Chilean Andes with particular species restricted to the branches and trunk (Mellado-Mansilla et al., 2017). Gradients in moisture availability and radiation intensity influenced the distribution of non-vascular epiphytes in temperate tree crowns in Japan (Hosokawa, Odani, & Tagawa, 1964); moss species that were more resistant to desiccation were found higher in tree crowns. The distribution of non-vascular epiphyte communities in northern temperate rainforest trees could be driven by tree structural variables, such as height, or variations in light and moisture availability.

Here we examined the influence of habitat heterogeneity on epiphyte communities in northern temperate rainforests by (a) documenting spatial patterns of epiphyte species within northern temperate rainforest trees; (b) measuring environmental and resource gradients within these host trees; and (c) examining the relationship between rarefied epiphyte richness, percent cover and composition with environmental gradients. Specifically, we asked the following questions: (a) how does epiphyte richness, percent cover and composition vary among trunk and branch zones within temperate rainforest trees; (b) are there steep gradients in environmental conditions, such as temperature, relative humidity and light or structural features within temperate rainforest trees; and (c) to what degree do species show specialization to particular zones within temperate rainforest trees? We hypothesized that habitat heterogeneity is high within temperate rainforest trees, which should influence patterns in epiphyte richness, percent cover and composition. We predicted that height of tree, light, and relative humidity would influence epiphyte distributions given that these factors influenced non-vascular epiphyte distributions in other temperate rainforests (Hosokawa et al., 1964; Mellado-Mansilla et al., 2017). We also predicted that species composition would differ between the trunk and the branches as was found in southern temperate rainforest trees (Hofstede et al, 2002; Mellado-Mansilla et al., 2017).

2 | METHODS

Our study was conducted in temperate rainforest located along the Hoh river on the Olympic peninsula of Washington State, USA (47°49′29″ N, 124°11′57″ W). The climate is mild with an average annual temperature of 10°C and annual rainfall of 3,200 mm (Harmon & Franklin, 1989). These forests are characterized by large and tall trees (>80 m) that are dominated by *Picea* and *Tsuga*, an abundance of nurse logs and bryophytes (Harmon & Franklin, 1989). *Acer macrophyllum* is a deciduous tree that occurs in groves of large trees in *Picea–Tsuga* forests, often in riparian areas where they dominate. There were approximately 20 maple trees in our grove that reached heights between 18 and 20 m, and had a minimum, mean, and maximum diameter at breast height (dbh) of 97.9 cm, 103.4 ± 2.3 (*SE*), and 113.4 cm, respectively. Many of these trees were leaning or had split trunks near the base of the tree. Understory plants were dominated by *Acer circinatum*, *Polystichum munitum*, and Ericaceous shrubs (e.g., *Vaccinium* spp.).

