Epiphyte diversity, abundance, and distribution in an old Sitka spruce crown

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Abstract. Preserving biodiversity in remaining old-growth forests is a high priority for many land managers. To this end, we inventoried the diversity, abundance, and distribution of epiphyte species in one 318-year-old, 86 m tall *Picea sitchensis* tree on the north coast of California. In 39 plots, we recorded species present and mean percent cover for each species. Our findings include the following: 1) 68 epiphyte species were found in this one tree; 2) epiphyte diversity increased with height; 3) lichens had the highest diversity of all epiphyte classes; and 4) mosses had the highest percent cover of all epiphyte classes. These findings highlight the capacity for old trees to serve as reservoirs of biodiversity in younger forests.

***Key words*. Lichen, moss, old-growth, *Picea sitchensis*, species richness.**

INTRODUCTION

Epiphytes are plants that grow on other plants in a non-parasitic fashion. Ferns, leafy liverworts, lichens, and mosses are common epiphyte functional groups found in the forests of northwestern California. Epiphytes are valuable members of forested ecosystems, as they perform invaluable ecological services. Lichens are important for forest nutrient cycling, and together with other cryptogamic organisms (bryophytes, algae, cyanobacteria, and fungi) are responsible for almost 50% of terrestrial nitrogen fixation (Elbert et al. 2012; Miller et al. 2017). Cyanolichens are particularly efficient at converting inert atmospheric nitrogen into a plant-available form due to cyanobacterial photobionts within the lichen thallus. Over three tons of cyanolichens per hectare can fix 16 kg of nitrogen annually, boosting ecosystem productivity (Sillett & Antoine 2004). In addition to nutrient cycling (Antoine 2004), epiphytes also serve as bio-indicators for air quality and climate. Air pollutants such as SO_2 can damage sensitive epiphyte species, rendering them rare or locally extinct (Nash & Wirth 1986; Sim-Siam et al. 2000; Sujetovienė 2015). Subtle disturbances in microclimate can also affect the diversity, abundance, and distribution of epiphytes while changing climate can shift the biogeographic ranges of epiphyte species (van Herk et al. 2002; Aptroot & van Herk 2007; Ellis et al. 2007; Zotz & Bader 2009; Miller et al. 2017).

Epiphyte communities support high levels of biodiversity. This diversity has been fairly well-studied in the Pacific Northwest, and has largely focused on redwood (*Sequoia sempervirens* (D.Don.) Endl.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) as host trees (e.g. McCune 1993; Williams & Sillett 2007), with a few studies (e.g. Ellyson & Sillett 2003) focused on Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Rich epiphyte communities also support greater animal diversity in forests. Bryophyte (mosses and leafy liverworts) mats act as habitat for a range of organisms including fungi, salamanders, mollusks, annelids, and arthropods, and are used by nesting bird species such as the endangered marbled murrelet (*Brachyramphus marmoratus* Gmelin; https://www.iucn.org/). Furthermore, decaying bryophyte mats in old-growth crowns can lead to soil accumulation, thereby promoting biodiversity as plant and animal communities develop in the presence of these canopy soils (Ellyson & Sillett 2003). Finally, lichens provide shelter for arthropods, forage for birds, and substrate for parasitic fungi, as well as nesting material for flying squirrels (Sillett & Antoine 2004).

Epiphyte diversity and abundance vary along environmental gradients at the ecosystem and individual tree scales. Gradients in light, moisture, temperature, and nutrients collectively

influence epiphyte assemblages (Sillett & Antoine 2004). For example, trees of the same age can have different epiphyte communities because of varying moisture regimes among individual trees (McCune 1993). Similarly, bryophytes are commonly found lower in the canopy and in more mesic conditions, while lichens are more commonly found in the relatively xeric, desiccating environment of the upper canopy (Lyons et al. 2000; Sillett & Rambo 2000). Generally, there is a positive correlation between height and lichen diversity and a negative correlation between height and bryophyte diversity (Ellyson & Sillett 2003). Overall, species richness typically increases with height, particularly as treetops often host rare species; thus, total tree height can be useful when trying to predict species richness (McCune et al. 2000).

