Diversity Begets Diversity: Structural Heterogeneity Determines Fine-Scale Epiphyte Community Structure in a Temperate Rainforest

Kaela M. Hamilton and Carrie L. Woods *

Biology Department, University of Puget Sound, Tacoma, WA 98416, USA; kaelahamilton@gmail.com
* Correspondence: cwoods@pugetsound.edu

Abstract: A foundational concept in ecology is the positive relationship between habitat heterogeneity and species diversity. Epiphytes demonstrate microhabitat specialization to particular areas within a tree; thus, epiphyte communities are potentially influenced by the structural heterogeneity of host trees. We evaluated the relationship between structural features of *Acer macrophyllum* and epiphyte distributions and abundance in a temperate rainforest in Washington, USA. Epiphytes and structural features of three *Acer macrophyllum* trees were systematically surveyed using the point-intercept method from the base to the crown and on three branches for each tree. Rarefied species richness increased with structural richness. Species richness along the trunk differed significantly among types of structural features (i.e., broken branches, burls, holes, rivets, branches, and trunks); broken branches had the highest species richness and branches had the lowest, followed by trunks. Rarefied species richness increased with height and peaked at 12 m, but the relationship between structural diversity and height was not significant. The species that occurred on branches were different to those that occurred on trunks, and species composition varied significantly among trunk features. The high structural diversity in northern temperate rainforest trees influenced the fine-scale distribution of nonvascular epiphytes and may explain their coexistence in tree crowns.

Keywords: *Acer macrophyllum*; bryophytes; epiphytes; microhabitat; old-growth forests; structural heterogeneity; temperate rainforest

1. Introduction

The habitat heterogeneity hypothesis posits that environmental complexity can promote species diversity and coexistence by offering a greater diversity of niches and reducing competitive exclusion [1–4]. Structural complexity, defined as the variation in the physical three-dimensional structure of an ecosystem, has been found to influence patterns of diversity in coral reefs [5,6], marine rocky shores [7], temperate forests [8], and canopy systems [9,10], among others. The variety of microhabitats that are generated by fine-scale structurally heterogeneous environments allow for specialization and, as a result, more diverse communities. Many studies have found that key structural components contribute disproportionately to diversity, such as particular coral species [6], large trees in human-modified landscapes [9–11], soil in tropical canopy trees [12,13], and rocks and crevices in intertidal zones [7]. Identifying these important keystone structures can be crucial for maintaining biodiversity and informing conservation efforts.

Large, old trees are critical components and keystone ecological structures of many ecosystems worldwide [9,14,15]. Their complex three-dimensional structures create a variety of microhabitats that influence the diversity and distribution of both fauna [2,16,17] and flora [12,15,18–21]. Epiphytes, structurally dependent non-parasitic plants, are distributed non-randomly within tree crowns due to their associations with microhabitats [1–3] created by gradients in light, relative humidity, substrate types, and structural features among different areas of the tree [12,18,20,22–24]. Bark traits and tree architecture have been found
to influence epiphyte communities [25–28], and tree size is known to be a predictor of epiphyte species richness [12,29–31]. However, the specific structural features of host trees that determine these preferences require further investigation [32].

Although much of the research focusing on epiphytic microhabitat associations has occurred in tropical rainforests (e.g., [12,20,33]), epiphyte distributions in temperate rainforests can also be influenced by tree factors [18,21,22,34–36]. In coastal temperate rainforests in New Zealand, distinct epiphyte communities were found among different areas of host trees, including trunks, inner branches, and outer branches [36,37]. Epiphyte distributions in Acer macrophyllum trees in Pacific Northwest northern temperate rainforests were found to be non-random across broad-scale Johansson zones, with distinct epiphyte communities on trunks and branches [18]. In Nothofagus temperate rainforests in the Chilean Andes, fine-scale epiphyte community composition varied with tree height, with some species restricted to trunks or branches [21]. These patterns have been hypothesized to be due to either physiological or morphological adaptations of epiphytes to variations in microclimate, particularly sunlight and water availability differences from the upper to lower parts of trees [21,37]. However, other studies have found structural features, such as the number and size of branches, to be more important than microclimate in determining epiphyte distributions [18,38].

