Forest Ecology and Management 392 (2017) 195–201

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Canopy distribution and survey detectability of a rare old-growth forest lichen

Jesse E.D. Miller [a,*], John Villella [b], Greg Carey [b], Tom Carlberg [c], Heather T. Root [d]

[a] Department of Environmental Science and Policy, University of California Davis, 1 Shields Avenue, Davis, CA 95616, United States
[b] Siskiyou Biosurvey, LLC, Eagle Point, OR 97524, United States
[c] Six Rivers National Forest, Eureka, CA 95501, United States
[d] Botany Department, Weber State University, Ogden, UT 84403, United States

ARTICLE INFO

*Article history:*
Received 24 January 2017
Accepted 5 March 2017

*Keywords:*
Adaptation
Cyanolichens
Epiphytic lichens
*Lobaria*
Range limits
Survey and manage

ABSTRACT

Forest managers in many parts of the world are charged with protecting rare lichen species, including species growing near their range limits. Rare lichens may be particularly vulnerable to effects of climate change, and conserving lichen diversity necessitates understanding factors that limit species distributions. Habitat suitability envelopes for lichens are shifting as the climate changes, but it is unclear whether and how local (e.g., within-tree) lichen species distributions will shift. Conserving lichen biodiversity also requires effective field surveys to detect and monitor rare lichen populations. However, the reliability of rare lichen survey methods currently used across global forest lands is rarely tested. In this study, we quantify the canopy distribution of an epiphytic old-growth forest cyanolichen near its southern range limit and test whether ground surveys reliably detect canopy populations. Near its southern range limit, *Lobaria oregana* was most abundant in two distinct zones within tree crowns: on branches of large trees in the mid-crown, and on boles of small trees near ground level. The abundance of this species near ground level suggests that lichens may benefit from cooler, wetter microclimates near the equatorial edges of their ranges. Maintaining these microclimate habitats may be a key to long-term viability of rear edge lichen populations. Targeted ground surveys reliably detected *L. oregana* in litterfall underneath trees where it was abundant in the crowns. However, ground surveys did not reliably detect the lichen underneath trees when it occurred in the crowns in low abundance. Our results suggest that ground surveys are useful for characterizing abundant lichen species, but that canopy surveys (e.g., tree climbing) may be needed to reliably detect lichens when they occur at low abundance.

© 2017 Elsevier B.V. All rights reserved.

## 1. Introduction

Lichens, although sometimes inconspicuous, contribute significantly to forest biodiversity and play key ecological roles. Lichens are important for forest nutrient cycling, and together with other cryptogammic organisms (bryophytes, algae, cyanobacteria, and fungi), are responsible for almost 50% of terrestrial nitrogen fixation (Elbert et al., 2012). Lichens can be sensitive to disturbances and small changes in ambient conditions, in part because they respond to the environment at fine scales (Esseen and Renhorn, 1998). Environmental changes at multiple scales, including those caused by climate change and forestry practices, can threaten lichen populations (Nascimbene and Marini, 2015). Rare species, including species growing near the edge of their ranges, may be especially vulnerable (Allen and Lendemer, 2016). Maintaining lichen diversity is a goal of forest managers in many parts of the world, and management efforts often focus on conserving populations of rare species.

Planning for lichen conservation in a changing climate requires understanding factors that control lichen distributions at both local and regional scales. While it is known that biogeographic lichen habitat suitability envelopes are shifting due to climate change (Allen and Lendemer, 2016; Rubio-Salcedo et al., 2016), it is less clear whether and how local (e.g., within-tree) lichen species distributions will shift in response to an altered climate. However, understanding species microclimate affinities is crucial for understanding the effects of climate change on populations (Potter et al., 2013). Studies of lichen distributions within the forest canopy have typically been conducted where lichens are abundant in the heart of their ranges (e.g., McCune et al., 1997), but the canopy distributions of lichens growing at their range limits have

* Corresponding author.
*E-mail address:* kawriver@gmail.com (J.E.D. Miller).

http://dx.doi.org/10.1016/j.foreco.2017.03.007
0378-1127/© 2017 Elsevier B.V. All rights reserved.

less commonly been quantified. If species growing near their range limits exhibit local habitat adaptations (e.g., growing in cooler microclimates at the warmer end of the range), this could inform the restoration and maintenance of habitat for lichens of conservation concern. For example, local assisted relocation to more benign microclimates could be effective, especially for dispersal-limited species, if species show signs of adaptations to these microclimates in the wild. Understanding habitat requirements of populations at the rear edge of a species' range (e.g., populations at the southern range limit of a species that is moving north) is particularly important because rear edge populations usually contain high genetic diversity and can be nuclei for future speciation (Hampe and Petit, 2005).