In addition to variations in microclimate, canopy and stand structure also influence epiphyte communities (McCune et al. 2000; Sillett & Antoine 2004). Within a crown, branches frequently die, exposing recently dead sapwood as a new and unique substrate for establishment. Some species are functionally limited to old-growth stands for dispersal reasons, but also because larger, older trees offer more surface area for epiphyte establishment across an assortment of substrates such as branchlets (< 4 cm diameter), branches, and trunks (Miller et al. 2017; Sillett & Antoine 2004). In large trees with complex crowns, there is a high turnover of substrate, fostering a variety of successional communities within individual crowns (Sillett & Antoine 2004). Another characteristic of large, old trees that supports high epiphyte diversity is the existence of ample horizontal branch surfaces and a variety of crotches, rot pockets, and cavities for successful spore germination and establishment. While old large trees are important centers of epiphyte diversity and abundance, younger trees in older forests serve as useful refugia for certain epiphyte species due to the low light levels and mesic conditions occurring under dense forest canopies (Miller et al. 2017). Due to favorable microclimates, diverse and abundant substrates, and sufficient time for epiphyte dispersal and establishment, old-growth forests store higher quantities of carbon in the form of epiphytic biomass compared to younger stands. For example, in Oregon and Washington, epiphyte biomass was approximately 2.6 tons per hectare in old forests and less than 1 ton per hectare in young forests (McCune 1993). As establishment of many epiphyte species can be limited by dispersal and suitable substrate availability, many are considered old-growth dependent and are therefore threatened by habitat loss due to extensive logging in the region.

Given their ecological importance, sensitivity to climate, and threats of habitat loss, more knowledge about epiphyte diversity and how it varies within large old trees is needed. The objective of this study was to evaluate how epiphyte species richness and percent cover vary within a large, old *Picea sitchensis* tree in northern California near the southern extent of this species range. More specifically, we hypothesized that: 1) *P. sitchensis* in this region supports high levels of epiphyte diversity due to favorable bark texture, benign bark chemistry, and a temperate climate; 2) Epiphyte diversity increases with height and percent cover decreases with height due to within-crown microclimatic trends; 3) Epiphyte diversity and percent cover are greatest on branches due to sufficient horizontal surface area; and 4) Among epiphyte classes, lichens are the most diverse due to tolerance of desiccating environments and bryophytes have the highest percent cover due to dominance of large old branches low in the crown.

METHODS

Study site
Field work took place in the Redwood Experimental Forest within Six Rivers National Forest (Taylor 1982), approximately 6 km north of Klamath, CA in February 2017. Redwood is the dominant overstory species in this forest, with subordinate species Douglas-fir, Sitka spruce, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Port Orford-cedar (*Chamaecyparis lawsoniana* (A. Murray) Parl.), and western redcedar (*Thuja plicata* Donn ex D. Don). One large (86 m), old (318 years) *Picea sitchensis* study tree was selected and its crown was non-destructively accessed using rope techniques (Jepson 2000; Kramer et al. 2018).

Epiphyte inventory

A stratified random sample of thirty-nine plots was established and exhaustively surveyed to quantify epiphyte diversity and abundance. Plots were stratified into three height classes (0-30 meters, 31-60 meters, and 61-87 meters) and three substrate classes (branchlets < 4 cm diameter, branches > 4 cm diameter, and trunk). Collectively, the plots covered 174 m^2, representing approximately 6% of the tree's total surface area. In each plot, all epiphyte species were recorded. For each species within each plot, percent cover was estimated using a modified Braun-Blanquet cover scale with nine cover classes ranging from 0.001-0.009% cover to 76-100% cover. Any questionable epiphytes were brought back to the lab for identification to species. Additionally, voucher specimens were collected for each species and deposited in cryptogamic herbaria at Humboldt State University (HSC) and Redwood National and State Parks.

Data analysis

Epiphytes were categorized into four classes: ferns, leafy liverworts, lichens, and mosses. Lichens were further categorized into foliose cyano-, foliose chloro-, fruticose, and crustose lichens. Due to decreasing surface area and therefore plot size with increasing height, species richness was standardized to the number of species per square meter to enable equal comparisons throughout the crown. From here forward, we refer to this standardized species richness as species richness. One-way analysis of variance (ANOVA) was used to test for differences in species richness and percent cover among height, substrate, and epiphyte classes. Data were analyzed using Microsoft Excel and JMP statistical software (SAS Inc., Cary NC). To test the assumption of equal variances among groups, Levine and Bartlett tests were used. When this assumption was violated, Welch tests were used to determine whether or not groups significantly differed. To test the assumption that our data are normally distributed, Shapiro-Wilk goodness-of-fit tests were used. When this assumption was violated, Kruskal-Wallis tests were used to determine whether or not groups significantly differed. If groups significantly differed, Tukey's HSD multiple means comparisons were used to identify significant differences among groups. For all statistical analyses, we used an α level of 0.05.