Explorations of fine-scale distribution patterns, including the contribution of structural features to epiphyte community patterns and how these structural features vary within trees, are needed to fully understand the relationship between host structural heterogeneity and epiphyte communities. They may also determine the key attributes of host trees for maintaining epiphyte biodiversity and inform forestry and conservation initiatives. The objective of this study was to evaluate the relationship between epiphyte community structure and host tree structural and spatial heterogeneity at a very fine scale in a northern temperate rainforest, where the epiphyte community was made up primarily of bryophytes. We surveyed epiphyte communities every meter from the base to as far up each of three trees as was logistically feasible, as well as every meter along at least three branches in each tree. We noted any structural features with each survey, including branches, broken branches, burls, holes, and rivets. We tested the hypothesis that epiphyte species richness and composition would be impacted by variations in host tree structural and spatial heterogeneity. We predicted that epiphyte species richness would increase with higher structural diversity and that epiphyte species would be specialized to unique microhabitats generated by host tree structures.

2. Materials and Methods

2.1. Study Area

Our study was conducted in the Hoh Rainforest just outside the entrance to the Olympic National Park in the Hoh River valley, Washington, USA (47°52′15″ N, 123°55′52″ W; Figure 1). The site is a flood plain along the Hoh River dominated by large bigleaf maples (Acer macrophyllum) with scattered Sitka spruce (Picea sitchensis) in the overstory and vine maple (Acer circinatum) and western sword fern (Polystichum munitum) in the understory. The climate is mild and wet, with temperatures fluctuating between −7 and 21 °C (average temperature: 10 °C) and the average precipitation fluctuating between 320 and 344 cm [39,40]. Within this temperate rainforest, Acer macrophyllum trees support more epiphyte biomass than any other tree in the Pacific Northwest, and the biomass of epiphytes can be four times that of their host tree’s foliage [41]. Therefore, Acer macrophyllum was selected as the focal host species for this study.
2.2. Study Design and Data Collection

Three large (>95 cm dbh) *Acer macrophyllum* trees were selected from a grove of approximately 20 maple trees. The three trees in this study were chosen based on previous findings of non-random distributions of epiphytes within trees across broad Johansson zones [18], the feasibility of establishing two clear climbing lines to allow access to all areas of the trunks, the absence of any dramatic lean or fork in the trunks, and clear access to at least three live branches.

To examine the effect of fine-scale structural and spatial characteristics of *Acer macrophyllum* on epiphyte community structure, the three trees were systematically surveyed every meter up the trunk until it was not feasible to climb any higher (12–17 m) and every meter along three branches for three meters (0 m, 1 m, and 2 m). The trees were climbed using single-rope climbing techniques [42]. The point-intercept method was used to measure the percent cover of epiphytes by identifying the epiphyte species and substrate type (i.e., bark or detritus) under each of 100 random dots on a 22 × 28 cm acetate sheet. The acetate sheets were connected using Command™ strips (3M, Maplewood, MN, USA) and wrapped around the entire circumference of the trunk and branches at every meter. We conducted a total of 576 surveys of epiphyte communities in the three *Acer macrophyllum* trees across two summer field seasons.

Substrate features were noted at each height on the trunk under the corresponding acetate sheets and included broken branches, burls, holes, and rivets (i.e., cavities or ruts running vertically up the trunk). At every meter surveyed on the trunk, canopy openness and bryophyte depth were recorded at each cardinal direction and averaged to obtain a measure of canopy openness and depth at each meter. Canopy openness and bryophyte depth were found to vary in these trees across broad Johansson zones [18], so we measured them as confounding variables. On the branches, canopy openness and bryophyte depth were recorded on the tops, bottoms, and both sides (facing outwards from the trunk) for each meter surveyed. Canopy cover was measured with a spherical densiometer (Forestry Suppliers, Jackson, MS, USA), and bryophyte depth was measured using calipers or a 5 m tape. The diameter at breast height (dbh) was measured for each tree surveyed and at each meter along the branches. Because previous research on these trees found no significant differences in microclimate (i.e., temperature, relative humidity, and vapor pressure deficit) across Johansson zones [18] or fine-scale distances (every 0.5 m; Woods, unpublished data), we did not include microclimatic variables in our study.
2.3. Statistical Analyses

We measured rarefied species richness as the total number of species found in each 1 m survey while accounting for the total area surveyed, and we measured structural richness as the number of structural features (i.e., broken branches, burls, holes, rivets, and branches) found at each 1 m survey. To evaluate the relationship between rarefied species richness and structural richness on the trunk, we used linear regression. A one-way ANOVA analysis was used to evaluate how rarefied species richness varied among structural features and was followed by Tukey HSD tests for pairwise comparisons across structures. We used two-way ANOVAs to determine if the way that structure affected richness depended on individual trees or heights in trees. Non-linear regressions were conducted to evaluate the relationship between structural richness and height and between rarefied species richness and height. For the analysis of structural richness and height, both variables were square-root-transformed to meet the normality assumptions of the model.

