Bark characteristics affect epiphytic bryophyte cover across tree species

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ABSTRACT

Forest tree communities are shifting as a result of changes in regional climate and human management, which has cascading effects on other members of the community such as epiphytic bryophytes. Epiphytic bryophytes play important roles in ecosystem function, and their distribution is highly dependent on the characteristics of their substrate. To see how epiphytic substrate characteristics affect bryophyte abundance, we measured bark thickness, pH, and water holding capacity as it varied with bryophyte coverage on five different species of trees in Northern California. We found that coniferous trees had more acidic bark and lower bryophyte cover. Additionally, bark thickness and water holding capacity predicted bryophyte coverage across individual trees of the Pacific madrone (Arbutus menziesii), but not in the other four species we measured. More research is necessary to determine which bark characteristics drive bryophyte coverage in species where bryophytes are highly successful. The tree species we measured that had the most bryophytic success are under threat of coniferous encroachment. These looming compositional changes must be further assessed to determine what effect they will have on the abundance and diversity of bryophyte communities that depend on them.

Keywords: bryophyte, epiphyte, bark characteristics, substrate suitability, forest community shifts

INTRODUCTION

Forest communities are rapidly changing with increasing human impact. Recent climate models predict compositional changes in the form of species range shifts (Chen et al. 2011), and range contractions in North American forests (Zhu et al. 2012). Additionally, some forest communities are shifting in response to changing management regimes (Valachovic 2015). However, while there has been a focus on tree community shifts due to human activity, less is known about how these shifting tree species will affect the less-charismatic plants that depend on them, like epiphytic bryophytes.

Bryophytes are a conglomerate of ancient non-vascular plant lineages which include mosses, liverworts, and hornworts. Ecologically, they play important roles in water cycling, nutrient cycling, and
providing microhabitats for invertebrates. Epiphytic bryophytes act as secondary interceptors of rainfall, decreasing the amount of rainfall reaching the ground and slowing the overall water velocity, which reduces erosion (Veneklaas et al. 1990). Bryophytes provide resource pools of many essential elements which are slowly released and available to the surrounding biomass in excess water shed from wet leaves (Rieley et al. 1979, Coxson 1991). Epiphytic bryophytes provide a moist habitat for invertebrates which assist in returning nutrients trapped in detrital matter back to the ecosystem level nutrient cycle (Glime 2017). Collectively, bryophytes are of great ecological importance.

Despite their ecological significance, bryophytes receive little attention in conservation and ecological research. Bryophyte species face a yearly extinction rate of 2-4% worldwide (Hallingbäck and Tan 2010), but in the United States there is no federal protection for any bryophyte species (USDA). Especially concerning is the lack of state-level protection for bryophytes in the Pacific Northwest (Northern California, Washington, Oregon), which was identified as a hotspot for global bryophyte diversity (Vanderpoorten and Hallingbäck 2008). To manage these susceptible species it is imperative to understand where they are able to establish themselves and thrive.

Bryophytes are able to grow on a wide variety of patchy substrates such as rocks, decaying logs, and live trees, yet individual species are renowned for their substrate specificity (Cleavitt 2001). Substrate characteristics like moisture (Li and Vitt 1995) and chemistry (Robinson et al. 1989) are some of the most important factors in determining bryophyte establishment (Wiklund and Rydin 2004). Many epiphytic bryophytes are not only specific to bark, but are only found on bark with favorable characteristics (Bates and Brown 1981). Thus, bark characteristics likely drive epiphytic bryophyte distributions. As tree communities shift, the amount of suitable bark for bryophyte establishment will also change.

In this study, we investigate how bark characteristics and bryophyte coverage vary between tree species. Further, we examine whether or not bark characteristics can predict bryophyte coverage within and across species. We measured bark thickness, pH, and water holding capacity across five tree species in a mixed coniferous forest of northern California. We considered bark thickness to be a proxy for bark age, with older bark giving more time for moss establishment, while pH and water holding capacities are our measures of bark chemistry and moisture. We hypothesize that bryophyte coverage would be greatest on thicker bark, with intermediate pH, and a high water holding capacity. Understanding what dictates bark suitability for bryophytes will help us forecast how changes in forest composition will affect bryophyte distribution and the ecological services they provide.