RESULTS

Height classes

We found a total of 68 epiphyte species in our one study tree: four ferns, one green alga, five leafy liverworts, 48 lichens, seven mosses, and three flowering vascular plants. (**Table 1**). We feel confident that we successfully captured the bulk of epiphyte diversity in this tree based on a species-area curve (**Figure 1**). When all species were pooled, species richness did not differ among height classes ($p = 0.0503$), although there was a positive trend between species richness and height (**Figure 2A**). When evaluated for each epiphyte class, species richness tended to increase between the lowest and highest height classes, although this difference in species richness among height classes was only significant in lichens ($p < 0.0001$, **Figure 2B**). When all species were pooled, epiphyte percent cover was significantly highest in the lowest height class ($p = 0.0228$, **Figure 3A**). When evaluated for each epiphyte class, epiphyte percent cover was generally higher in the lowest height class for ferns, leafy liverworts, and mosses, although these differences among height classes were not significant ($p > 0.05$, **Figure 3B**). Contrastingly, epiphyte percent cover in lichens was significantly greatest in the highest height class ($p = 0.0014$, **Figure 3B**).

Substrate classes

When all species were pooled, species richness was highest on branchlets compared to the trunk and branches ($p = 0.0338$, **Figure 4A**). Likewise, when evaluated for each epiphyte class, branchlets supported significantly higher species richness than other substrate types (**Figure 4B**). When all species were pooled, epiphyte percent cover did not differ among substrate classes ($p > 0.05$, **Figure 5A**). Similarly, when evaluated for each epiphyte class, percent epiphyte cover did not significantly vary among substrates ($p > 0.05$, **Figure 5B**).

Table 1. Epiphyte classes and species found in one 318-yr-old Sitka spruce tree near Klamath, CA in February 2017.

