

Patterns in the occupancy and abundance of the globally rare lichen *Erioderma pedicellatum* in Denali National Park and Preserve, Alaska

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ABSTRACT. We investigated habitat attributes related to the occupancy of the globally rare and endangered epiphytic lichen, *Erioderma pedicellatum*, in a newly discovered (2009) population center in Denali National Park and Preserve (DNPP), Alaska. We measured forest, tree and epiphytic lichen community characteristics on eighty-five systematically selected plots in four study areas. We aggregated these data at three spatial scales (tree, plot and study area) at which to compare *E. pedicellatum* occupancy (probability of occurrence) and abundance to environmental covariates. We observed 2,035 *E. pedicellatum* thalli on 278 individual *Picea glauca* stems. The species occurred in 61% of the plots measured. Occupancy of *E. pedicellatum* at the individual tree-scale was influenced by stem diameter, study area, live crown length, plot *P. glauca* basal area, plot canopy cover and distance to open water. Our models for *E. pedicellatum* occupancy at the plot-scale identified study area, *P. glauca* density, deciduous basal area (*Betula neoalaskana* and *Populus trichocarpa*), and tall shrub cover (≥ 200 cm in height) as significant covariates. Our estimates of the DNPP population size increase the world population by at least tenfold to approximately 100,000 thalli. We suggest important topics for further research on *E. pedicellatum*.

KEYWORDS. Boreal forest, cyanolichens, habitat model, logistic regression, Pannariaceae.



Erioderma pedicellatum (Hue) P. M. Jørg. (Pannariaceae) is a foliose, epiphytic cyanolichen, considered one of the most endangered lichens in the northern hemisphere (Scheidegger 2003). It is one of only two lichens included on the International Union for the Conservation of Nature's Red List of Threatened Species where it is ranked Critically Endangered due to its limited distribution and documented population declines (Scheidegger 2003). The distribution of *E. pedicellatum* is limited to four population centers worldwide: Scandinavia (Ahlner 1948; Holien et al. 1995), Atlantic Canada (Ahti & Jørgenson 1971; Cameron 2004; Maass 1983), Alaska (Nelson et al. 2009) and most recently, Russia (Stepanchikova & Himmelbrant 2012). Dramatic declines in *E. pedicellatum* populations over the last 50 years in Scandinavia and Atlantic Canada have been attributed to disturbance from forestry activities (Goudie et al. 2011; Holien et al. 1995; Maass 1980) and acid deposition (Maass

& Yetman 2002). Excluding Alaskan localities, the estimated remaining world population is approximately 8,100 thalli (Goudie et al. 2011), 99% of which occur in Newfoundland, although no population information has been collected in Russia.

Habitat studies in Atlantic Canada indicate *E. pedicellatum* primarily occupies boles of *Abies balsamea* trees in areas of mature forest with persistent cool, moist conditions (Cameron & Neily 2008; Maass & Yetman 2002). Preliminary observations of the Alaskan *Erioderma pedicellatum* population (Nelson et al. 2009), indicated that it occupies branch tips of *Picea glauca* in mixed forests (*Picea-Betula* or *Picea-Populus*) of maritime-influenced areas south of the Alaska Range. Differences in phorophyte species, forest type, and location on host between the Alaskan and other North American population centers, in combination with the great geographic distance (5,000 km) between them, highlighted the need for in-depth habitat studies of the Alaskan population to understand the specific ecological preferences of this species in Alaska compared to other populations.

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DOI: 10.1639/0007-2745-116.1.002

Our goals for this study were to describe patterns of *Erioderma pedicellatum* occupancy and abundance within and among areas where this species was known to occur in the Denali National Park and Preserve, Alaska (DNPP), and to develop statistical models predicting *E. pedicellatum* occupancy at the individual tree and the plot levels in relation to measured physical and biotic attributes. Additionally, we aimed to quantify the size and local extent of this recently discovered population in four distinct study areas.

We expected that both individual host-tree characteristics and plot-scale attributes would significantly influence *Erioderma pedicellatum* occupancy. At the tree-scale, we hypothesized that occupancy of *E. pedicellatum* would be greatest on large, live *Picea glauca* stems (>10 cm diameter at breast height (dbh; 1.37 m in height)), because optimal light and moisture conditions for cyanolichen growth occur on such trees, especially on branch tips lower in the canopy (Sillett & Neitlich 1996; Liu et al. 2000). At the plot-scale, we hypothesized *E. pedicellatum* would be most abundant in forests possessing variation in canopy structure (e.g., not too closed nor too open), introduced either by deciduous tree or shrub species or forest openings, such as forests interspersed with wetlands (see Cameron & Neily 2008). Additionally, we expected *E. pedicellatum* to be most frequent and abundant on plots closer to water since other studies have found cyanolichen richness and biomass to be highest near streams (Howe 1978; McCune et al. 2002). Information obtained through statistical models will aid in conservation of this globally rare species by identifying the attributes of areas that are likely to support populations of the species in south-central Alaska and by documenting the population size of *E. pedicellatum* in DNPP.