To examine how epiphyte communities varied among trunk and branch zones within temperate rainforest trees, the epiphyte communities in six large (>95 cm dbh) *A. macrophyllum* trees in the Hoh rainforest on the Olympic Peninsula in Washington State were systematically surveyed in six tree zones in the summer of 2016 and 2017 (modified from Johansson, 1974; Woods et al., 2015). These zones included the basal part of the trunk (LowerTrunk; 0–3 m from the ground), the rest of the trunk until the first branch (MidTrunk), the trunk above the first branch (UpperTrunk), the inner branch (Inner; 0–2 m along the branch from the trunk), the mid-branch (Mid; 2–5 m along the branch) and the outer branch (Outer; >5 m along the branch; Figure 1). The first 3–4 branches were chosen for our surveys as the branches above this were logistically impossible to reach and properly survey, particularly given that the small size of most of the epiphytes required close proximity for proper identification. Branches in the outer crown (Outer) were very difficult to access using our climbing techniques, so we often surveyed small branches in the inner and mid-crown, and small branches that were accidentally broken off the tree while setting lines. This tree species was chosen because it carries the largest biomass of epiphytes in the Hoh rainforest (Nadkarni, 1984; C. Woods, personal observation). We avoided trees that were leaning or had split trunks because they were unsafe to climb and this would minimize variation in microhabitats among trees; as a result, we were able to only survey six trees. Tree crowns were accessed by modified rope-climbing techniques (Perry, 1978). In each zone within each tree, epiphytes were surveyed with the point intercept method using a 22 cm × 28 cm acetate sheet with 100 randomly placed dots (Bonham, 2013). Thick branches were only surveyed on the top surface, and the sheet was wrapped around smaller branches to survey all surfaces. Under each dot, we noted the epiphyte species, bare bark or detritus (woody debris, leaves, cones, etc.). For small branches, the sheet wrapped around the branch and had some left over space in which it was not covering the branch. In these cases, we calculated percent cover from the dots that had something under them (i.e., not air). This survey plot size was chosen given the small size of the epiphytes within these trees and the use of a similar-sized sampling unit in previous temperate rainforest epiphyte research on *A. macrophyllum* (Kenkel & Bradfield, 1986). Each trunk zone was surveyed at least once per tree, except for the upper trunk, which was not surveyed in one tree, and each branch zone was surveyed at least three times per tree, except for the outer branch, which was surveyed only once in one of the trees. In total, each zone was surveyed with the following replicates: LowerTrunk: *n* = 11, MidTrunk: *n* = 12, UpperTrunk: *n* = 9, Inner: *n* = 19, Mid: *n* = 19, Outer: *n* = 14.

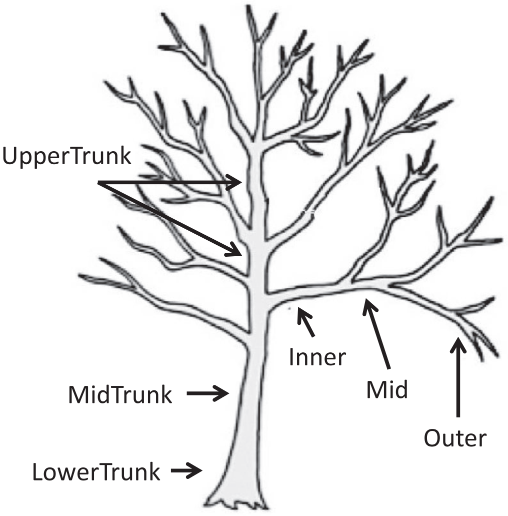
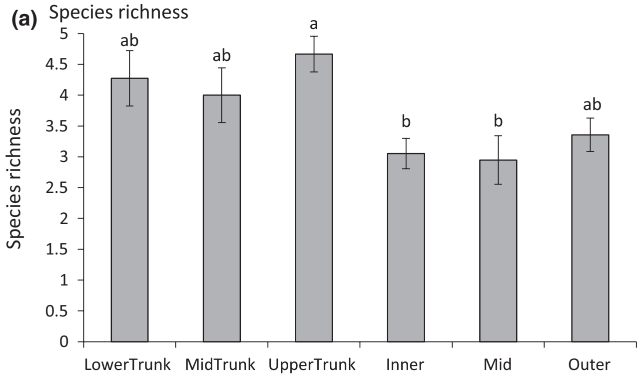


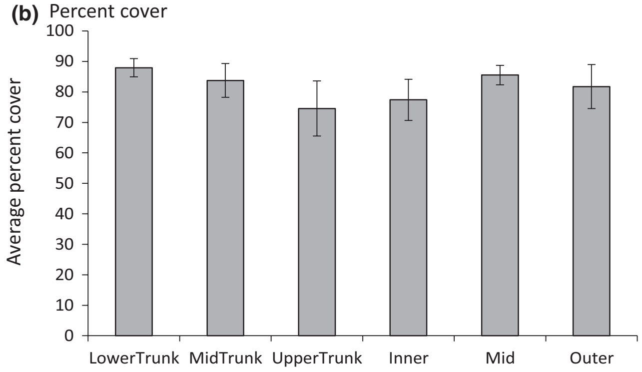
FIGURE 1 Diagram of the three trunk and three crown zones used for surveying epiphytes in six *Acer macrophyllum* trees in temperate rainforests of the Hoh river watershed, Olympic peninsula, Washington, USA