| Epiphyte Class	Species	Epiphyte Class	Species
Crustose Lichens	*Buellia* cf. *muriformis*	**Fruticose Lichens**	*Alectoria sarmentosa*
	Calicium glaucellum		*Alectoria vancouverensis*
	Chrysothrix xanthina		*Bryoria* sp.
	Chrysothrix granulosa		*Cladonia bellidiflora*
	Cliostomum griffithii		*Sphaerophorus tuckermannii*
	Graphis cf. *scripta*		*Usnea ceratina*
	Lecanactis megaspora		*Usnea cornuta*
	Lecanora expallens		*Usnea flavocardia*
	Lecanora impudens		*Usnea longissima*
	Lepraria sp.		*Usnea pacificana*
	Loxosporopsis corallifera		*Usnea rubicunda*
	Ochrolechia arborea		*Usnea wasmuthii*
	Ochrolechia juvenalis		*Usnea* sp. 1
	Pertusaria carneopallida		*Usnea* sp. 2
	Pertusaria sp. 1	**Green Algae**	*Trebouxia* sp.
	Pertusaria sp. 2	**Leafy Liverworts**	*Douinia ovata*
	Pyrrhospora quernea		*Frullania nisquallensis*
	Thelotrema lepadinum		*Porella navicularis*
	Variolaria amara		*Radula bolanderi*
Foliose Lichens	*Cetraria chlorophylla*		*Scapania bolanderi*
	Heterodermia leucomela	**Mosses**	*Antitrichia gigantea*
	Hypogymnia apinnata		*Dicranoweisia cirrata*
	Lobaria oregana		*Dicranum fuscescens*
	Lobaria pulmonaria		*Isothecium myosuroides*
	Nephroma laevigatum		*Leucolepis acanthoneura*
	Parmelia hygrophila		*Neckera douglasii*
	Parmelia squarrosa		*Rosulabryum gemmascens*
	Parmelia sulcuta	**Ferns**	*Polypodium glycyrrhiza*
	Parmotrema arnoldii		*Polypodium scouleri*
	Parmotrema crinitum		*Polystichum munitum*
	Parmotrema perlatum		*Selaginella oregana*
	Platismatia glauca	**Vascular Plants**	*Cardamine californica*
	Sticta limbata		*Claytonia perfoliata*
	Tuckermannopsis chlorophylla		*Oxalis oregana*
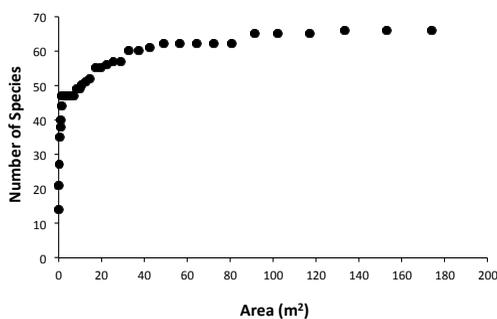
Figure 1. Species area curve showing a decrease in new epiphyte species found as the area sampled increased in one 318-yr-ol[...] [...]ruary 2017
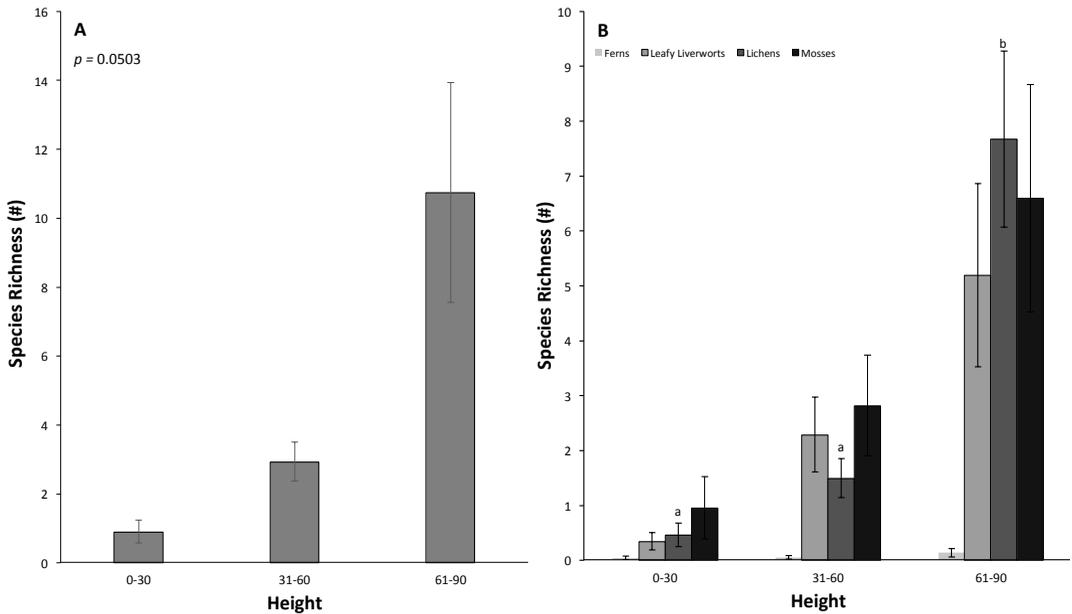
Figure 2. Species richness (mean ± standard error) of A) all species among height classes and B) each epiphyte class among heights. Data were collected from one 318-yr-old Sitka spruce tree near Klamath, CA in February 2017. In panel B, lichen height classes not sharing the same letter are significantly different.
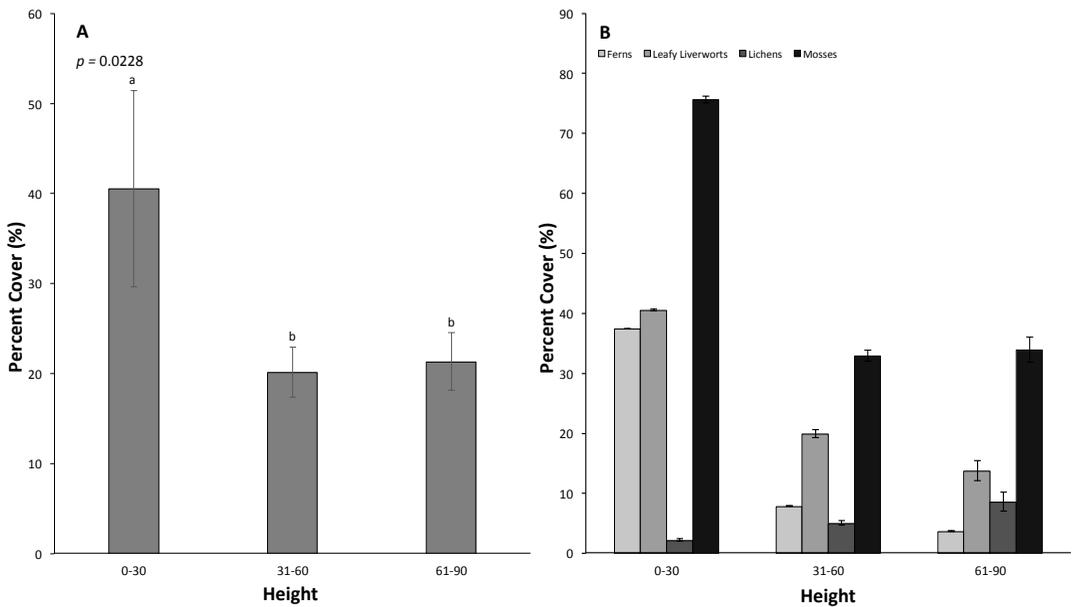