STUDY AREA

We investigated patterns of *Erioderma pedicellatum* occupancy and abundance in four study areas arrayed along the southern escarpment of the Alaska Range in the upper Cook Inlet Basin of DNPP in south-central Alaska (Fig. 1). We chose study areas based on their proximity to documented locations of *E. pedicellatum* within DNPP (Nelson et al. 2009), their representation of a diversity of forest types and topographic positions extant in this region, and accessibility. Annual precipitation in this area ranges from 728–937 mm, with average January minimum temperatures of -4.5°C , and average maximum July temperatures of 5.7°C . General characteristics of the study areas from west to east are described below.

The Cascade Creek study area (centered at $62^{\circ}25.75' \text{ N}$, $152^{\circ}1.91' \text{ W}$) is located in a hanging valley near the junction of the East and West Fork of

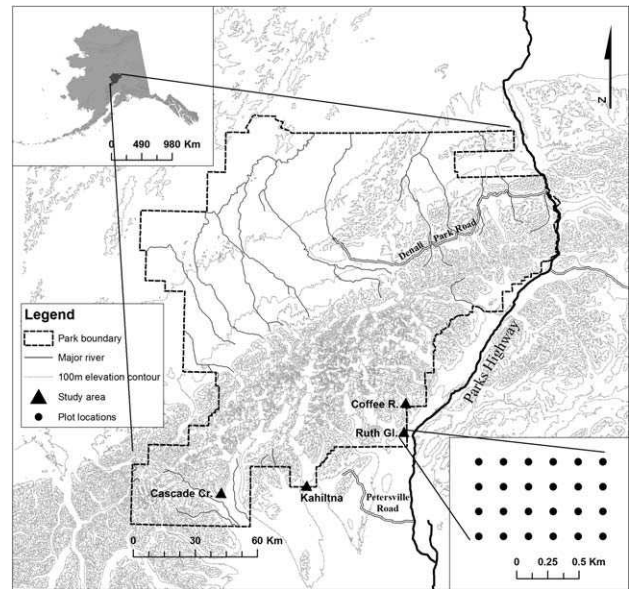


Figure 1. Map showing the location of Denali National Park and Preserve (DNPP) within Alaska and the locations of the four *Erioderma pedicellatum* study areas within DNPP. The Ruth Gl. study area is shown in the inset, although not all study areas were a symmetrical grid.

the Yentna River on alluvium and till-mantled valley slopes (Clark & Duffy 2006). Open *Picea glauca* forest was the most common forest type, with trees generally scattered and interspersed with areas dominated by deciduous shrubs. Linear fens throughout the study area also contributed to the patchy forest mosaic (Fig. 2a). The understory in Cascade Cr. was comprised of a high cover of herbaceous taxa, including a lush assortment of forbs, ferns and graminoids. *Salix* spp. were also abundant in the understory, sometimes forming thickets up to 2 m in height.

The Kahiltna study area (centered at $62^{\circ}28.16' \text{ N}$, $151^{\circ}15.40' \text{ W}$, located 40 km east of Cascade Cr.) is located in the outwash plain and alluvium at the Kahiltna Glacier terminus. The Kahiltna study area was characterized by well-developed *Picea glauca* forest with relatively large trees and high understory cover of *Alnus*, *Salix*, *Ribes*, and *Rubus* spp. (Fig. 2b). Areas more recently disturbed by flooding or debris flows supported stands of *Populus trichocarpa* or closed tall *Alnus* scrub.

The Ruth Glacier study area (centered at $62^{\circ}42.38' \text{ N}$, $150^{\circ}19.51' \text{ W}$, 55 km east of Cascade Cr.) is located in the rolling till plain east of the Ruth Glacier terminus, three km north of a large area of ponds and wetlands. The forest mosaic is composed of mostly closed *Betula neolaskana* or mixed *Picea-Betula* forest (Fig. 2c). Understory vegetation was largely determined by topographic position, as this study area was a jumble of small ridges and steep-sided valleys. Valleys