METHODS

2.1 Study System

We collected data in May of 2019 on Black Oak Mountain trail (39.7313 N, -123.6262 W) in Angelo Coast Range Reserve, a UC Natural Reserve System managed area located in the Northern California Coast Ranges. Our research was conducted on the north-facing slope in a mixed coniferous forest dominated by
Douglas fir (*Pseudotsuga menziesii*). Our study focused on Douglas fir, tanoak (*Notholithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), Pacific madrone (*Arbutus menziesii*), and bay laurel (*Umbellularia californica*), all of which were abundant in the area. These species were chosen for their array of bark characteristics and bryophyte cover. The dominant epiphytic bryophyte in the area was *Homalothecium nuttallii*, but smaller amounts of *Porella* sp. and *Frullania* sp. were also observed on some trees. Our sampling was limited to an elevational range between 500–600 m to control for plant community changes at different elevations.

### 2.2 Experimental Design

#### 2.2.1 Tree Sampling

One tree of each species was sampled in randomly chosen locations along the trail to control for differences in bryophyte spore exposure based on location. For each tree, we recorded the species and measured the diameter at breast height (DBH) and canopy cover. A 33 cm x 33 cm quadrat was placed on the north side of each tree to obtain a visual assessment of percent bryophyte cover. The Douglas fir, tanoak, canyon live oak, and Pacific madrone trees we sampled had a minimum DBH of 20 cm to ensure that the quadrat did not reach the tree’s south side. Bay laurels were allowed to have a minimum DBH of 13 cm due to their smaller growth form, and the quadrat was scaled down proportionally. To obtain a measurement for bark thickness, we used a hatchet to cut into a bark furrow until reaching the layer of cork cambium (bark producing cells within a tree) and used a ruler to measure the distance from the cork cambium to the outermost layer of the bark. Additionally, we removed 15 g of bark from 10 Douglas firs, tanoaks, canyon live oaks, and Pacific madrones, and 5 bay laurels to test water holding capacity and pH.

#### 2.2.2 Water Holding Capacity Tests

To measure water holding capacity, we chose 10 bark samples of similar surface area and mass from each species (5 from bay laurel) and submerged them in water for 30 minutes to completely saturate the bark. After saturation, the wet mass of each sample was recorded. Then, bark was placed in drying pockets (window screen mesh stapled into 10 cm pockets) and hung in the sun to dry. After 9 hours, bark samples were re-weighed for a final dry mass. Water holding capacity was calculated by \((\text{wet mass} - \text{dry mass})/\text{(wet mass)}\).

#### 2.2.3 pH Tests

To find the bark pH, we made 10 cups of ‘bark tea’ for each species (5 for bay laurel). We cut and ground 3 g of bark from each tree until all chunks were less than 5 mm thick, most being less than 1 mm. The ground samples were placed within 100 mL of boiling water and left to steep for 15 minutes. After 15 minutes, the pH of each sample was taken with the H198128 pHeP®5 pH/Temperature Water Tester with 0.01 pH Resolution (HANNA Instruments, https://hannainst.com/). The pH meter was calibrated after every 5 samples. Samples were processed in monospecific groups of five with an additional control cup of water without bark.
2.3 Statistical Analysis

Statistical analyses were conducted using JMP student v. 14. Larger trees naturally had thicker bark, so we used a linear regression between DBH and bark thickness of all trees sampled and saved the residuals for statistical analyses. The residuals yielded a size-independent measurement of bark thickness, which allowed us to characterize a tree’s bark as thicker or thinner than its DBH would predict. For within-species analyses, separate linear regressions of DBH and bark thickness were used for each species. ANOVA and Tukey Kramer tests were used to assess the difference in percent bryophyte cover, pH, water holding capacity, and residual bark thickness across species. ANCOVAs were used to test how residual bark thickness, canopy cover, DBH, water holding capacity, and pH interact to affect bryophyte cover across and within each species.