Locating and monitoring rare lichen populations is crucial for informing management practices that further lichen conservation, and for studying lichen distributions and global change impacts on lichen populations. Field surveys for rare lichens are often conducted over large areas, such as in timber sales covering hundreds to thousands of hectares, thus representing significant financial cost (Molina et al., 2006). Surveys for rare canopy-dwelling lichens are usually conducted entirely from the ground, and rely on finding lichen thalli in litterfall to detect populations (e.g., Derr et al., 2003), in part because tree climbing for canopy lichen surveys is labor intensive. While the survey detectability of organisms such as birds has received substantial consideration (e.g., Royle et al., 2005), there has been less work testing lichen detectability and the effectiveness of lichen survey protocols. Studies of canopy lichen survey protocols have mostly focused on comparing various ground-survey techniques (e.g., Britton et al., 2014; Frati and Brunialti, 2006). While litterfall is known to be coarsely representative of canopy lichen abundance (McCune, 1994), there has been little direct investigation of whether lichens present in the canopy in low abundance are reliably represented in litterfall (but see Rosso et al., 2000).

In this study, we quantify canopy distributions of an old-growth forest lichen species near its southern (equatorial) range limit and test whether ground surveys that examine lichen litterfall can effectively detect canopy populations. *Lobaria oregana* is a lichen that is endemic to the Pacific Northwest of North America, where it occurs as an epiphyte in old-growth rainforest trees (Brodo et al., 2001) and often becomes the most abundant cyanolichen (McCune, 1994). *Lobaria oregana* plays important ecological roles in northwest rainforests, particularly by providing a major source of available nitrogen for plants (Holub and Lajtha, 2004; Pike, 1978). It is also a major nutrient source for canopy-dwelling heterotrophic organisms (Cooper and Carroll, 1978), and it is rapidly consumed by ground dwelling arthropods once it accumulates as litterfall on the forest floor (McCune and Daly, 1994). Despite the fact that *L. oregana* can occur in all forest age classes when transplanted, poor dispersal and/or establishment functionally limit its occurrence to primarily old-growth stands (Sillett et al., 2000; Werth et al., 2006).

In Oregon and Washington—near the heart of its range—*L. oregana* is most abundant in the "light transition zone" of the mid-canopy at around 20 m above the ground (McCune, 1993; McCune et al., 1997). The light transition zone is a vertical portion of the canopy characterized by intermediate levels of light and moisture, between the drier, brighter upper canopy and wetter, darker lower canopy (McCune et al., 1997). There has been little work testing whether this distribution remains constant near range edges, but it has been suggested that lichens may take refuge in buffered microsites lower in the forest profile near their range limits (McCune, 1993). Understanding where such habitat shifts occur is crucial for planning management activities that are compatible with lichen population persistence. For example, small trees are frequently thinned in forests where *L. oregana* occurs, but the effects of thinning on lichen populations growing near their range limits has been little studied. Because large cyanolichens are often sensitive to anthropogenic influences and are among the lichens most threatened by climate change, survey detectability and canopy distributions of *L. oregana* have implications for other rare lichens as well (Nascimbene et al., 2016; Rubio-Salcedo et al., 2016).

Here, we examine the distribution of *L. oregana* within trees in northwest California, USA, with two specific objectives. First, we ask where on trees *L. oregana* is most likely to be found in these southern habitats and compare these microhabitat associations to other parts of the species' range. Second, we ask whether ground-based surveys consistently detect the species, even when it is found in low abundance using canopy surveys.

## 2. Material and methods

### 2.1. Site selection

*Lobaria oregana* reaches the southern edge of its range in northwest California (McCune and Geiser, 2009) where it occurs only sporadically and is listed as a Survey and Manage Category A species (USDA & USDI, 2001). This designation requires the U. S. Forest Service to conduct surveys for *L. oregana* to protect sites where it occurs from disturbance caused by management activities such as logging. Ground-based pre-disturbance surveys for *L. oregana* have been conducted in Six Rivers National Forest since 2001. Surveys generally follow "intuitive-controlled" methods, in which a surveyor searches for the lichen in litterfall, focusing on areas that seem likely to have the species based on the species' ecology and the surveyor's experience (Derr et al., 2003). These surveys have documented 55 occurrences of *L. oregana* populations within the Forest.

To select study sites, we grouped the 55 known sites on the forest by their distributions across 14 sub-watersheds of the Smith River. Within each sub-watershed, we selected a single site for study. We attempted to capture the greatest possible variation in vegetation type, seral stage, size class, canopy cover, and stand composition. We also attempted to maximize variation in elevation, aspect, and soil. To explore vegetation types and environmental variables, we used California's Wildlife Habitat Relationships information system (California Interagency Wildlife Task Group, 2008) and the USDA Existing Vegetation Classification Framework (Tart et al., 2005). Of the fourteen sites chosen, ten were prioritized for study and the remaining four were reserved as alternate sites if any of the first ten could not be accessed (Fig. 1). Our sites were well-dispersed among the three main branches of the Smith River watershed (North, Middle, and South Forks). The minimum distance between study sites was 1.3 km.