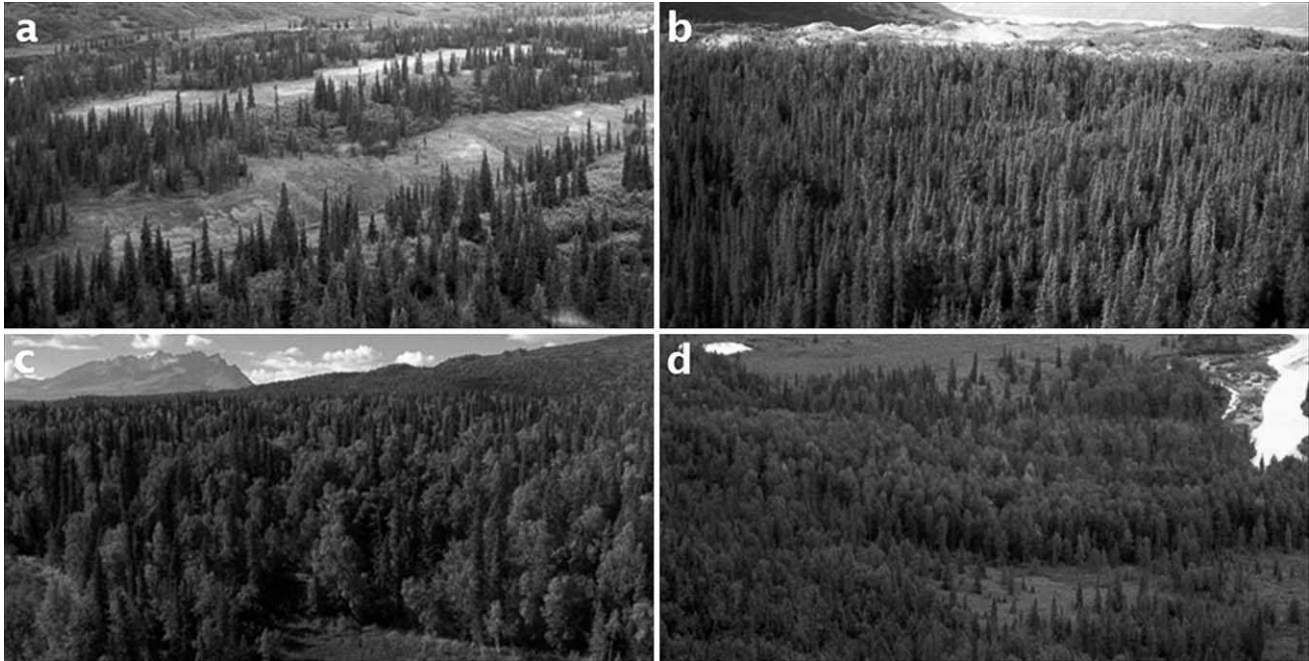


Figure 2. Aerial photographs of the four study areas: (a) Cascade Cr. with open *Picea glauca* forest interspersed among linear fens, (b) Kahiltna with closed *P. glauca* forest, glacier in background, (c) Ruth Gl. with evenly mixed *P. glauca*-*Betula neoalaskana* forest, and (d) Coffee R. with less evenly mixed *P. glauca*-*B. neoalaskana* forest.

supported a lush assemblage of large ferns and forbs with occasional thickets of *Oplopanax horridus*. Ridges were dominated by *Cornus suecica* and low ericaceous shrubs including *Vaccinium vitis-idaea*.

The Coffee River study area (centered at 62°49.56' N, 150°17.96' W, 14 km north of the Ruth Glacier study area), is located in a subalpine valley, underlain by alluvium and till-mantled valley slopes (Clark & Duffy 2006). Here the forest was a mosaic of *Picea glauca*-*Betula neoalaskana*, *P. glauca*-*Populus trichocarpa*, open *P. glauca* woodland, pure broadleaf forest (primarily *B. neoalaskana*), and tall alder or willow scrub with scattered trees (Fig. 2d). Coffee R. plots supported a dense understory, with high cover of forbs, ferns, graminoids and shrubs of the genera *Alnus*, *Ribes*, *Salix*, *Spiraea* and *Sorbus*.

METHODS

Plot selection. For each study area we identified a forested area in the vicinity of a collection site for *Erioderma pedicellatum* (using remotely-sensed imagery), then generated a sample grid over each of these forest patches with a random start based on a DNNP-wide, 100 m systematic grid. In the Kahiltna, Ruth Gl., and Coffee R. study areas, a random “seed” plot from the 100 m grid was chosen to be the south-east corner of the sample grid. From this start point, plots were selected with either 100 or 200 m spacing among sample plots, chosen a priori based on estimated ease

of travel. Instead of creating a grid of sample plots in the Cascade Cr. study area, where *P. glauca* forests occur in relatively narrow bands parallel to the stream course, we limited potential plot locations to the systematic 100 m grid points falling within forested polygons. For all study areas, we excluded clearly non-forested potential plot locations from the samples by examining high-resolution satellite imagery prior to fieldwork. Additional plot locations found to be without stems of the presumed phorophyte species (*Picea glauca*) were also excluded.

We measured 82 plots on sampling grids in four study areas (Cascade Cr., Coffee R., Kahiltna, and Ruth Gl.). We visited nine additional plots, but did not sample them due to an absence of *Picea glauca*. We sampled one additional plot in the Ruth Gl. study area that was dominated by *P. mariana* but it did not support *Erioderma pedicellatum*. These ten plot locations were excluded from the plot- and tree-scale models, but included as absences when estimating the population. Due to the limited presence of *E. pedicellatum* in the Coffee R. study area, we selected two additional plots containing the species to add to our knowledge of host-tree characteristics and population estimates in that study area. We excluded these plots from plot-scale analyses since they were not systematically selected.