RESULTS

We observed a total of 80 trees, with 19 Pacific madrones, 19 tanoaks, 18 canyon live oaks, 15 Douglas fir, and 9 bay laurels. We sampled only 15 Douglas fir trees because of their low variation in variables measured. Additionally, only 9 bay laurels were sampled due to the difficulty of finding trees at our site that exceeded our minimum DBH. We found that bryophyte coverage varied between tree species (N=80, F=21.25, p<0.0001; Figure 1a). Mean coverage was highest in the bay laurel (65%), canyon live oak (61%), and tanoak (53%). Bryophyte coverage was intermediate in the Pacific madrone (32%) and lowest in the Douglas fir (2%).

Bark characteristics also varied between tree species. Bark pH was greater in deciduous than coniferous trees (N=45, F=100.85, p<0.0001; Figure 1b). Deciduous trees had an intermediate bark pH (6.5-7.0) and our coniferous Douglas fir had an acidic pH (4.5). Water holding capacity was highest in the Pacific madrone (x̄=1.75) and lowest in the tanoak (x̄=0.22) (N=45, F=24.32, p<0.0001; Figure 1c). Finally, diameter-independent bark thickness, calculated using residuals of a linear regression between DBH and bark thickness (R²= 0.76, p<0.0001), was greater in the bay laurel, tanoak, and Douglas fir, than in the canyon live oak and Pacific madrone (N=80, F=19.90, p<0.0001; Figure 1d).

Within species, our models of covarying factors did not predict bryophyte coverage for tanoak (N=10, R²=0.41, p=0.73), canyon live oak (N=10, R²=0.28, p=0.88), and Douglas fir (N=10, R²=0.41, p=0.86). We were not able to fit a model to bay laurel as our sampling size when including all characteristics was too small (N=5). However, in the Pacific madrone, our model predicted moss coverage on individual trees within the species effectively (N=10, R²=0.96, p=0.008; Table 1). In the madrone model, bark thickness (p=0.003), DBH (p=0.005), and water holding capacity (p=0.01) had a positive effect on bryophyte coverage, whereas canopy cover had a negative effect (p=0.005).
Figure 1. Tree species vary in bryophyte coverage and bark characteristics. Five different tree species were sampled at the same site in Angelo Coast Range Reserve. Between species mean measurements are shown to vary in a. percent bryophyte cover, b. pH, c. water holding capacity, and d. size-independent bark thickness. Vertical bars are one standard error from the mean in either direction. Different letters indicate significant differences. a. Bryophyte percent cover was estimated using a quadrat at DBH. b. pH was obtained by making ‘bark tea’. c. Water holding capacity was calculated by \((\text{wet mass} - \text{dry mass})/\text{wet mass}\). d. Size-independent bark thickness was derived from the residuals of a linear fit between DBH and actual bark thickness across all tree species.

DISCUSSION

We observed clear differences in bark characteristics across tree species, but only some of these characteristics predicted bryophyte coverage. Across species, our hypothesis that intermediate pH would produce high bryophyte coverage was supported. The Douglas fir trees we observed often had no bryophyte coverage, and their bark pH was dramatically lower than all other deciduous species we sampled. Because Douglas fir had comparable water holding capacity and bark thickness to other species with more moss cover, pH may be driving its low bryophytic coverage (Figure 1). Previous studies have shown that the low bark pH of conifers correlates with decreased bryophyte species abundance and richness (Drew and Billings 1938). Within species, pH did not have a strong influence in predicting bryophyte coverage, potentially due to the low variability of bark pH within species. Our findings indicate that pH may be an initial filter for bryophyte establishment across tree species, with a low pH inhibiting bryophytic growth.