The height of each plot in each zone was measured using a clinometer (Suunto, Finland), and percentage of canopy cover at each sampling site (i.e., above each acetate sheet) was measured using a handheld densiometer (Forestry Suppliers Inc., Jackson, MS). The diameter of the substrate was measured at each sampling site in the branch zones. Measuring canopy humus cover alone was impossible as canopy humus was buried under thick epiphyte mats on large branches and patchily distributed under epiphytes on trunks. Thus, in lieu of a direct measure of canopy humus, we measured the depth of the epiphyte mats from the top of the plants to the branch using calipers with the assumption that canopy humus cover was proportional to the depth of the epiphyte mats (hereafter referred to as moss depth).

To register microclimate variables on epiphyte communities, LogTag dataloggers (MicroDAQ) were suspended in the first two trunk zones and all three branch zones of three *A. macrophyllum*



(a) Species richness



(b) Percent cover

FIGURE 2 Average (±*SE*) rarefied species richness of epiphyte species (a) and percent cover of the epiphyte community (b) among trunk and crown zones of six *Acer macrophyllum* trees in temperate rainforests of the Hoh river watershed, Olympic peninsula, Washington, USA. Zones follow Figure 1. Rarefied species richness varied significantly among crown zones ($p = 0.02$) but percent cover of epiphytes did not significantly vary among crown zones ($p = 0.21$). In (a), bars with different letters are significantly different according to least square means contrasts ($p < 0.05$)

during the summer of 2016, and recorded temperature (T) and relative humidity (RH) approximately every hour for an entire year. The UpperTrunk zone was not considered. All values were adjusted for individual datalogger variation using data collected under standard conditions in the lab. The dataloggers were hung from small ropes above each zone with plastic coverings over them to protect them from precipitation and sunlight. For each datalogger we calculated the daily maximum, daily minimum, and daily average for temperature, relative humidity, and vapor pressure deficit, which we calculated from temperature and relative humidity data.

2.1 | Statistical analysis

Due to uneven sampling efforts across our zones we calculated the rarefied species richness using the rarefy function in the vegan package in R (Oksanen et al., 2010). To examine differences in rarefied epiphyte species richness and percent cover among tree zones we used a linear model followed by least-square means contrasts for all tree zones. We also tested differences in rarefied species richness and percent cover between all trunk and all branch zones using a Welch's two-sample t test due to the uneven sample size across zones. We used analysis of variance (ANOVA) followed by Tukey's HSD tests to determine whether environmental conditions and resources (temperature, relative humidity, canopy cover, moss depth, height) differed among tree zones.

To examine turnover in epiphyte species composition among tree zones and along environmental and resource gradients, we calculated the dissimilarity among our zones using the Jaccard index and the turnover component of that dissimilarity. We created a dissimilarity matrix of species turnover using the beta.pair function in the betapart package in R (Baselga & Orme, 2012) and used this matrix to run a non-metric multi-dimensional scaling (NMDS) ordination, an indirect gradient analysis approach. We used the metaMDS function in the vegan package in R to run our NMDS (Oksanen et al., 2010). A Monte Carlo test was performed with 1,000 iterations in order to determine to what degree the NMDS ordination differed from random; the stress level of the Monte Carlo test had to be greater than the stress level of the NMDS analysis to be considered different from random (McCune, & Grace, 2002). We fit the measured environmental conditions and resources (canopy cover, moss depth, branch diameter, and height) to the NMDS ordination with the envfit function in the vegan package in R (Oksanen et al., 2010). R version 3.0.1 was used for all statistical analyses (R Development Core Team, 2009).

3 | RESULTS

In the summers of 2016 and 2017, we conducted a total of 78 surveys of epiphyte communities in six *A. macrophyllum* trees in the Hoh river watershed in the Olympic National Forest. We observed 27 epiphyte species during our survey and were able to identify 21 to genus or species. Within these 27 species, we found 21 mosses, 3 liverworts, 1 lichen, 1 lycophyte and 1 fern (Appendix S1). We observed a maximum of 13 and a minimum of 10 epiphyte species in a single tree. Grouping observations from all six trees by zone, there was a maximum of 15 species in the inner branch zone and a minimum of 8 species in the upper trunk zone. Overall, we observed a total number of occurrences of 6,674 for all species (Appendix S1).