Field sampling. Field methods were similar to those used for characterizing vegetation and physical

attributes for the National Park Service Central Alaska Network Vegetation Monitoring Program (Roland et al. in press). The plot size was larger (25 m diameter (490.9 m²) rather than 16 m diameter) in the current study to increase epiphytic lichen species capture. Within plots, we censused trees (≥ 1.37 m in height and ≥ 12 cm in dbh) and saplings (≥ 1.37 m in height and < 12 cm dbh). We recorded species, dbh, condition (live or dead), crown class and crown length (% of entire tree bole occupied by live branches) for each tree (Roland et al. 2004). For each sapling, we recorded species, dbh, and condition. We examined each tree and sapling for *Erioderma pedicellatum* thalli from the ground to approximately 2 m, which is the maximum search height for the average field technician without means to observe higher in the canopy. We recorded the number of thalli (0–10 thalli) on each stem, assigning a default value of 15 thalli when > 10 thalli were observed on one stem (which happened for 6% of stems). We assessed the epiphytic lichen community by recording each macro-lichen species encountered within the plot either on woody substrate > 0.5 m above ground-level or litterfall. For each species, we assigned a plot-level abundance code based on methods used by the United States Department of Agriculture (USDA) Forest Inventory and Analysis Program (Geiser 2004). Two vertically-integrated 16 m point-intercept transects were used to quantify vegetation vertical structure, cover by species and general ground cover (e.g., terricolous moss, lichen, litter; see Roland et al 2004). We made eight spherical densiometer readings per plot to estimate canopy closure. To estimate minimum stand age, we took penetrating increment cores (which yield two samples of each annual ring because the corer penetrates the entire tree diameter) near the base of 4–8 dominant *Picea glauca* in each plot, 8–16 m from plot center. Cores were extracted and placed in paper straws in the field, then dried, mounted, and sanded in the lab in preparation for counting and cross-dating. Stand minimum age was determined by identifying the oldest annual ring measured in each plot.

Analyses. We aggregated our data into two spatial scales, tree and plot level, for modeling *Erioderma pedicellatum* occupancy (probability of occurrence). We used logistic regression to identify predictors significantly associated with the occupancy of *E. pedicellatum* on *Picea glauca* stems. Variables used in our tree-scale modeling included field measured and geographic information system (GIS) derived values selected to capture tree and plot-scale variability in stem size and canopy cover, stand structure and composition, understory composition, and landscape

position (**Table 1**). A reference category was chosen for categorical variables with more than two categories, and all other categories were compared to it in the regression analysis. To reduce the suite of potential predictors, we used a hierarchical selection process by first fitting a univariate logistic regression with each variable to remove those that were not significantly associated with the response (Hosmer & Lemeshow 2000). Remaining variables were then grouped into tree-scale, plot-scale biotic, and plot-scale abiotic groups (**Table 1**) and added to the model in order, based on our hypotheses that *E. pedicellatum* would occur most frequently on larger *P. glauca* trees in stands exhibiting variation in canopy structure. Due to the large number of possible covariates (60) and our goal of identifying the most important factors governing occupancy and abundance of *E. pedicellatum*, while avoiding over-fitting, we limited our modeling to first-order effects and did not investigate interactions among variables. Because of the violation of the assumption of independence of samples at the tree-scale, and our interest in reducing the probability of falsely rejecting the null hypothesis (type II error), we were strict in our inclusion of model predictors, retaining only those variables associated with occupancy of *E. pedicellatum* at the $p < 0.001$ level. We used the Akaike information criterion (AIC) to select the model that provided the best fit with the fewest number of predictors. We used proportional reduction in deviance (deviance of the best-approximating model divided by deviance of the intercept-only model) to assess fit (Zheng & Agresti 2000). We found a unimodal relationship between dbh and occupancy, so a quadratic term was included to improve model fit (**Table 1**). Trees identified as outliers or highly influential to estimates were investigated, but ultimately retained because we found no ecological rationale for their removal. All variables were assessed for correlation based on a Pearson's correlation coefficient of > 0.70 . We assessed multicollinearity of variables in the models by calculating the variance inflation factor (VIF) using a threshold of 10 and investigated all variables with a VIF over two (Fox 2012; O'Brien 2007). If high correlation or collinearity between variables was detected, the variable thought to be the most biologically significant and easiest to measure in the field was retained in the model.

We used logistic regression to identify predictors associated with *Erioderma pedicellatum* occupancy and abundance (number of thalli) at the plot-scale. Our data had a greater proportion of zeros than would be expected for either a negative binomial or Poisson distribution because 30 out of 82 plots had zero *E.*

Table 1. Variables used to model *E. pedicellatum* occupancy and abundance at the tree- and plot-scale. Mean or actual values are followed by minimum-maximum in parentheses when applicable. Tree species include the conifers *Picea glauca*, *P. mariana*, and deciduous *Betula neolaskana* and *Populus trichocarpa*. Derived abiotic data came from GIS data layers. Distance measures from plot to emergent wetland and to open water used a minimum mapping unit 0.2 ha.