Figure 3. Percent cover (mean ± standard error) of A) all species among height classes and B) each epiphyte class among heights. Data were collected from one 318-yr-old Sitka spruce tree near Klamath, CA in February 2017. Within a panel, columns not sharing the same letter are significantly different.
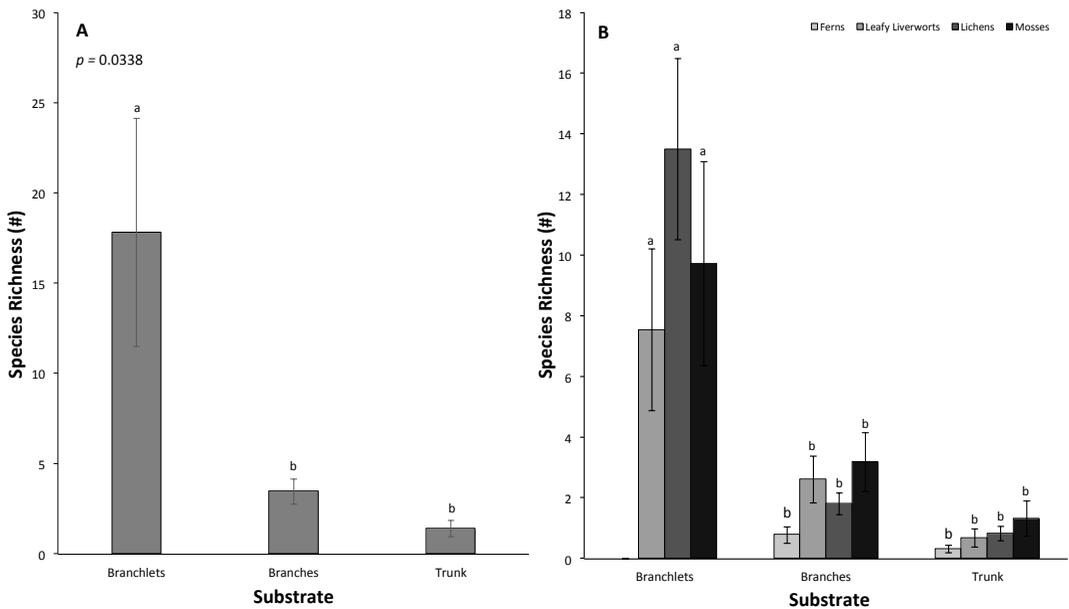
Figure 4. Species richness (mean ± standard error) of A) all species among substrate classes and B) each epiphyte class among substrates. Data were collected from one 318-yr-old Sitka spruce tree near Klamath, CA in February 2017. Branchlets are branches with diameter < 4 cm. Columns not sharing the same letter are significantly different.
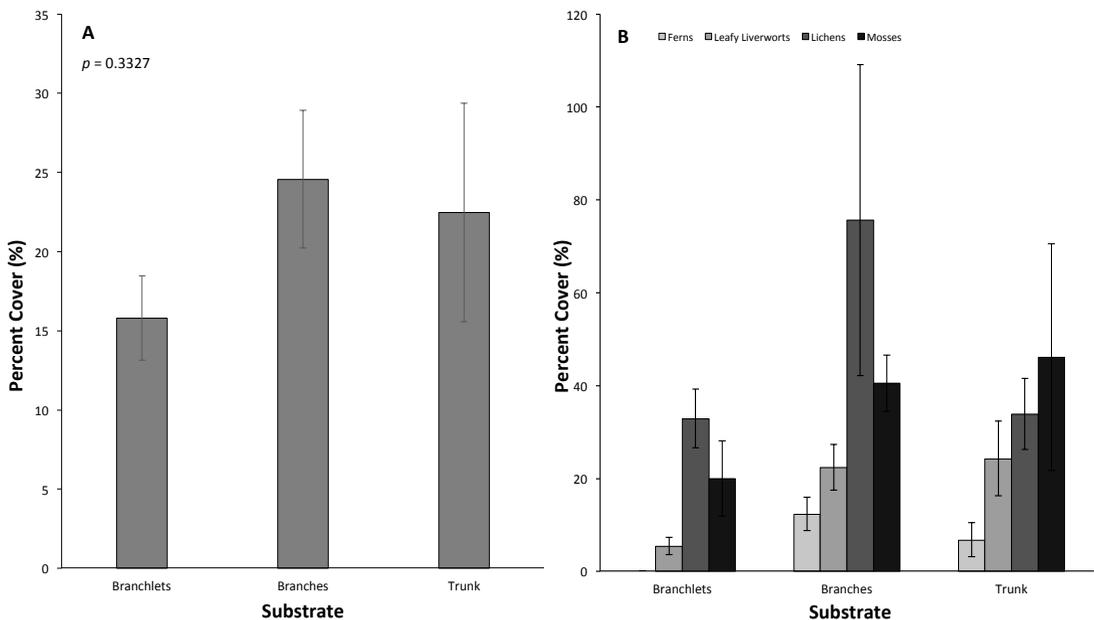