Non-metric multi-dimensional scaling (NMDS) ordination was used to evaluate variation in species composition among structural and spatial features (i.e., trunks, broken branches, burls, holes, and rivets, as well as the tops, sides, and bottoms of branches). We used the Morista–Horn index with 1000 iterations using the vegan package in R [43]. We tested whether the NMDS was significantly different from random using the Monte Carlo test with 1000 iterations. To be considered statistically different from random, the stress level of the Monte Carlo test had to be larger than the NMDS stress level [44]. We examined whether bryophyte depth, canopy openness, and height in tree correlated with variations in species composition using the envfit() function in the vegan package with 1000 iterations [43]. The direction of vectors represents their maximum correlation with the ordination axes and their length represents the strength of the correlation. We used the adonis function in the vegan package and the pairwiseAdonis package in github to test for significant differences in species composition among structures and branch zones with 1000 permutations [43,45]. Statistical analyses were performed using R v. 4.0.2 or R v. 4.2.0 in RStudio [46].

3. Results

Overall, we found a total of 22 species, which were mostly bryophytes, including 16 mosses and 3 liverworts. In addition, we also found one lichen and two vascular plant species (one lycophyte and one fern) (Table 1). Bryophyte species showed specialization to structures on the trunks and to zones on the branches. While most bryophyte species were found on the trunk, the mosses Antitrichia curtipendula, Hylocomium splendens, and Rhytidiadelphus loreus had a higher average percent cover on trunk structures than on the trunk, and the liverwort Scapania bolanderi was only found on burls. In contrast, the mosses Claopodium crispifolium, Hypnum subimponens, and Metaneckera menziesii and the lichen Lepraria spp. had the greatest percent covers on trunks. Polypodium glycerrhiza, the only epiphytic fern, was found exclusively on trunks, although by June and July in the Hoh Rainforest, this species has lost its leaves and its rhizome is buried under moss mats, so this is likely an underestimate. Among branch zones, bryophyte species also showed specialization. The mosses Antitrichia curtipendula, Dicranum fuscenscens, Kindbergia oregana, Kindbergia praelonga, Neckera douglasii, and Rhytidiadelphus triquestrus were restricted to the sides of branches, and this pattern was also observed for Lepraria spp. Except for the moss Kindbergia oregana, these species were also abundant on trunks, which suggests a preference for vertical structures.
Table 1. Average percent cover of epiphyte species found on trunk structures and branch zones of *Acer macrophyllum*. For each epiphyte species, average percent cover represents the total count of a species on each trunk structure or branch zone divided by the total count of the species across all trunk structures or branch zones, averaged across the three trees surveyed.

<table>
<thead>
<tr>
<th>Species</th>
<th>Code</th>
<th>Family</th>
<th>Life Form</th>
<th>Broken Branch</th>
<th>Bawl</th>
<th>Hole</th>
<th>Rivet</th>
<th>Trunk</th>
<th>Top</th>
<th>Bottom</th>
<th>Side</th>
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<td>0.77</td>
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<td>14.32</td>
<td>1.38</td>
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<td>Neckeraeaceae</td>
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<td>0.28</td>
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<td>11.29</td>
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<td>Moss</td>
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<td>0.00</td>
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<tr>
<td><em>Neckera douglasii</em></td>
<td>NecDou</td>
<td>Neckeraeaceae</td>
<td>Moss</td>
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<td>Hylocomiaceae</td>
<td>Moss</td>
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<td>52.39</td>
<td>0.00</td>
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<td>45.83</td>
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<td>Hylocomiaceae</td>
<td>Moss</td>
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<td>0.00</td>
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<td>Selaginellaceae</td>
<td>Lycophyte</td>
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<td>Liverwort</td>
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<td>0.00</td>
<td>0.00</td>
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</table>