Variable	Cascade	Kahiltna	Ruth	Coffee	All study areas	All n with <i>E. pedicellatum</i>
<i>Tree-scale</i> n =	206	752	363	286	1606	280
<i>P. glauca</i> dbh (cm)	20.3 (0.5–57.7)	13.02 (0.1–48)	12.5 (0.4–43.1)	14.6 (0.4–54.9)	14.1	19.7 (1.5–57.7)
Condition (live; or dead)	196; 10	612; 139	315; 48	259; 26	1382; 223	256; 21
Crown class (open grown; dominant or co-dominant; intermediate or overtopped)	0; 118; 78	1; 211; 400	1; 76; 237	11; 89; 159	13; 494; 874	1; 146; 110
Crown length (≥ 70% live crown; < 70% live crown; sapling)	22; 119; 65	288; 40; 424	53; 99; 211	42; 87; 156	405; 345; 856	74; 119; 87
<i>Plot-scale</i> Biotic n =	20	20	19	23	82	52
Mean stand age (years)	118.9 (86.9–178.3)	122.8 (79.9–160.4)	124.9 (85.9–164.4)	133.1 (62.1–349.3)	125.4	126.9 (79.9–178.3)
Mean <i>P. glauca</i> ring width (mm)	1.5 (0.9–2.2)	1.2 (0.6–2.2)	1.0 (0.4–1.5)	1.2 (0.6–2.5)	1.3	1.2 (0.4–2.2)
% Canopy closure	47.1 (26.8–73.6)	65.2 (28.5–84.9)	69.5 (23.2–86.6)	64.4 (14.6–88.1)	61.7	61.0 (26.8–86.6)
Live <i>P. glauca</i> density (stems ha ⁻¹)	199.6 (20.4–631.59)	623.3 (203.7–1588.9)	337.7 (20.4–774.1)	203.7 (40.7–448.2)	336.1	418.2 (0–1752)
Live <i>P. glauca</i> basal area (m ² ha ⁻¹)	9.3 (1.0–22.7)	14.9 (4.1–26.4)	7.5 (0.0003–15.1)	5.8 (2.0–10.4)	9.2	10.9 (0–29.9)
Live deciduous basal area (m ² ha ⁻¹)	2.2 (0–13.7)	4.1 (0–21.5)	14.8 (6.6–26.1)	11.1 (0.2–34.1)	8.1	7.5 (0–26.2)
% Terricolous moss cover	48.3 (1.7–89.8)	58.7 (23.7–94.9)	29.3 (0–67.8)	15.3 (0–40.7)	37.2	48.4 (0–94.9)
% Shrub cover (all strata)	56.4 (6.8–83.1)	65.3 (37.3–94.9)	33.6 (0–79.7)	59.8 (16.9–94.9)	54.3	49.6 (0–84.7)
% Shrub cover between 50–200 cm	37.6 (3.4–72.9)	41.8 (5.1–67.8)	20.4 (0–50.8)	28.7 (0–57.6)	32.1	31.6 (0–72.9)
% Shrub cover ≥ 200 cm	1.4 (0–11.3)	6.5 (0–15.3)	2.9 (0–35.0)	10.0 (0–54.2)	5.5	10.0 (0–54.2)
% Tree species cover (all strata)	18.8 (0–67.8)	17.2 (1.7–37.3)	49.1 (1.7–79.7)	37.8 (1.7–84.7)	31.0	31.4 (0–83.1)
% Tree species cover ≥ 200 cm	18.0 (1–66.1)	16.2 (0–37.3)	46.1 (1.7–79.7)	38.8 (1.7–84.7)	31.0	29.8 (0–83.1)
<i>Plot-scale</i> Abiotic n =	20	20	19	23	82	52
Plot center elevation (m)	328.7 (291–348)	249.5 (232–266)	223.5 (192–265)	350.4 (313–406)	290.3	275.7 (192–406)
Plot slope (degrees)	4.9 (1–13)	2.0 (1–3)	10.7 (1–44)	11.6 (1–33)	7.4	7.0 (1–44)
Annual solar radiation (derived; watt hours (km ²) ⁻¹)	0.66 (0.40–0.80)	0.74 (0.70–0.75)	0.68 (0.26–0.88)	0.71 (0.66–0.75)	0.70	0.70 (0.26–0.88)
Southness (aspect off of 180°)	54.1 (1–141)	38.0 (3–92)	86.3 (11–168)	91.3 (7–158)	68.0	60.9 (1–168)
Equivalent latitude (derived index of potential radiation; degrees)	60.2 (52–70.4)	61 (60.3–63.1)	62 (34.9–76.3)	60.5 (41.2–75.8)	60.9	60.7 (35.0–76.3)
Distance to wetland (derived; m)	79.4 (19.3–370)	460.5 (58–940)	129.8 (0–438)	288.7 (38–486)	239.6	234.9 (19.3–843)
Distance to water (derived; m)	165.6 (19–514)	281.8 (81–553)	289.2 (3–806)	262.8 (30–510)	249.9	325.6 (3–1116)

pedicellatum thalli. To help account for this overdispersion, we used a multilevel, zero-inflated, negative binomial model (Zuur et al. 2009) to separately identify the factors associated with either plot occupancy (hospitable vs. inhospitable) or plot abundance. This multilevel approach allows inclusion of different variables for each model component, and thus better model fit when predicting both occupancy and abundance. We chose logistic regression to model occupancy and negative binomial regression to model abundance. Because the number of occupied stems was highly correlated ($r = 0.69$) with the number of available stems, we used density of *Picea glauca* as an independent variable in all models, log-transformed to achieve normality. Additionally, we included a categorical variable for study area in all of our models to capture unmeasured sources of variation caused by differing location of the study areas. All additional variables added to the model with *P. glauca* density and study area found to be significant at the 0.05 level were then added to the full, zero-inflated model. We then removed variables based on significance until all remaining variables were significant at the $p < 0.001$ level.