### 2.2. Field surveys

During the winter of 2014 we conducted fieldwork to quantify *Lobaria oregana* canopy distributions and ground survey detection. At each of the ten sites, we selected 10–15 trees for crown surveys. Because *Pseudotsuga menziesii* was the dominant tree species at all sites—making up an average of 86% of site-level tree occurrences—and other trees species were not abundant enough to draw reliable inference, we studied only *P. menziesii* trees. We climbed using the doubled rope technique (Adams, 2007). We assessed the abundance of *L. oregana* on tree boles and branches within vertical divisions of 6.1 m for each tree. Height in the tree was measured using marked ropes or tape measures lowered to the ground. For each 6.1 m division, we envisioned a cylinder with the bole of the tree as its axis and a radius equal to the length of the longest branch

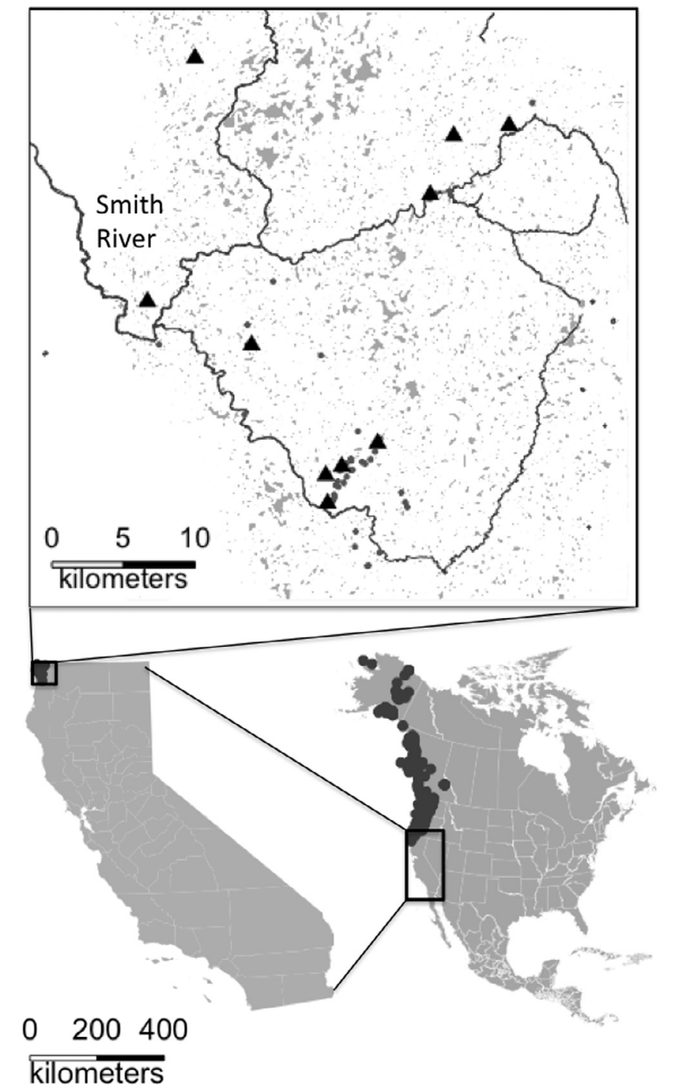


**Fig. 1.** Map of study sites in the Smith River Watershed. Study sites are shown as triangles, and *Lobaria oregana* populations that were not studied are shown as small grey circles. Light grey polygons represent late successional forest stands. In the insets of North America and California, the dark shaded areas represent the range of *L. oregana*.

falling within that division. The radius of each cylinder was further divided into three equal lengths, resulting in three concentric cylinders: inner, middle and outer (Fig. 2). An ocular estimate of the percent cover of *L. oregana* was made separately for the bole of the tree and for each of the three cylinders within each 6.1 m vertical division. Trees in full view and in close proximity to the climbed trees were also analyzed using the above methodology resulting in a sample size of 169 trees across the ten study sites. At each site, we climbed three or four trees and assessed seven to ten neighboring trees from adjacent climbed trees.

We conducted ground surveys for *L. oregana* thalli in litterfall underneath each of the trees for which crown surveys were performed. All fieldwork was conducted by TC, GC, and JV, who routinely conduct surveys for rare lichens. Ground-survey methods employed here are representative of typical rare lichen surveys conducted on public lands in the USA following survey and manage protocols (Derr et al., 2003). These surveys involved thoroughly walking the area underneath each tree canopy examining canopy litter for *L. oregana* thalli.

**Fig. 2.** Schematic diagram showing how trees were divided into vertical and horizontal zones for surveys. Vertical space was divided into 6.1 m tall zones, and horizontal space was divided into four zones: the tree bole and the inner, middle and outer branches.

## 2.3. Analysis

Because the dataset was zero-inflated and some predictor variables had nonlinear relationships with *L. oregana* abundance, we used nonparametric multiple regression (NPMR; McCune, 2006) in the software HyperNiche v. 2.16 (McCune and Mefford, 2010) to analyze drivers of *L. oregana* canopy distributions. We used tree diameter at breast height (DBH), survey height, and survey horizontal position (bole or inner, middle or outer branches) as predictors of *L. oregana* presence at each of 4140 individual survey locations within the 169 individual trees. NPMR develops response curves using a local mean estimator multiplied across predictors with a Gaussian kernel function (Bowman and Azzalini, 1997). The breadth of the kernel function was estimated as the "tolerance" optimized using leave-one-out cross-validation to maximize the logarithm of the likelihood ratio. The neighborhood size reflects the average number of data points contributing to estimates and was set to at least 207. We report sensitivity, which measures the effect size of each predictor as a ratio relative to the range of the predictor. A *P*-value for the model was calculated using 100 randomizations of the data.