3.1. Effect of Structure

Rarefied species richness increased as the number of structural features increased (linear regression, $F_{1,35} = 7.66, p = 0.009$; Figure 2). Further, rarefied species richness significantly varied among types of structures (one-way ANOVA, $F_{5,447} = 22.43, p < 0.001$; Figure 2). Mean (±SE) rarefied species richness was highest on broken branches (4.32 ± 0.28) and lowest on branches (2.28 ± 0.08), followed by trunks (3.03 ± 0.09; Figure 2). Rarefied species richness on holes, burls, and rivets was also higher than on bare trunks (Figure 2). Rarefied species richness on trunks was 28.25% higher than richness on branches ($p < 0.001$), but 25.36% lower than on burls ($p < 0.001$) and 35.10% lower than on broken branches ($p = 0.006$). In addition, rarefied species richness on branches was 44.90% lower than on rivets ($p = 0.014$), 52.67% lower than on burls ($p < 0.001$), and 61.82% lower than on broken branches ($p < 0.001$). All other pairwise comparisons among structures were not statistically different from each other. The way that structure affected richness did not depend on the tree (two-way ANOVA, $F_5 = 0.54, p = 0.74$) and it did not depend on height (two-way ANOVA, $F_4 = 2.21, p = 0.071$), indicating that the patterns of species richness and structure were consistent across trees and heights.
Richness on holes, burls, and rivets was also higher than on bare trunks (Figure 2). Rarefied species richness on trunks was 28.25% higher than richness on branches ($P < 0.001$), but 25.36% lower than on burls ($P < 0.001$) and 35.10% lower than on broken branches ($P = 0.006$). In addition, rarefied species richness on branches was 44.90% lower than on rivets ($P = 0.014$), 52.67% lower than on burls ($P < 0.001$), and 61.82% lower than on broken branches ($P < 0.001$). All other pairwise comparisons among structures were not statistically different from each other. The way that structure affected richness did not depend on the tree (two-way ANOVA, $F_{5,30} = 0.54$, $P = 0.74$) and it did not depend on height (two-way ANOVA, $F_{4,30} = 2.21$, $P = 0.071$), indicating that the patterns of species richness and structure were consistent across trees and heights.

Figure 2. There was a positive effect of structure on rarefied species richness of epiphytes in *Acer macrophyllum*. (a) An increase in structural richness on the trunk led to a corresponding increase in rarefied species richness of epiphytes ($p = 0.009$). (b) Average ($\pm SE$) rarefied species richness of epiphytes also varied among structural features ($p = 0.001$) and was lowest on branches and bare trunks. Bars with different letters are significantly different from each other according to a Tukey’s HSD test ($p < 0.05$).

3.2. Effect of Height

Average rarefied species richness showed a non-linear relationship with height in the trees and reached a maximum at 12 m (non-linear regression, $F_{1,149} = 4.89$, $p = 0.029$; Figure 3). Average structural richness demonstrated a similar trend with height, but the effect was not significant (non-linear regression, $F_{2,36} = 0.44$, $p = 0.648$; Figure 3).

Species varied in their percent covers along the trunks with height in the trees (Figure 4). *Metaneckera menziesii* and *Isothecium myosuroides* were found in almost equal abundance across all heights on the trunk (Figure 4). *Leucolepis acanthaneuron* occurred on the lower parts of the trunk, while *Porella navicularis*, *Selaginella oregana*, *Rhytidiales loreus*, and *Hypnum subimponens* occurred higher up the trunk (Figure 4).
Acer macrophyllum (n = 3). Hypnum subimponens 0.06. species composition did not significantly differ across all heights on the trunk (Figure 4). Leucolepis acanthaneuron 0.28, 0.069. Species composition could vary in another dimension, which could explain the significant differences in species composition between all trunk structures and branch zones (Adonis, R² = 0.43, P < 0.001). There were significant differences in species composition among trunk structures and branch zones (Adonis, R² = 0.43, P < 0.001). Species varied in their percent covers along the trunks with height in the trees (Figure 3).

Our NMDS was significantly different from that on broken branches (pairwise Adonis, R² = 0.24, P = 0.005), and the composition on rivets was significantly different from the branches (pairwise Adonis, R² = 0.04, P = 0.014). Among the species found on branches were Isothecium myosuroides, Metaneckera menziesii, and Selaginella oregana, which were all significantly different from each other (pairwise Adonis, R² = 0.27, P = 0.648). Among the species found on branches were Isothecium myosuroides, Metaneckera menziesii, and Selaginella oregana, which were all significantly different from each other (pairwise Adonis, R² = 0.27, P = 0.648). Among the species found on branches were Isothecium myosuroides, Metaneckera menziesii, and Selaginella oregana, which were all significantly different from each other (pairwise Adonis, R² = 0.27, P = 0.648).