Figure 5. Percent cover (mean ± standard error) of A) all species among substrate classes and B) each epiphyte class among substrates. Data were collected from one 318-yr-old Sitka spruce tree near Klamath, CA in February 2017. Branchlets are branches with diameter < 4 cm.

Epiphyte classes

Lichens had significantly higher species diversity than any other epiphyte class ($p < 0.0001$, **Figure 6A**). Among lichen classes, foliose lichens had significantly lower species richness compared to crustose and fruticose lichens ($p < 0.0001$, **Figure 6B**). Among epiphyte classes, mosses had the highest percent cover ($p < 0.0001$, **Figure 7A**) and among lichen types, fruticose lichens had the highest percent cover ($p < 0.0001$, **Figure 7B**).
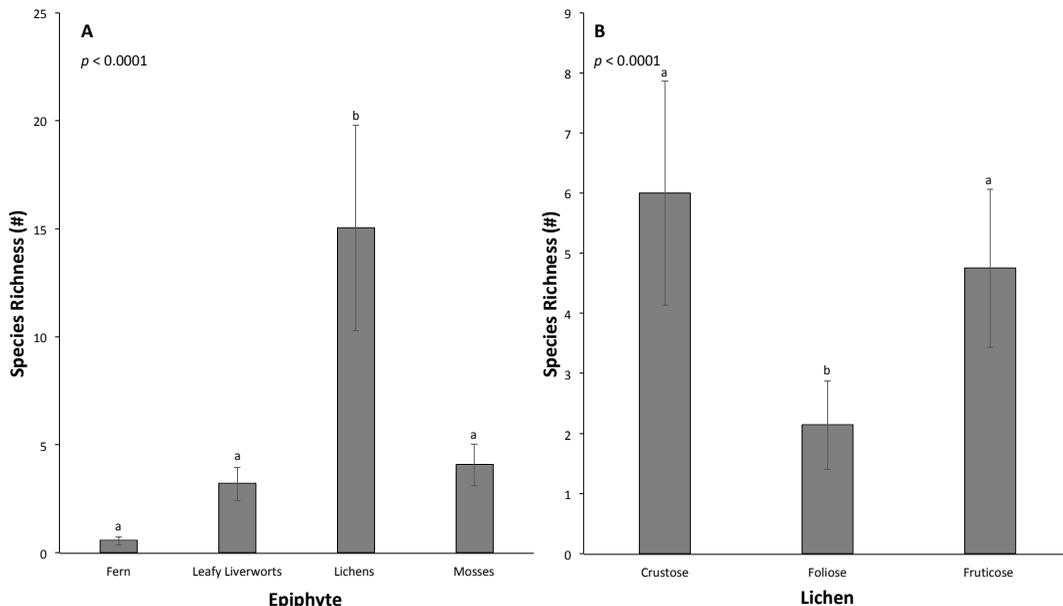

Figure 6. Species richness (mean ± standard error) of A) all species among epiphyte classes and B) specific lichen types. Data were collected from one 318-yr-old Sitka spruce tree near Klamath, CA in February 2017. Columns not sharing the same letter are significantly different.