To assess whether *L. oregana* crown abundance affected the probability of its detection in litterfall underneath trees in which it occurred in the crown, we began by running a generalized linear mixed model with total *L. oregana* crown abundance as the predictor variable and the probability of detecting *L. oregana* on the ground as the response variable. We used a log likelihood test to determine whether a stand-level random effect significantly improved the model. Because there was not a significant difference between models with and without the random effect (Likelihood ratio test: c2 = 2.26, df = 1, $P = 0.13$), we proceeded with a generalized linear model.

## 3. Results

### 3.1. Stand conditions

The 10 known *L. oregana* populations that we surveyed all occurred in late-successional forest, but the size of trees in the vicinity of *L. oregana* populations varied. Stands at some sites contained only large, old (>30 cm DBH) trees, while other sites contained a mix of large and small (<30 cm DBH) trees. The median height of trees we sampled across all plots was 38.1 m (First quartile [Q1]: 25.9 m, Third quartile [Q3]: 45.7 m). We did not age trees, and it is common for small trees to be quite old as a result of shade-stunted growth in our study area. Tree composition ranged from pure stands of *Pseudotsuga menziesii* to mixed stands with *P. menziesii* and, in various combinations, *Notholithocarpus densiflorus*, *Quercus chrysolepis,* and *Acer macrophyllum*. *Arbutus menziesii*, *Chrysolepis chrysophylla,* and *Taxus brevifolia* also occurred once in a single plot each.

### 3.2. Canopy distribution

Total stand-level *L. oregana* abundance varied substantially among the 10 populations we sampled. At most sites, *L. oregana* was present in several of the approximately ten trees we surveyed, but at one site only a single thallus occurred in a single tree. Of the 169 trees we surveyed, 94 (56%) contained at least one *L. oregana* thallus. *L. oregana* occurred in various positions throughout the crowns of *P. menziesii* trees—vertically, from ground level to 60 m above ground, and horizontally, from the tree boles to outer crown branches. *L. oregana* occurred at 11% of the individual canopy locations that we sampled. At canopy locations where it was present, median *L. oregana* cover was 1% (Q1: 0.5%, Q3: 3%). At a few survey locations *L. oregana* cover was much higher, reaching a maximum cover of 35%.

Tree DBH, vertical position, and horizontal position (bole or inner, middle or outer branches) were all significant predictors of *L. oregana* occurrence (Table 1; Fig. 3). *L. oregana* was generally most abundant in two distinct zones within the canopy. It reached high local cover on small (<20 cm DBH) trees, where it usually was most abundant on the boles of the trees at low vertical positions (<15 m) near ground level, and on larger (>30 cm DBH) trees, where it was most abundant on the inner and middle branches of trees at mid-crown heights (~30 m). Across all sites, *L. oregana* was uncommon in outer branch positions and in the upper vertical third of the tree crowns.

### 3.3. Ground survey detection

The occurrence of *L. oregana* thalli in litterfall under individual trees where it occurred in the crown increased significantly as its abundance in the crown increased (Fig. 4, GLM, binomial distribution, $T_{1,90} = 35.4$, $P < 0.001$). Of the 92 trees where *L. oregana* occurred in the crown, it was found as litterfall on the ground beneath 57 trees (62%). It was detected beneath 97% of trees that had high *L. oregana* abundance in the crown (trees in the upper tertile of *L. oregana* cover), 60% of trees with intermediate *L. oregana* crown abundance (trees in the middle tertile), and only 17% of trees with low *L. oregana* crown abundance (trees in the lower tertile). *L. oregana* thalli were detected in litterfall at least once at nine of the ten forest stands we surveyed, even though it was not reliably found underneath individual trees where it occurred in the crown. At the one site where *L. oregana* was not found in litterfall, only a single thallus was observed in the canopy.

## 4. Discussion

### 4.1. Canopy distribution

*Lobaria oregana* tends to occur in two distinct zones within trees in old-growth forests near the southern end of its range. It is particularly abundant on the lower boles of small trees, and also abundant in the branches of larger trees at intermediate vertical positions. The latter distribution – in the "light transition zone" on large trees – has been well documented near the heart of *L. oregana*'s range (Lyons et al., 2000; McCune et al., 1997; Rosso et al., 2000; Sillett, 1995). Although it has been previously observed that old-growth forest lichens shift their ranges to lower canopy positions at drier sites (McCune, 1993), we are unaware of other studies that have quantitatively documented shifts towards lower canopy positions and smaller trees at lichen species range limits (but see Rosso et al., 2000).