There were significant differences in rarefied species richness among tree zones ($F_{5,78} = 2.8$, $p = 0.02$, Figure 2a). The upper trunk had significantly higher rarefied species richness than the mid-branch zone (Figure 2a); there were no other significant differences in rarefied species richness among tree zones (Figure 2a). The average rarefied species richness in the trunk zones (2.9 ± 0.2 *SE*) was 25% higher than in the branch zones (2.3 ± 0.1; Welch's t test, $t = -3.2$, $df = 66.9$, $p = 0.002$). There was no significant variation in percent cover of epiphytes among zones ($F_{5,78} = 0.8$, $p = 0.5$, Figure 2b). This was not surprising given that *A. macrophyllum* trees were almost completely covered in epiphytes (Appendix S2).

Canopy cover varied significantly among tree zones with the highest values being in the lower trunk zone and generally decreasing with increasing height ($F_{5,27} = 4.7$, $p = 0.003$, Table 1). Moss

TABLE 1 Average (±*SE*) percent canopy cover, moss depth, and height among all six tree zones and branch diameter among the three branch zones in six *Acer macrophyllum* trees in a lowland temperate rainforest along the Hoh river watershed, Olympic peninsula, Washington, USA

Zone	Canopy cover	Moss depth	Height	Branch diameter
LowerTrunk	97.8 ± 0.8^{a}	3.2 ± 0.8^{c}	1.7 ± 0.1^{c}	
MidTrunk	96.8 ± 0.8^{ab}	4.8 ± 1.6^{bc}	8.2 ± 0.1^{b}	
UpperTrunk	95.9 ± 1.1^{abc}	13.1 ± 1.3^{ab}	15.5 ± 3.4^{a}	
Inner	93.9 ± 0.8^{bc}	16.2 ± 2.8^{a}	15.1 ± 1.0^{a}	35.4 ± 4.3^{a}
Mid	93.4 ± 0.4^{c}	1.7 ± 0.5^{c}	15.2 ± 0.8^{a}	34.3 ± 2.8^{a}
Outer	95.5 ± 0.5^{abc}	6.5 ± 2.7^{bc}	14.8 ± 2.5^{ab}	3.6 ± 0.9^{b}
$F_{5,27}$	4.7^{*}	11.0^{**}	16.7^{**}	35.5^{**}

Averages with different letters denote significant differences according to Tukey HSD tests.

* $p < 0.01$.

** $p < 0.001$.

depth varied significantly among tree zones with the inner and mid-branches having a moss depth that was 266% higher than all other zones ($F_{5,27} = 10.9$, $p < 0.001$, Table 1). Height varied significantly among zones ($F_{5,20} = 16.7$, $p < 0.001$, Table 1). Not surprisingly, the branches in the inner and mid-branch zones had a similar diameter that was significantly higher than that of the small branches in the outer crown ($F_{2,15} = 35.5$, $p < 0.001$, Table 1, Appendix S3).

Epiphyte species composition differed among tree zones (Figure 3). There was a clear pattern in species turnover from the lower trunk up the tree and then into the branches, such that very few species found on the trunk were found on the branches and vice versa (Figures 3, 4). This was supported by the high degree of beta diversity (Jaccard dissimilarity = 0.96) and the large degree to which turnover was a part of that dissimilarity (turnover fraction of Jaccard dissimilarity = 0.93). There was overlap in species composition among the trunk zones and almost complete overlap in species composition among the inner and mid-branch zones (Figure 3). Trunk zones were dominated by *Metaneckera menziesii* and *Leucolepis acanthoneura*, and the inner and mid-branch zones were dominated by *Rhytidiadelphus loreus* and *Selaginella oregana* (Figure 4). The outer branch zone had a unique species composition, which was made up mostly of *Neckera douglasii* and *Isothecium myosuroides* (Figures 3, 4). The NMDS ordination resulted in a stress of 0.17, which was lower than the randomly generated Monte Carlo stress of 0.22 indicating that the NMDS ordination was different from random. Moss depth ($p = 0.04$) and branch diameter ($p = 0.004$) significantly influenced turnover in epiphyte species, and they were highest in the inner and mid-branch zones. Percent canopy cover (CC) was highest in the lowest trunk zone but this was not significant ($p = 0.25$). Height did not significantly influence turnover in epiphyte species composition ($p = 0.85$). None of the microclimate variables from the dataloggers (temperature, relative humidity and vapor pressure deficit) varied significantly among tree zones (Appendix S4) nor did they explain turnover in species composition.