We used field data to calculate two different estimates of the total number of *Erioderma pedicellatum* thalli in each study area. One estimate was based on host (*Picea glauca*) density (estimated study area size \times mean *P. glauca* density \times mean # thalli per stem), while the other was based on area sampled and area of inference (# of possible plots in study area \times mean # thalli per plot). A 95% confidence interval was calculated for the population mean using a *t*-distribution. In addition, to detect differences in the general characteristics of each study area we used analyses of variance (ANOVA) testing in conjunction with Tukey's range test to compare means.

RESULTS

Forest characteristics. There was considerable variation in stand attributes within and among the four study areas. The most common forest types (for definitions see Viereck et al. 1992) surveyed were open *Picea glauca* forest (35% of plots) and closed and open *P. glauca*-*Betula neoalaskana* forests (31% of plots). Average stand age was approximately 125 years (Table 1). We measured 4,667 individual stems across all study areas, of which 57% were *B. neoalaskana*, 34% were *P. glauca*, 6% were *Populus trichocarpa*, and 3% were *P. mariana*. The size-class distributions of the two primary tree species, *P. glauca* and *B. neoalaskana*, were strongly skewed towards smaller size classes. The majority of stems (30.1% for *P. glauca* and 75.3% for

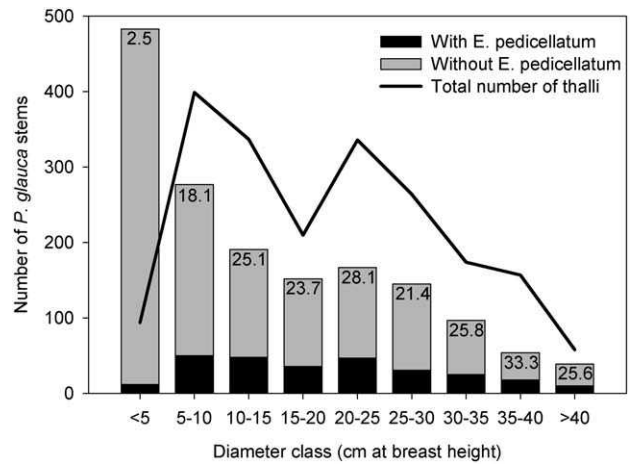


Figure 3. Distribution of *Picea glauca* among diameter size classes, showing proportion of stems occupied by *Erioderma pedicellatum* across four study areas. Percentage of *P. glauca* stems occupied per class displayed in bar. Line shows the total number of thalli observed in each class.

B. neoalaskana) occurred in the smallest dbh size-class (< 5 cm) and few stems (11.8% for *P. glauca* and 0.8% for *B. neoalaskana*) occurred in classes ≥ 30 cm (*P. glauca* shown in Fig. 3). A notable exception was observed for *P. glauca* in the Cascade Cr. study area, where only 17.5% of stems were in the < 5 cm size class, while 27.2% of stems occupied size classes ≥ 30 cm.

Picea glauca was the most abundant tree species, with a mean live basal area (BA) of $9.1 \text{ m}^2 \text{ ha}^{-1}$ across all study areas (Table 2). However, live BA of *Betula neoalaskana* was higher than *P. glauca* in the Ruth Gl. and Coffee R. study areas, where *P. glauca* BA was lowest ($7.0 \text{ m}^2 \text{ ha}^{-1}$ and $5.8 \text{ m}^2 \text{ ha}^{-1}$ respectively). Live BA for *P. glauca* was significantly ($p < 0.001$) higher in the Kahiltna study area ($14.9 \text{ m}^2 \text{ ha}^{-1}$) than all other study areas. *Betula neoalaskana* was the most frequently encountered tree species, with a mean density of $576.5 \text{ stems ha}^{-1}$ across all study areas. However, mean *P. glauca* density was higher than *B. neoalaskana* density in the Cascade Cr. and Kahiltna study areas (Table 2). The mean density of *B. neoalaskana* was highest in the Coffee R. study area ($1198.3 \text{ stems ha}^{-1}$). The mean density of *P. glauca* stems was highest in the Kahiltna and lowest in the Cascade Cr. and Coffee R. study areas (Table 2).

There was considerable variation in understory attributes within and among the four study areas. Mean canopy closure of plots based on densiometer readings also varied (Table 1), with Cascade Cr. having a significantly ($p < 0.01$) more open canopy than all other study areas. The Ruth Gl. study area had significantly ($p < 0.001$) lower shrub cover (36%) than the Kahiltna (65%) and Coffee Cr. (59%) study

Table 2. Mean basal area and density of all tree species across 83 plots in four study areas. BA = basal area ($\text{m}^2 \text{ha}^{-1}$) and Dens = density (stems ha^{-1}).