This distribution pattern raises the question of whether *L. oregana* uses small trees as a refuge habitat near its range limits. The mid-canopy, where *L. oregana* is most abundant in the heart of its range, is relatively hot and dry at the southern range limit of the species. Since the lowest part of the forest canopy is the darkest and wettest (Geiger, 1965; Lyons et al., 2000), boles of small trees may provide a microclimate that facilitates the persistence of this rainforest lichen in the area of its range with the harshest conditions. These results highlight that maintaining or restoring such mesic microclimates may be a key to conserving old-growth lichens near their range limits. They also suggest that local managed relocations into dark, wet microclimates could be successful. We are not aware of previous research that tests how environmental conditions (especially light and moisture) at forest floor and mid-canopy habitats vary between lichen range centers and edges, and such work would help us understand drivers of population distributions within forest canopies at their range limits. Assessing whether southern populations contain uniquely adapted genotypes, as research with other organisms has found, could also be useful for rare lichen conservation under a changing climate (Hampe and Petit, 2005).

Transplant studies have suggested that *L. oregana* is generally restricted to old-growth forests because of dispersal and/or establishment limitation (Sillett et al., 2000; Werth et al., 2006). Our results show that *L. oregana* can thrive on small trees in natural environments, providing further evidence that it is not dependent on the substrate provided by large trees. However, even if *L. oregana* can theoretically live outside old growth forests, for practical

**Table 1**
Non-parametric multiple regression models predicting *Lobaria oregana* occurrence. AUC represents how well the model predicts presence or absence of *L. oregana* and is equal to 1 when the model perfectly predicts species occurrences. $N^*$ is the average number of plots contributing to an estimate. Tolerance reflects how broadly an estimate is based on predictors, and sensitivity estimates the average effect size as a ratio relative to the range of the predictor.

| # plots | AUC | $N^*$ | *P*-value | Predictors | Tolerance | Sensitivity | Range |
|---|---|---|---|---|---|---|---|
| 4140 | 0.723 | 209.2 | 0.01 | DBH | 9.52 | 0.187 | 68 |
| | | | | Lateral | 0.60 | 0.121 | 3 |
| | | | | Vertical | 2.70 | 0.123 | 18 |

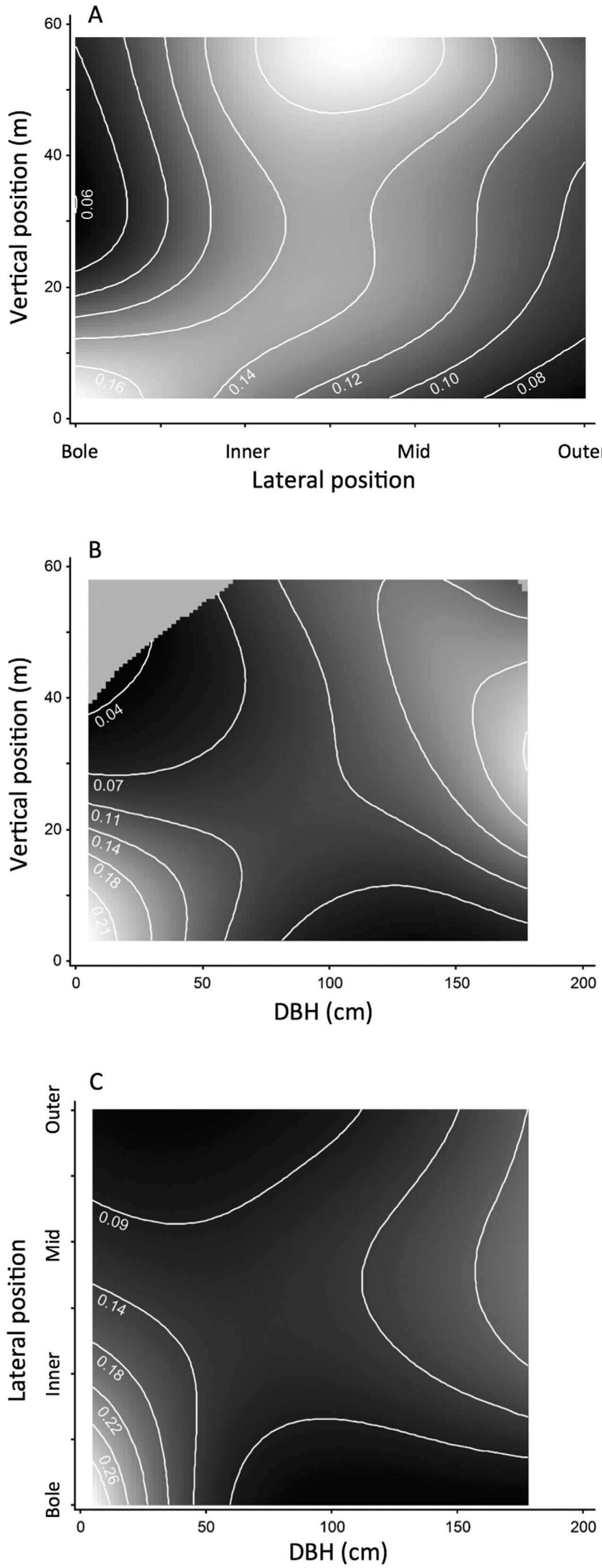


**Fig. 3.** Response surfaces from non-parametric multiple regression models showing the probability of *Lobaria oregana* occurrence as predicted by tree diameter (DBH) and vertical and horizontal canopy position (see model details in Table 1). Modeled probability of occurrence is represented by shading with light-colored areas representing high probability, black representing low probability, and white topographic lines representing isoclines. The grey area in the upper left corner of panel B was not modeled because of insufficient data with that combination of predictors.