4 | DISCUSSION

We found that epiphyte species richness and composition varied among tree zones. Trunk zones hosted a unique flora that was 25% more species rich than the branch zones, and there was a high degree of turnover in species composition along the trunk. There was a high degree of similarity in epiphyte composition among the inner and mid-branch zones but low similarity to the epiphyte community in the outer crown — patterns that were driven by branch diameter and moss depth. Percent cover of epiphytes did not significantly vary among tree zones, which was anticipated given that these large *A. macrophyllum* trees are covered almost completely in epiphytes (Appendix S2). The structural heterogeneity of the different zones (branch diameter, height in tree, and moss depth) played a larger role in structuring epiphyte communities than did microclimate factors, such as relative humidity or vapor pressure deficit. Thus, our results are similar to epiphyte studies in other temperate rainforests where epiphyte species composition differs between trunk and branch zones (Hofstede et al, 2002; Mellado-Mansilla et al., 2017); however, we did not find that microclimate factors (canopy cover, relative humidity, temperature, and vapor pressure deficit) influenced epiphyte distributions, which is contrary to other temperate rainforest research (Hosokawa et al., 1964; Kenkel & Bradfield, 1986; McCune, 1993). Alternatively, microclimatic variations in northern temperate rainforest trees in our study could be at a finer scale than what we measured.

We found support for our hypothesis that epiphyte species composition was non-random within trees. There was a clear turnover in species composition along the trunk with increasing height in the tree. The unique composition of epiphytic species in the lower trunk is consistent with another study that examined epiphyte distributions up to 5 m on *A. macrophyllum* trees at varying sites in British Columbia and found turnover in species composition with height (Kenkel & Bradfield, 1986). Height was also found to influence epiphyte communities in other temperate forests (Bates, 1992; Coxson & Coyle, 2003; Hofstede et al, 2002; Lyons, Nadkarni, & North, 2000; Mellado-Mansilla et al., 2017; Oksanen, 1988). Canopy cover was significantly higher in the lower trunk zones than in all other tree zones and declined with increasing tree height, which was also found in beech trees in Japan (Omura, Nishihara, & Hosokawa, 1955), and in an old-growth Douglas fir and Western Hemlock Forest in Southern Washington State (Parker, 1997). This suggests that the species that dominated in the lower trunk zones (*Leucolepis*