Figure 3. Mean rarefied species richness (a) and structural richness (b) of epiphytes with height in Acer macrophyllum (n = 3). (a) Points represent average (±SE) rarefied epiphyte species richness with height (p = 0.014). (b) Points represent average (±SE) structural richness with height (p = 0.648).

Figure 4. Average percent cover of epiphyte species found on trunks and all trunk structures with height zones in three Acer macrophyllum trees in the Hoh Rainforest. Species found on branches were not included. See Table 1 for species codes.
3.3. Species Distributions

Our NMDS was significantly different from random (stress = 0.16, Monte Carlo stress = 0.26; Figure 5). There were significant differences in species composition among trunk structures and branch zones (Adonis, $R^2 = 0.43$, $F_{7,253} = 26.93$, $p < 0.001$), which were supported by the lack of overlap in species composition between all trunk structures and branches and the pairwise comparisons that showed that the trunks and trunk structures were all significantly different from the branches (pairwise Adonis, $p < 0.001$). Among the trunk structures, the composition on the trunk was significantly different from that on burls (pairwise Adonis, $R^2 = 0.04$, $F_{1,136} = 6.02$, $p < 0.001$) and broken branches (pairwise Adonis, $R^2 = 0.03$, $F_{1,113} = 3.82$, $p = 0.005$), and the composition on rivets was significantly different from that on broken branches (pairwise Adonis, $R^2 = 0.24$, $F_{1,10} = 2.88$, $p = 0.027$; Figure 5). While there was some overlap in species composition among trunk structures, species composition could vary in another dimension, which could explain the significant differences. All branch zones were significantly different from each other (pairwise Adonis, $p < 0.001$). Species composition was significantly related to bryophyte depth (MD; $r^2 = 0.28$, $p < 0.001$) and height ($r^2 = 0.37$, $p < 0.001$), both of which were highest on branches. Species composition did not significantly relate to canopy openness (CO, $r^2 = 0.02$, $p = 0.06$).

Figure 5. Non-metric multidimensional scaling ordination (NMDS) of epiphyte species composition by structural features of trunks (i.e., trunks (black squares), burls (gray diamonds), broken branches (white triangles), holes (white squares), and rivets (white diamonds)) and branches (i.e., tops (black circles), sides (gray circles), and bottoms (white circles)). The Marista–Horn similarity index was used on abundance data. Ellipses show the covariance matrix centered on the mean of each structure; overlapping ellipses indicate similar species composition. Two-dimensional stress = 0.16, Monte Carlo stress with 1000 iterations = 0.26. Species codes are shown in red (see Table 1 for species codes). Environmental variables are shown as blue vectors. Bryophyte depth (MD, $r^2 = 0.28$, $p < 0.001$) and height ($r^2 = 0.37$, $p < 0.001$) explained a significant proportion of the variation in species composition, but canopy openness (CO, $r^2 = 0.02$, $p = 0.06$) did not.

4. Discussion

The positive effect of structural complexity on species richness and diversity is well documented across ecosystems [5,6,12,47]. Our results on epiphytes in a northern temperate rainforest, which were mostly composed of bryophytes, support this trend in the literature,
as species richness increased with increasing structural richness. It has been long established in the literature that epiphytes are found in different microhabitats within trees [12,19,48]. Here, we provide evidence that fine-scale structural heterogeneity created by particular structures within a tree explains non-random patterns of epiphyte community structure and species distributions.

We found support for the prediction that epiphytes would be specialized to unique structural features of the trees. Broadly, we found distinct epiphyte communities on the trunks and branches, consistent with previous findings from other studies in temperate rainforests [18,21,37]. The epiphyte species on the trunks were primarily bryophytes but also included the lichen Lepraria spp. and a fern. On the trunks, richness varied significantly with the presence of structural features. Rarefied species richness on branches and bare trunks was surprisingly low compared to all other trunk structures, and, further, richness varied among types of structural features. The mosses Metaneckera menziesii and Isothecium myosuroides dominated the trunks and were quite rare on trunk structures, which suggests a preference for vertical substrates. These findings are consistent with those of other studies which found that M. menziesii and I. myosuroides were abundant on trunk surfaces [22,49].