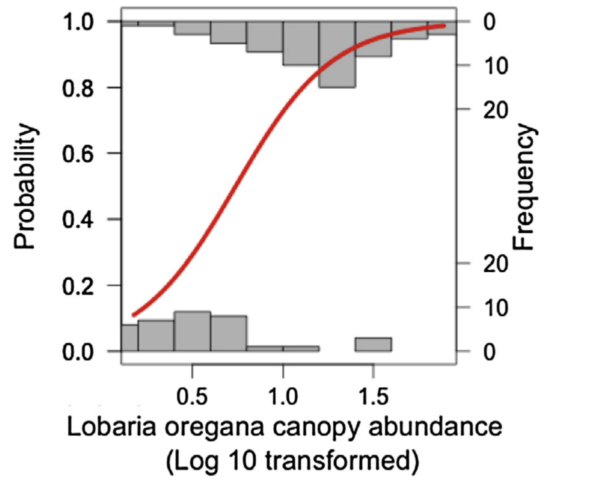


**Fig. 4.** The probability of *L. oregana* being detected in ground surveys beneath trees where it occurs (Y-axis; modeled as logistic regression line) as predicted by tree-level *L. oregana* canopy abundance (X-axis). Grey bars are histograms of *L. oregana* canopy abundance in trees beneath which it was detected (top) and was not detected (bottom).

management purposes it should be considered primarily an old-growth-forest-dependent species—albeit one that can grow across a range of tree sizes, and perhaps ages, within the greater old-growth landscape. Because *L. oregana* and other rare cyanolichens (e.g., *Nephroma occultum*, Rosso et al., 2000) are often largely limited by dispersal and/or establishment, they may be good candidates for assisted relocation.

### *4.2. Ground survey reliability*

Our test of survey methods shows that ground surveys that rely on litterfall can effectively detect large *Lobaria oregana* populations, but detection of small populations appears to be less reliable. Our results highlight that populations can be most reliably detected by ground surveys when the entire stand is thoroughly explored for litterfall, since populations often span multiple trees. Surveys under individual trees only found litterfall when the lichen was abundant in the tree crown. However, at the stand level, nine out of ten *L. oregana* populations were detected via at least one thallus found on the ground. Together, these results suggest that ground surveys may not be highly accurate for detecting tree-to-tree variation in lichen presence, but that they are still likely to detect intermediate- to large-sized populations at the stand level.

Our results suggest that when high survey accuracy is desired, ground surveys should be augmented by more focus on the tree canopy in some circumstances. In occasional situations, canopy surveys could potentially be a more effective use of survey time than ground surveys. For example, when a single, large old-growth tree occurs within a 16 ha timber unit of otherwise young, uniformly aged trees, a given amount of survey time might be more likely to detect a *L. oregana* population by climbing the one old-growth tree than by exploring the rest of the silvicultural landscape where it is unlikely to occur. However, it would be impractical to implement universal canopy surveys as a forest management practice, since surveys must cover large areas. An integrated method in which ground surveys are used across the landscape in combination with occasional targeted canopy surveys in promising habitats seems pragmatic. Populations that occur at the lowest canopy positions can be readily observed from the ground with the naked eye, and ground surveyors should also use binoculars to increase detection of *L. oregana* populations growing above ground-level, since *L. oregana* and other rare cyanolichens often have relatively large, visible thalli.

The survey detection implications of this study are likely applicable to many species beyond *L. oregana*. Numerous species of canopy cyanolichens with old-growth affinities are species of conservation concern that are tracked and monitored in many areas of the world (e.g., Rubio-Salcedo et al., 2016). For example, in Oregon, *Nephroma occultum* has similar ecological affinities to *L. oregana*, and often occurs in very low abundance, suggesting that it may be under-detected by ground surveys (Rosso et al., 2000). *Lobaria amplissima* and *Lobaria retigera* are other rare forest canopy epiphytes for which surveys are conducted in Europe and Alaska, respectively, and our findings likely apply to survey detection of these species, in addition to many others (Cornejo and Scheidegger, 2017; Park et al., 2002).