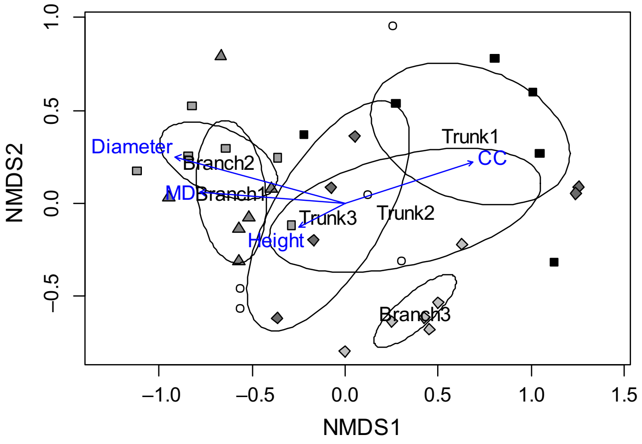


FIGURE 3 Non-metric multi-dimensional scaling (NMDS) ordination of epiphyte community composition among tree zones in the canopies of six large *Acer macrophyllum* trees in a lowland temperate rainforest along the Hoh river watershed, Olympic peninsula, Washington, USA. We used a Bray--Curtis distance matrix for all zones (two-dimensional stress = 0.17, and Monte Carlo stress with 1,000 iterations = 0.22). The ellipses show the covariance matrix centered on the mean of each zone, which are described in Figure 1. Only epiphyte species found more than once were included in the analysis. Moss depth (MD) explained a significant amount of variation in epiphyte species composition ($p = 0.004$) as well as branch diameter ($p = 0.002$), while canopy cover (CC) ($p = 0.06$) and height in tree ($p = 0.07$) were marginally significant

acanthoneura and *Metaneckera menziesii*) are likely shade tolerant, while those that dominated in the outer branch zones may have higher temperature or light tolerances (Mellado-Mansilla et al., 2017; Turetsky, 2003). Kenkel and Bradfield (1986) argued that light and the availability of water influences epiphyte distributions in *A. macrophyllum* as varying heights and inclinations of the trunk can influence moisture and light availability. While many species were found in varying degrees among the zones, we found two species, *Porella navicularis* and *Antitrichia curtipendula*, that appeared to be generalist species as they were found more evenly distributed among all tree zones (Figure 4). *Porella navicularis* and *Antitrichia curtipendula* were found as epiphytes in the shaded understory of *Pseudotsuga menziesii* forests in Oregon, which extended from 5 to 20 m (Pike, Denison, Tracy, Sherwood, & Rhoades, 1975). The wide distribution of *Porella navicularis* and *Antitrichia.curtipendula* in *A. macrophyllum* trees may, therefore, be due to the fact that *A. macrophyllum* trees may be predominantly within the understory of northern temperate forests. Controlled studies examining the performance of epiphyte species under varying light and moisture levels could determine the importance of these variables in influencing their distributions.

There were clear trends within the branch zones that showed turnover in species composition from the inner to the outer crown, which were driven by changes in branch diameter and moss depth, suggesting that canopy humus influences epiphyte distributions. These results are supported by those in tropical rainforests that show epiphyte distributions are influenced by branch diameter and the presence of canopy humus (Freiberg, 1996; Hietz & Hietz-Seifert, 1995; ter Steege & Cornelissen, 1989; Woods et al., 2015) as well as in other temperate rainforests that showed that epiphyte distributions are influenced by the presence of canopy humus or "duff" (Hofstede et al, 2002; Mellado-Mansilla et al., 2017) and location on branches (Pike et al., 1975). This suggests that species in the inner and mid-branch zones, such as the moss *Rhytidiadelphus loreus* and the lycophyte *Selaginella oregana*, establish on large surface areas, and either *require* thick moss mats because of the underlying canopy humus, which can provide nutrients or water (Aubrey, Nadkarni, & Broderick, 2013; Freiberg, 1996; Woods et al., 2015), or *create* the thick moss mats themselves by their growth patterns. *Rhytidiadelphus loreus* creates large mats on top of the branches and *Selaginella oregana* hangs below the branches (Appendix S3), so it could be a combination of the three-dimensional structure of the branches along with variations in substrate requirements of these two species that explains their specialization to these branch zones; *Rhytidiadelphus loreus* might require more light or atmospherically deposited nutrients than *Selaginella oregana*, which might require less light and depend more on canopy humus to root in and gain nutrients from. *Selaginella oregana* was also found in the lower trunk zones (LowerTrunk and MidTrunk), which supports its tolerance to low light (Figure 4). The outer crown, which has neither a thick moss mat nor any canopy humus, was dominated by two species, *Neckera douglasii* and *Isothecium myosuroides*. These species dominate thin, bare branches not only in the large *A. macrophyllum* trees in our study but also on the vine maple (*Acer circinatum*) (Peck & Moldenke, 2011) and other trees in the understory (Pike et al., 1975) of Pacific Northwest forests. These results are supported by other studies that found some epiphyte species specialized to bare bark (Benzing, Seeman, & Renfrow, 1978; Hofstede et al, 2002; Woods et al., 2015). The specialization of these two moss species to small branches is likely due to the way they grow, beginning predominantly flat on the branch and then growing pendulous as they hang from the branches. Their absence in the inner and mid-branch zones could be due to their inability to grow above the large mats created by *Rhytidiadelphus loreus* and *Selaginella oregana*, or because they require small branches for their pendulous growth.