Our hypothesis that bryophyte coverage would be greater on thicker bark and bark with a high water holding capacity was not supported. Across species, bark thickness and water holding capacity differed, but they did not serve as predictors for bryophyte coverage. Amongst the three species with the highest bryophyte coverage, bay laurel and tanoak had thick bark and intermediate water holding capacity, whereas canyon live oak had thin bark and low water holding capacity. Despite this, these three species did not differ in moss coverage (Figure 1a,c,d). Our measure of water holding capacity did not account for water retention rates, which has been shown to support greater abundances of bryophytes (Drew and Billings 1938). Furthermore, bark thickness may be a better proxy for growth or bark peeling rate in many species, rather than bark age. These between species differences should be characterized in order to determine what the implications of bark thickness are on bryophyte coverage.

Within species, our variables were successful in predicting bryophyte coverage in the Pacific madrone, but not in our other four species. The madrone may serve as a
good model system for studying bryophytic substrate suitability because it had intermediate bryophyte coverage. This implies that the factors we studied played an important role in limiting the establishment of bryophytes on the madrone’s trunk. Bryophyte coverage in madrone was higher in bark with a higher water holding capacity (Table 1), pointing to bryophytic dependence on moisture for establishment and reproduction. Additionally, bark thickness had a positive effect on bryophyte coverage in the madrone. This pattern may be due to the rapid rate of bark peeling this tree experiences, with thicker bark being older and shedding less frequently (Bressette and Hamilton 1999). In tropical systems, tree trunk/limb microhabitats with higher peeling rates are shown to have negative effects on the epiphyte abundance (López-Villalobos 2004). Thus, it is likely that bryophytes are more successful at establishing on older bark with a lower peeling rate in the Pacific madrone. In our non-peeling deciduous species (bay laurel, tanoak, canyon live oak), the effects of bark thickness may not be important in the success of bryophytes. Future studies should investigate other potential drivers of moss distributions within non-peeling trees where bryophytes are successful.

Table 1. Covarying bark characteristics affect moss coverage within Pacific madrone. ANCOVA of bryophyte cover at DBH based off of covarying factors: pH, water holding capacity, size-independent bark thickness, canopy cover, and DBH.

<table>
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<th>Characteristic</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
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<td>pH</td>
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<td>0.032</td>
<td>3.999</td>
<td>0.116</td>
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<tr>
<td>Water Holding Capacity (g)</td>
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<td>0.159</td>
<td>19.541</td>
<td>0.012*</td>
<td>positive</td>
</tr>
<tr>
<td>Size-Independent Bark Thickness (mm)</td>
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<td>0.315</td>
<td>38.947</td>
<td>0.003**</td>
<td>positive</td>
</tr>
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<td>Canopy Cover (%)</td>
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<td>32.292</td>
<td>0.005**</td>
<td>negative</td>
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<td>DBH (cm)</td>
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<td>Total</td>
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Regardless of what drives the success of the bryophytes we observed on individual deciduous trees in the Pacific Northwest, these epiphytic species still face the continuing threat of shifting host communities. Our findings support previous literature which suggest that increasing bark acidity decreases bryophyte abundance. For example, in Europe Vanderpoorten et al. found that bryophyte abundance decreased in conifer-dominated (low pH) forest stands (2004). When available bark types shift from neutral to acidic pH levels, bryophytes that are adapted for the former will be unable to survive and establish themselves in the shifted community. This threat is especially prevalent in California, where a drastic change in management regimes has allowed for conifer encroachment into oak woodlands (Cocking et al. 2015). Studies assessing how these forest shifts might
affect bryophyte communities are imperative for conservation of species that are dependent on the mixed forests of the Pacific Northwest. Understanding microhabitat suitability for specific bryophyte species will ultimately help us understand where these bryophytes can survive. This could lead to increased pressure to manage forests in a way that considers their importance as functional members of the ecosystem.

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REFERENCES