### 4.3. Forestry implications

Thinning forest stands benefits lichen diversity in some contexts (Root et al., 2010). However, the affinity that *L. oregana* has for cool, wet microclimates near its southern range limit suggests that thinning old forests could be detrimental to rare cyanolichens if it increases light and heat low in the canopy. When thinning accelerates the restoration of old growth conditions in previously logged stands, though, it could potentially benefit old-growth lichens in the long-term. Increased fire frequency and severity is also a significant management concern in many parts of the world where rare lichens occur (Enright et al., 2015), and thinning could reduce the intensity of future fires, which could ultimately benefit rare lichen populations. Further experimental studies with surveys before and after thinning stands are needed to assess effects of thinning on rare lichen populations. Until such studies have been conducted, forest managers should proceed cautiously in areas where rare lichens occur.

## Acknowledgements

We thank Lisa Hoover, Forest Botanist, Six Rivers National Forest, for initiating this project. We thank Richard Brock for assisting with fieldwork. We are very grateful to Phil Hahn, Cristina Herren, and Tony Ives for statistical advice. We thank Bruce McCune and two anonymous reviewers for helpful comments that improved the manuscript. We thank Patty Hensley and Arianna Stokes for their editorial assistance. This work was supported by Six Rivers National Forest (USDA Forest Service).

## References

Adams, M., 2007. Safe and efficient tree ascent: doubled rope techniques (DdRT), part two. Arborist News 15, 50–53.

Allen, J.L., Lendemer, J.C., 2016. Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. Biodivers. Conserv. 25, 555–568. http://dx.doi.org/10.1007/s10531-016-1071-4.

Bowman, A.W., Azzalini, A., 1997. Applied Smoothing Techniques for Data Analysis: The Kernel Approach with S-Plus Illustrations. OUP, Oxford.

Britton, A.J., Mitchell, R.J., Potts, J.M., Genney, D.R., 2014. Developing monitoring protocols for cost-effective surveillance of lichens. Lichenologist 46, 471–482. http://dx.doi.org/10.1017/S0024282913000728.

Brodo, I.M., Duran-Sharnoff, S., Sharnoff, S., 2001. Lichens of North America. Yale University Press, New Haven & London.

California interagency wildlife taskforce, 2008. California Wildlife Habitat Relationships Information System.

Cooper, G., Carroll, G.C., 1978. Ribitol as a major component of water-soluble leachates from *Lobaria oregana*. Bryologist 81, 568–572.

Cornejo, C., Scheidegger, C., 2017. Morphological aspects associated with repair and regeneration in *Lobaria pulmonaria* and *L. amplissima* (Peltigerales, Ascomycota). Lichenologist 45, 285–289. http://dx.doi.org/10.1017/S0024282912000813.

Derr, C., Helliwell, A., Ruchty, A., Hoober, L., Geiser, L., Lebo, D., Davis, J., 2003. Survey protocols for Survey & Manage category A & C lichens in the Northwest Forest Plan area.

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M.O., Pöschl, U., 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. Nat. Geosci. 5, 459–462. http://dx.doi.org/10.1038/ngeo1486.

Enright, N.J., Fontaine, J.B., Bowman, D.M.J.S., Bradstock, R.A., Williams, R.J., 2015. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Front. Ecol. Environ. 13, 265–272. http://dx.doi.org/10.1890/140231.

Esseen, P., Renhorn, K., 1998. Edge effects on an epiphytic lichen in fragmented forests. Conserv. Biol. 12, 1307–1317. http://dx.doi.org/10.1046/j.1523-1739.1998.97346.x.

Frati, L., Brunialti, G., 2006. Long-term biomonitoring with lichens: comparing data from different sampling procedures. Environ. Monit. Assess. 119, 391–404. http://dx.doi.org/10.1007/s10661-005-9032-5.

Geiger, R., 1965. The Climate Near the Ground. Harvard University Press, Cambridge.

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8, 461–467.

Holub, S.M., Lajtha, K., 2004. The fate and retention of organic and inorganic 15N-nitrogen in an old-growth forest soil in western Oregon. Ecosystems 7, 368–380. http://dx.doi.org/10.1007/s10021-004-0239-z.

Lyons, B., Nadkarni, N.M., North, M.P., 2000. Spatial distribution and succession of epiphytes on *Tsuga heterophylla* (western hemlock) in an old-growth Douglas-fir forest. Can. J. Bot. 78, 957–968. http://dx.doi.org/10.1139/cjb-78-7-957.

McCune, B., 2006. Non-parametric habitat models with automatic interactions. J. Veg. Sci. 17, 819–830. http://dx.doi.org/10.1658/1100-9233(2006) 17[819:NHMWAI]2.0.CO;2.

McCune, B., 1994. Using epiphyte litter to estimate epiphyte biomass. Bryologist 97, 396–401. http://dx.doi.org/10.2307/3243905.

McCune, B., 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in Western Oregon and Washington. Bryologist 96, 405–411. http://dx.doi.org/10.2307/3243870.