Structural features, such as branch size, height in tree, and branch diameter, were found to be more important in explaining the distribution of moss species in temperate rainforest trees than microclimate variables. This was surprising given the strong influence of microclimate on vascular epiphyte distributions in tropical forests (Reyes-García, Mejia-Chang, & Griffiths, 2012; Woods et al., 2015), and the hypothesized importance of moisture availability for non-vascular epiphyte distributions in a previous study (Kenkel & Bradfield, 1986). It could be that microclimate varies at a much finer scale than was measured in our study. For instance, Kenkel and Bradfield (1986) examined epiphyte distributions at approximately 1 m increments along the trunk and found compositional differences with height. In our study, the first 5 m of the trunk were grouped into one tree zone. Thus, a more fine-scale survey of epiphytes within *A. macrophyllum* trees along with a finer-scale measure of

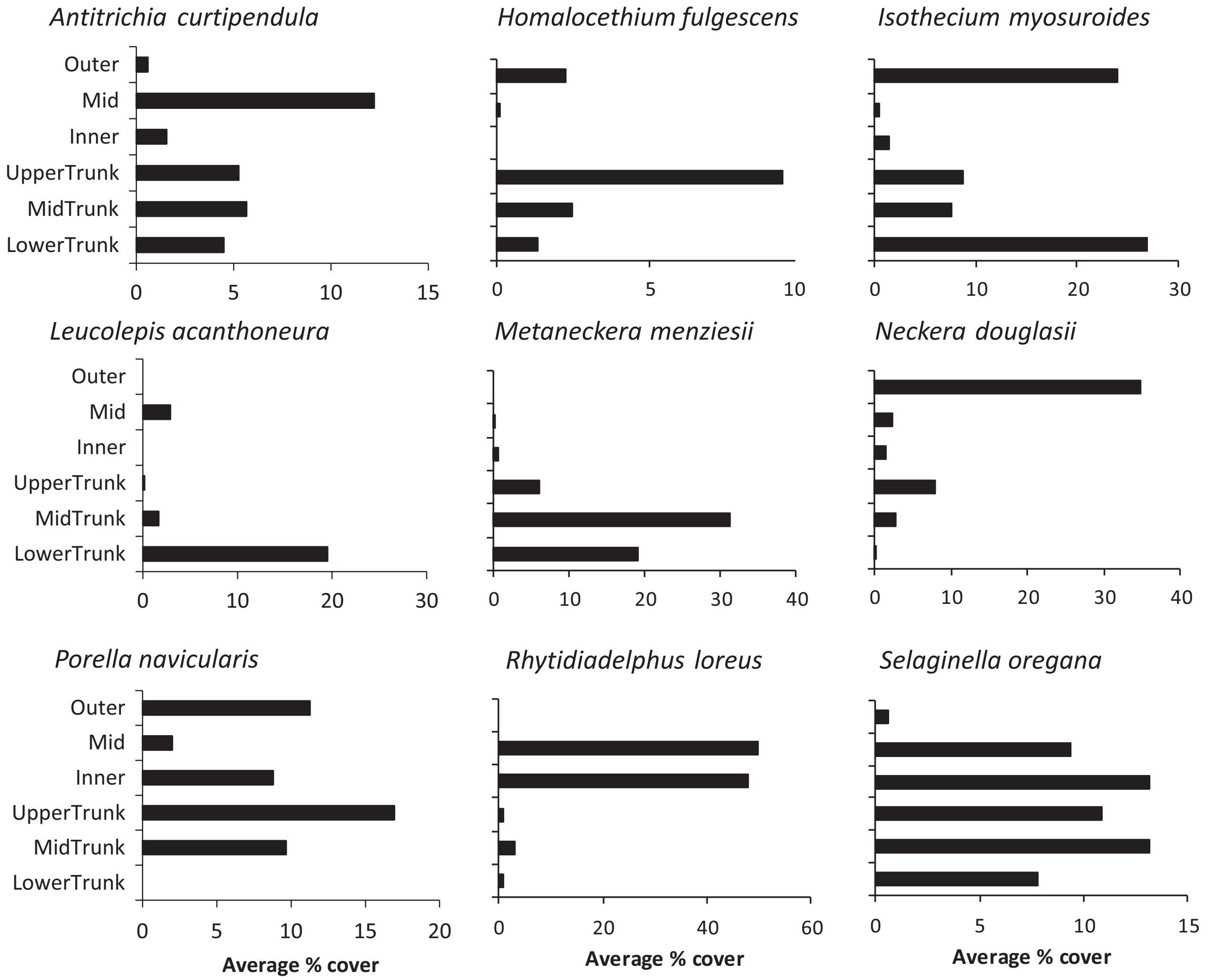


FIGURE 4 Average % cover of the nine most abundant and widespread epiphytes in six tree zones (Figure 1) in six *Acer macrophyllum* trees in a lowland temperate rainforest along the Hoh river watershed, Olympic peninsula, Washington, USA

microclimate and structure may uncover even more variations in epiphyte species composition and habitat selection than was seen in our study. It could also be that the variation in microclimate among zones within these trees is low given that *A. macrophyllum* is almost completely in the understory of these northern temperate rainforests (Pike et al., 1975). Alternatively, the adapted high dessication tolerance that is characteristic of many non-vascular epiphyte species could negate the effects of temperature and moisture in determining species distributions (Proctor, 2000; Turetsky, 2003).

Ours is the first study to document the distribution of epiphytes within entire *A. macrophyllum* trees in northern temperate rainforests, and relate them to structural and microclimatic features. We found that a single tree can host up to 13 different epiphyte species, many of which were dominant in particular areas within the trees. Variations in structural features, more