Tree species	Condition	Cascade		Kahiltna		Ruth		Coffee		All study areas	
		BA	Dens	BA	Dens	BA	Dens	BA	Dens	BA	Dens
<i>Picea glauca</i>	Live	9.3	199.6	14.9	623.4	7.0	320.9	5.8	203.7	9.1	332.1
	Dead	0.3	10.2	2.0	141.6	0.8	48.9	0.7	21.3	1.0	54.2
<i>Picea mariana</i>	Live	0	0	0	0	0.1	112.0	0	0	0.02	27.0
	Dead	0	0	0	0	0.1	39.7	0	0	0.02	9.6
<i>Betula neoalaskana</i>	Live	0.7	103.9	0.3	5.1	11.3	905.5	7.5	1198.3	5.2	576.5
	Dead	<0.01	5.1	0.1	6.1	2.0	60.1	0.9	137.3	0.7	55.2
<i>Populus trichocarpa</i>	Live	1.2	23.4	3.5	19.4	0	0	2.3	163.9	1.78	55.7
	Dead	0.3	4.1	0.2	2.0	0.8	1.0	0.3	137.3	0.38	4.9

areas. Fern cover was relatively high at Cascade Cr. (35%), Ruth Gl. (48%) and Coffee R. (51%) but significantly ($p < 0.0001$) lower at Kahiltna (9%). The Kahiltna study area also had significantly ($p < 0.0001$) lower graminoid cover (4%) than all other study areas. Terricolous moss cover was significantly ($p < 0.0001$) lower at Ruth Gl. (30%) and Coffee R. (16%) than at Cascade Cr. (48%) and Kahiltna (59%).

Epiphytic lichen community. Eighty-five epiphytic lichen species were observed across all plots in all study areas (**Supplementary Table S1**). The median number of species encountered per plot was 23, with a minimum of 10 and a maximum of 37. Ten species occurred in $\geq 85\%$ of plots, including *Hypogymnia austerodes*, *H. physodes*, *Lobaria scrobiculata*, *Nephroma parile*, *Parmelia sulcata*, *Parmeliopsis ambigua*, *P. hyperopta*, *Ramalina roesleri*, *Tuckermannopsis chlorophylla*, and *Vulpicida pinastri*. The majority of these species were observed in common (>10 individuals per plot) or greater abundance levels. Of these frequent and abundant species, *Lobaria scrobiculata* and *Nephroma parile* are cyanolichens. Including *Erioderma pedicellatum*, 26% of epiphytic lichen species encountered were cyanolichens (**Supplementary Table S1**). In plots occupied by *E. pedicellatum*, we found ten species (five of which were cyanolichens) that occurred in $\geq 90\%$ of plots (**Supplementary Table S1**). On average, plots with *E. pedicellatum* supported more than twice as many cyanolichens (10 species) than plots without *E. pedicellatum* ($p < 0.001$).

General patterns in *E. pedicellatum* occupancy and abundance. We observed a total of 2,035 *Erioderma pedicellatum* thalli on 278 stems, occurring in 63% of the plots measured. Of *P. glauca* stems supporting *E. pedicellatum* thalli, 73% of stems had thalli occurring on twigs exclusively, while 23% of stems had thalli occurring on twigs and primary branches. We observed one instance of six thalli growing on the bole of an Alaska birch (*Betula neoalaskana*) tree.

Erioderma pedicellatum occupied 18.3% of all *Picea glauca* stems measured across all study areas (**Table 3**). Occupancy was highest in the Cascade Cr. study area, where the species occurred on 40% of *P. glauca* stems and in 85% of plots, and was lowest in the Coffee R. study area, where we observed it on 1.8% of *P. glauca* stems and in 16% of plots (**Table 3**), including two auxiliary plots chosen based on observed *E. pedicellatum* occurrence. Across the four study areas, the mean dbh of occupied and unoccupied *P. glauca* stems was 19.7 cm, and 13 cm, respectively. Thus, the average size of occupied *P. glauca* stems was skewed toward larger trees relative to the population of *P. glauca* stems in the study area (**Fig. 3**). Average age of occupied stands was 126.9 ± 7.1 years, but was not significantly different from unoccupied stands.

Variation in the number of *Erioderma pedicellatum* thalli (abundance) showed a somewhat different pattern among study areas than variation in occupancy, with the highest mean number of thalli per plot (55 thalli) recorded in the Kahiltna study area. This was more than double the mean number of thalli per plot in the Cascade Cr. study area (23 thalli), even though *E. pedicellatum* occurred most frequently there. Not surprisingly, the Coffee R. study area, which had the lowest occupancy of *E. pedicellatum* thalli, also had the lowest mean abundance of the species with only 0.6 thalli per plot (**Table 3**). We recorded ≥ 10 *E. pedicellatum* thalli on 33% of stems (92 individuals), while 14% of stems supported only one thallus (40 individuals).