Broken branches and burls were covered with epiphytes and had the greatest numbers of species on them, including some species that were specialized to these structures. These results are supported by other studies in the Pacific Northwest and elsewhere that found the highest covers of epiphytes on the oldest structures closest to the trunk [12,34,50]. The bryophytes Antitrichia curtipendula, Rhytidiodelphus loreus, and Scapania bolanderi were most abundant on burls, and Hylocomium splendens was most abundant on broken branches. A. curtipendula and R. loreus are large mosses that form bushy mats on horizontal surfaces, whereas S. bolanderi is a small liverwort that forms tufts or turfs and often occurs on the sides of trees or logs and on tree trunks [49,51,52]. Thus, burls may offer a variety of microhabitats that support large mat-forming bryophyte species on the top and small, turf-forming species on the sides and bottom. H. splendens is a large feather moss that is very abundant on old, decaying logs and on the forest floor in this forest [39,51]. Thus, it may be able to colonize the horizontal surfaces that broken branches offer. The specialization of species to structures along the trunk supports structural richness as a driver of species richness.

Fine-scale partitioning of tree crowns was evident on branches, as species composition varied across the tops, sides, and bottoms of branches. Branches were dominated by particular bryophyte species, as well as one vascular plant species. The mosses Claopodium crisipfolium, Hypnum subimponens, and Leucolepis acanthaneuron were restricted to the tops of branches, while seven species were restricted to the sides of branches. The most abundant species on the tops of branches were the mosses Rhytidiodelphus loreus and L. acanthaneuron, while the most abundant on the sides were R. loreus and Metaneckera menziesii, which supports the notion that M. menziesii is a vertical specialist. R. loreus forms large bushy mats on large branches close to the trunk, which suggests that it requires a large surface area and might be a competitive dominant on old branches. The bottoms of the branches were dominated by Selaginella oregana and Isothecium myosuroides. S. oregana is a pendulous lycophyte that requires canopy soil to root into. Canopy soil forms on burls, broken branches, along the trunk, and on large branches [37,41]. S. oregana was found on all these structures, suggesting canopy soil presence as a requirement for S. oregana establishment. I. myosuroides has dimorphic phyllids that form both tufts close to the bark and pendulous, stringy tails that hang below branches. Pendant bryophytes and vascular epiphytes have been found hanging below branches in other systems [12,37]. Thus, S. oregana and I. myosuroides hang in large mats below branches, which explains their dominance on the bottoms of branches as well as the greater bryophyte depth in this zone.

Rarefied epiphyte species richness increased with height but was highest at intermediate–upper trunk zones. A concentration of epiphytes at intermediate heights in a tree is a common trend across systems [19,34,53,54] and could be due to various factors. Some researchers have suggested that this relationship is due to gradients in abiotic factors, such as humidity and light, with height in the tree [12,19,21,22,37], while others found
structural features to be more important \cite{18,38}. We found support for the prediction that epiphyte species richness is correlated with structural richness because structural richness also peaked at intermediate heights on the trunk. Microclimate was found not to vary with broad-scale zones or correlate with epiphyte communities in our system \cite{18}. *Acer macrophyllum* trees are much shorter than the dominant conifers that surround them, such as *Picea sitchensis* (Sitka spruce) and *Pseudotsuga menziesii* (Douglas fir), and they are therefore considered part of the understory. We found support for this in the lack of a significant relationship of canopy cover with species composition in the NMDS. As a result, there is likely less of a gradient in microclimate and light than in other temperate rainforests where trees are much taller \cite{21,37}. The positive relationships between structural richness and height and between structural richness and epiphyte richness in our study suggest that structural heterogeneity is more important than height in influencing the vertical distribution of epiphytes in these northern temperate rainforest trees.

The unique structures within a tree likely create microhabitats to which epiphyte species can become specialized. Thus, trees with more structural complexity should, in theory, support a greater diversity of epiphytes. While strict host specificity is uncommon in epiphytes \cite{32,33,55,56}, network analyses of epiphytes and host trees reveal that epiphyte–host relationships are not completely random \cite{32,57–60}. Epiphyte colonization patterns are known to be impacted by bark traits \cite{26,27,32,61,62} and tree architecture \cite{28}. Epiphyte richness and diversity also increase with tree size due to increased time for colonization and increased heterogeneity in old tree crowns (e.g., \cite{10,29,61}). Microhabitat partitioning of trees by epiphytes may also be favored under more constant environmental conditions \cite{63}, such as those found in our study system and others \cite{37,38}. This study builds on this research by highlighting the importance of structurally diverse trees in the maintenance of epiphyte diversity. Given our finding of the contribution of particular structural components of large, old-growth trees to epiphyte richness, our study provides further support for the protection of large, old trees with complex architectures \cite{9,14,28}.

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