Figure 7. Percent cover (mean ± standard error) of A) all species among epiphyte classes and B) specific lichen types. Data were collected from one 318-yr-old Sitka spruce tree near Klamath, CA in February 2017. Columns not sharing the same letter are significantly different.
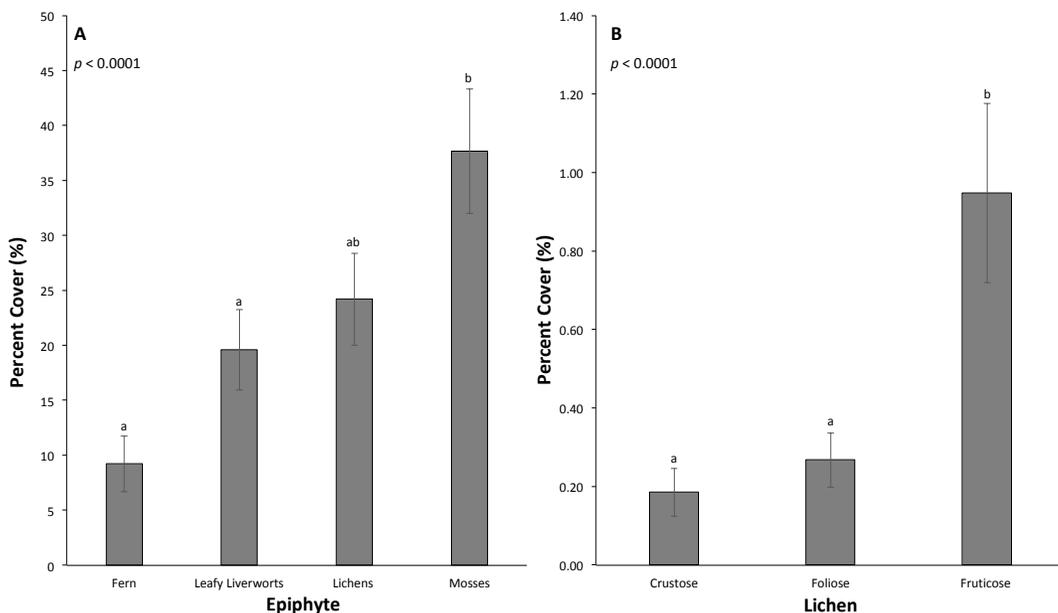
DISCUSSION

Diversity and abundance

Epiphyte diversity totaled 68 species on the *Picea sitchensis* tree that we surveyed. As other studies have documented up to 91 epiphyte species in old-growth *P. sitchensis* across multiple trees (Ellyson & Sillett 2003), expanding our study to include additional trees would likely increase observed species richness due to the inclusion of more microsite/microclimate variations. While the species richness observed in our one tree is impressive, over 275 epiphyte species have been observed across multiple old *S. sempervirens* trees (Williams & Sillett 2007). Given that dispersal is often a limiting factor for epiphyte establishment (Sillett & Antoine 2004), this extreme biological diversity in *S. sempervirens* crowns is likely due, in part, to the host tree's long life, as this species can live upwards of 2,000 years (Sillett et al. 2015). Thus, the accumulation of 68 species on our study tree in only approximately 300 years is temporally quite impressive. Although spore colonization in *Pseudotsuga menziesii* can be more rapid on smooth bark compared to rough bark (Sillett et al. 2000), we speculate that flakey bark with relatively neutral chemistry (Rogers & Rozon 1970) makes *P. sitchensis* a notably hospitable host to epiphytes. Large flakes in *P. sitchensis* bark likely provide abundant footholds for spore and asexual fragment establishment and relatively benign bark chemistry likely makes this host tree compatible with a broad spectrum of epiphytic species. We also note that because epiphytes provide food and shelter to a multitude of difficult-to-survey animals including invertebrates, amphibians, birds, and mammals, there is the potential for epiphyte diversity to indirectly inform on forest animal diversity.

As hypothesized, with increasing height, epiphyte diversity increased and epiphyte percent cover decreased. This relationship is likely due to lichens comprising the bulk of total diversity in this tree. As lichen diversity increases with height, total diversity increases with height. The decrease in percent cover is likely due bryophytes favoring the lower, less-desiccating conditions lower in the crown (Lyons et al. 2000). The relationships among height, epiphyte diversity, and epiphyte abundance are important to understand when managing forests, as forest structure can have a strong influence on epiphyte communities in numerous forest types. These observed patterns provide important information about microclimatic influences on epiphyte diversity and abundance and how these influences vary within large tree crowns. Improved understanding of these relationships between microclimates and epiphytes is needed, as epiphyte ranges appear to be shifting in response to changing climate and little is known about how new distributions will vary on a site-by-site basis (Miller et al. 2017).

Among substrate types, diversity was highest on branchlets. This finding is surprising and warrants further investigation, given the small diameter and vertical orientation of branchlets. We speculate that the small, pendant inter-leaf spaces along foliated shoots function like a net to catch epiphyte spores and asexual fragments in air currents passing by the outer crown, leading to high epiphyte diversity in this substrate type. It is also possible that our standardized metric of evaluating species richness per square meter somehow overestimated diversity on this substrate type.