McCune, B., Amsberry, K.A., Camacho, F.J., Clery, S., Cole, C., Emerson, C., Felder, G., French, P., Greene, D., Harris, R., Hutten, M., Larson, B., Lesko, M., Majors, S., Markwell, T., Parker, G.G., Pendergrass, K., Peterson, E.B., Peterson, E.T., Platt, J., Proctor, J., Rambo, T., Rosso, A., Shaw, D., Turner, R., Widmer, M., 1997. Vertical profile of epiphytes in a Pacific Northwest old-growth forest. Northwest Sci. 71, 145–152.

McCune, B., Daly, W.J., 1994. Consumption and decomposition of lichen litter in a temperate coniferous rainforest. Lichenologist 26, 67–71.

McCune, B., Geiser, L., 2009. Macrolichens of the Pacific Northwest. Oregon State University Press, Corvallis, Oregon.

McCune, B., Mefford, M.J., 2009. HyperNiche. Nonparametric Multiplicative Habitat Modeling. Version 2. MjM Software, Gleneden Beach, Oregon, USA.

Molina, R., Marcot, B.G., Lesher, R., 2006. Protecting rare, old-growth, forest-associated species under the survey and manage program guidelines of the Northwest Forest Plan. Conserv. Biol. 20, 306–318. http://dx.doi.org/10.1111/j.1523-1739.2006.00386.x.

Nascimbene, J., Casazza, G., Benesperi, R., Catalano, I., Cataldo, D., Grillo, M., Isocrono, D., Matteucci, E., Ongaro, S., Potenza, G., Puntillo, D., Ravera, S., Zedda, L., Giordani, P., 2016. Climate change fosters the decline of epiphytic *Lobaria* species in Italy. Biol. Conserv. 201, 377–384. http://dx.doi.org/10.1016/j.biocon.2016.08.003.

Nascimbene, J., Marini, L., 2015. Epiphytic lichen diversity along elevational gradients: biological traits reveal a complex response to water and energy. J. Biogeogr. 42, 1222–1232. http://dx.doi.org/10.1111/jbi.12493.

Park, L., Council, N.C., Nature, E., 2002. A transplant operation involving *Lobaria amplissima*; the first twenty years. Lichenologist 34, 267–269. http://dx.doi.org/10.1006/lich.2002.0387.

Pike, L.H., 1978. The importance of epiphytic lichens in mineral cycling. Bryologist 81, 247–257.

Potter, K.A., Arthur Woods, H., Pincebourde, S., 2013. Microclimatic challenges in global change biology. Glob. Chang. Biol. 19, 2932–2939. http://dx.doi.org/10.1111/gcb.12257.

Root, H.T., McCune, B., Neitlich, P., 2010. Lichen habitat may be enhanced by thinning treatments in young *Tsuga heterophylla-Pseudotsuga menziesii* forests. Bryologist 113, 292–307. http://dx.doi.org/10.1639/0007-2745-113.2.292.

Rosso, A.L., McCune, B., Rambo, T.R., 2000. Ecology and conservation of a rare, old-growth-associated canopy lichen in a silvicultural landscape. Bryologist 103, 117–127. http://dx.doi.org/10.1639/0007-2745(2000) 103[0117:EACOAR]2.0.CO;2.

Royle, J.A., Nichols, J.D., Kéry, M., 2005. Modelling occurrence and abundance of species when detection is imperfect. Oikos 110, 353–359. http://dx.doi.org/10.1111/j.0030-1299.2005.13534.x.

Rubio-Salcedo, M., Psomas, A., Prieto, M., Zimmermann, N.E., Martínez, I., 2016. Case study of the implications of climate change for lichen diversity and distributions. Biodivers. Conserv. http://dx.doi.org/10.1007/s10531-016-1289-1.

Sillett, S.C., 1995. Branch Epiphyte assemblages in the forest interior and on the clearcut edge of a 700-year-old Douglas fir canopy in western Oregon. Bryologist 98, 301–312.

Sillett, S.C., Mccune, B., Peck, J.E., Rambo, T.R., Applications, S.E., Jun, N., 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. Ecol. Appl. 10, 789–799.

Tart, D., Williams, C., DiBendedetto, J., Crowe, E., Girard, M., Gordon, H., Sleavin, K., Manning, M., Haglund, J., Short, B., Wheeler, D., 2005. Section 2: Existing vegetation classification protocol Gen. Tech. Rep. WO-67. In: Brohman, R.,

Bryant (Eds.), Existing Vegetation Classification and Mapping Guide. U.S. Department of Agriculture, Forest Service, Ecosystem Management Coordination Staff, Washington, D.C., pp. 2-1–2-34.
US Department of Agriculture Forest Service, US Department of the Interior Bureau of Land Management, 2001. Record of decision and standards and guidelines for amendments to the Survey and Manage, Protection Buffer, and other mitigation measures standards and guidelines. Portland, OR.
Werth, S., Wagner, H.H., Gugerli, F., Holderegger, R., Csencsics, D., Kalwij, J.M., Scheidegger, C., 2006. Quantifying dispersal and establishment limitation in a population of an epiphytic lichen. Ecology 87, 2037–2046. http://dx.doi.org/10.1890/0012-9658(2006) 87[2037:QDAELI]2.0.CO;2.