than microclimatic features, influenced the distribution of epiphytes, which adds to the growing body of literature on the importance of habitat heterogeneity for epiphyte species diversity and distribution (Hofstede et al, 2002; Mellado-Mansilla et al., 2017; Pike et al., 1975; Woods et al., 2015). In northern temperate rainforests, large bigleaf maple trees house the greatest biomass of epiphytes of all tree species in the forest, a biomass that can be four times that of their host tree (Nadkarni, 1984). These trees also host some unique epiphyte species found on no other tree. For example, the two species that dominated the inner branches in our study, *Rhytidiadelphus loreus* and *Selaginella oregana*, were not found in the understory or on *Pseudotsuga menziesii* trees in northwest forests in Oregon (Pike et al., 1975) nor on the trunks of *A. macrophyllum* trees in coastal forests in southern British Columbia (Kenkel & Bradfield, 1986). The distinctive epiphyte loads found on *A. macrophyllum* in northern temperate rainforests are indicative of the value of the trees, as they could be host to epiphyte assemblages and relationships that are found nowhere else in these rainforests. Studies such as these are necessary to contribute to our understanding of the factors driving the distribution of non-vascular epiphytes, and the importance of particular tree species to supporting diversity in temperate rainforests.

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AUTHOR CONTRIBUTIONS

CLW conceived of the research idea; CLW, LMN and ED collected data; CLW performed statistical analyses; CLW, with contributions from LMN and ED, wrote the paper; all authors discussed the results and commented on the manuscript.

DATA ACCESSIBILITY

The data that support the findings of this study are available in Appendix S1.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1 List of epiphyte species found in each zone of each *Acer macrophyllum* trees

APPENDIX S2 Images of two of the *Acer macrophyllum* trees surveyed

APPENDIX S3 Image of a single branch of an *Acer macrophyllum* tree

APPENDIX S4 Summary of microclimate data from three *Acer macrophyllum* trees

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