Another interesting observation worthy of further study is that percent cover did not vary among substrate classes. It is likely that our use of the Braun-Blanquet cover class system was too coarse of an approach, such that our resulting data were too noisy to detect significant differences in cover among substrates. Nevertheless, our findings of comparably high epiphyte cover on branches and trunks suggest that the benign bark chemistry of Sitka spruce (Rogers & Rozon 1970) make this species highly hospitable to epiphytes, regardless of substrate size or orientation (vertical v. horizontal surface).

Among epiphyte classes, lichens had the highest level of diversity while mosses had the highest percent cover. These trends are again likely due to lichen diversity increasing with height due to a tolerance of more xeric, desiccating environments, while mosses favor the more mesic, less-desiccating microclimates lower in the crown. It also reasons that we observed the highest level of diversity in lichens, as this diverse group of "plants" includes approximately 20,000 species

(http://www.ucmp.berkeley.edu/fungi/lichens/lichensy.html), roughly twice the level of specific diversity found in each of the other investigated epiphyte classes (Christenhusz & Byng 2016).

Management implications

Many epiphytes are rare, associate with late-successional forests, occur within the Northwest Forest Plan area, and are therefore classified as "Survey and Manage" species (USDA & USDI 2001). Two such species, *Lobaria oregana* and *Usnea longissima*, were found on our study tree and require old-growth conditions for dispersal. In our study, while ground-based surveys could have likely detected *L. oregana* and *U. longissima*, it is unlikely that these surveys would have been able to detect the bulk of epiphyte diversity present in the crown. For land managers needing to inventory and monitor biological diversity, we therefore recommend the use of both tree- and ground-based surveys. Because tree climbing is time-consuming, expensive, and requires a specific skill set, a management approach using a combination of survey techniques can be realistic and effective. Under this approach, a small subset of old, large trees should be climbed to document rare Survey and Manage species and complementary ground-based surveys should be used to document more common epiphyte species not dependent on old-growth trees for dispersal (Miller et al. 2017).

While thinning stands can be beneficial to epiphytes, the more sensitive species might not thrive well under the sudden increase in light and temperature and decrease in moisture (Sillett & Antoine 2004). However, management practices that accelerate old-growth stand structure could have long-term benefits to sensitive species that favor sheltered, mesic, and heterogeneous conditions (Miller et al. 2017). For example, in young, mixed conifer-hardwood stands, removal of young conifers often promotes shrub growth around residual hardwoods, and these shrubs serve as habitat for epiphytic species (Sillett & Antoine 2004). Mangers should therefore consider leaving clumps of hardwoods (and removing some young conifers) in harvest units to promote the recruitment of shrubs and the eventual establishment of epiphytes. The use of uneven-age silvicultural practices can also create structural diversity and complexity in a stand, thereby increasing the diversity and complexity of substrates that can be used for epiphyte establishment. However, it is important to note that regardless of management practices, some species are just too sensitive to disturbance to benefit from restoration (Sillett & Antoine 2004). Thus, managers should also consider leaving larger, older trees, especially those in mesic microsites, in their stand matrix to conserve sensitive epiphyte habitat and diversity.

Our findings highlight the fact that, to whatever extent possible, old, large trees should be preserved in managed stands due to their ability to serve as reservoirs of biological diversity. We recommend that managers aim to maintain and promote a mix of tree heights, substrate types, and live and dead canopy structures to maximize epiphyte diversity and cover in forests (Sillett & Antoine 2004). Thus, uneven-aged management practices that promote multiple cohorts and therefore structural complexity at the stand-level can improve epiphyte conservation and perpetuation. Furthering this concept of active management to promote structural and ultimately biological diversity, recent work suggests that canopy manipulations in mature second-growth forests can quickly and significantly increase structural heterogeneity in treetops, an important first step in creating suitable habitat for epiphyte recruitment and establishment (Sillett et al. 2018). Epiphytes should be a serious consideration in forest restoration and timber production, as they provide essential services such as nutrient cycling that are imperative to ecosystem productivity. Furthermore, once lost, epiphytes and their ecological services can be difficult to recover.

Future research

Future studies are needed to investigate the importance of epiphyte fog water use, particularly if fog frequency is decreasing, as well as the possible mutualisms between epiphytes and their host trees. For example, do epiphytes measurably increase within-crown relative humidity, thereby influencing host tree physiology? Additionally, more work is needed to understand how changes in climate and air quality will affect epiphyte ranges and distributions.

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