Statistical models. The best tree-scale model (overall proportional reduction in deviance = 0.24) indicated that tree dbh, live crown length, size class (sapling or not), and plot BA of *Picea glauca* were positively associated with *Erioderma pedicellatum* occupancy on individual *P. glauca* stems (**Table 4**). Canopy cover, distance to open water, and location in the Coffee R. study area were negatively associated with *E. pedicellatum* occupancy on *P. glauca* stems (**Table 4**).

Table 3. Frequency and population estimates of *E. pedicellatum* thalli in four study areas. Population estimates are derived from a calculation of $N = n^*(A/a)$. Subscripts denote which statistic was used in which estimate. A 95% confidence interval is given around the estimates. The confidence interval for the estimates across study areas are pooled variation across variable “a” (plots or trees), and not representative of the difference in estimates among study areas.

Statistic	Cascade	Kahiltna	Ruth Gl.	Coffee R.	All study areas
% Plots occupied by <i>E. pedicellatum</i>	85	80	75	13	63.25
% <i>P. glauca</i> stems occupied by <i>E. pedicellatum</i>	40	19	13	1	18.25
n Total # of thalli observed on <i>P. glauca</i>	535	1,160	318	16	2029
Estimated study area size (ha)	38	84	88	26	236
A ₁ Possible # of 0.04909 ha plots in study area	774	1,711	1,793	530	4,808
a ₁ # Plots sampled	23	21	22	26	92
Mean # <i>E. pedicellatum</i> thalli per plot	23.26	55.24	14.73	0.38	22.05
Mean <i>P. glauca</i> density (stems ha ⁻¹)	182.46	728.54	336.13	199.02	348.54
A ₂ Estimated # of <i>P. glauca</i> stems in study area	6,933.48	61,197.36	29,579.44	5,174.52	82,255.44
a ₂ # of <i>P. glauca</i> sampled	206	751	363	285	1605
Mean # <i>E. pedicellatum</i> thalli per stem	2.60	1.54	0.88	0.06	1.26
N ₁ Population estimate based on area sampled (thalli)	18,005 ± 7,889	94,520 ± 73,550	26,400 ± 15,178	203 ± 277	106,026 ± 50,572
Estimated thalli per ha	474 ± 208	1,125 ± 875	300 ± 172	8 ± 11	449 ± 214
N ₂ Population estimate based on <i>P. glauca</i> density (thalli)	18,006 ± 4,479	94,525 ± 17,898	25,912 ± 9,231	290 ± 288	103,985 ± 14,678
Estimate thalli per ha	474 ± 117	1,125 ± 213	294 ± 105	11 ± 11	440 ± 62

We found that optimal stem dbh for *E. pedicellatum* occupancy was approximately 35 cm, generally declining at stem diameters both greater and less than this value (Fig. 4a). Occupancy of *E. pedicellatum* was significantly lower on stems in the Coffee R. study area as compared to the three other study areas we investigated, whereas occupancy of this species was statistically indistinguishable among these three remaining study areas. Thalli of *E. pedicellatum* were 3.4

times more likely to be found on trees with ≥ 70% live crown than on those with < 70% live crown and 3.3 times more likely to be found on saplings than on trees with < 70% live crown (Fig. 4b).

The best plot-scale model indicated that *Erioderma pedicellatum* occupancy was strongly associated with study area, with conspicuously low occupancy in the Coffee R. study area relative to the other study areas. Plot abundance of *E. pedicellatum* was positively associated with the density of *Picea glauca* and negatively associated with deciduous BA (*Betula neolaskana* and *Populus trichocarpa*) and percent cover of tall shrubs (≥ 200 cm; Table 4).

Population size. Our population estimates indicate that the four study areas combined contained an estimated 106,026 ± 50,572 *Erioderma pedicellatum* thalli in the vertical stratum within 2 m of the ground (based on estimating from area sampled, ± 95% confidence interval; or 103,985 ± 14,678 thalli if estimating based on measured *Picea glauca* density; Table 3). Because the size of the study areas varied, we compare density estimates (# thalli hectare⁻¹) rather than total population estimates, for *E. pedicellatum* populations among study areas. The Kahiltna study area supported the highest number of thalli per hectare, while Cascade Cr. and Ruth Gl. supported similar numbers of thalli per hectare and Coffee R. supported the lowest *E. pedicellatum* density of all the study areas (Table 3). The high proportion of plots occupied by this species in the relatively restricted areas that we studied suggest that the overall population of the species in DNPP is very likely considerably higher

Table 4. Direction of significant associations between model covariates and *E. pedicellatum* occupancy at the tree-scale and *E. pedicellatum* occupancy and abundance at the plot-scale across four study areas. Deciduous species include *P. trichocarpa* and *B. neolaskana*. Dispersion parameter for the plot-scale model was 7.02.

Predictor	Sign	p-value
<i>Tree-scale Model</i>		
<i>P. glauca</i> dbh	+	< 0.001
(<i>P. glauca</i> dbh) ²	-	< 0.001
Study area (Coffee Cr. vs. others)	+	< 0.001
Crown length (>70% live vs. <70% live)	+	< 0.001
Crown length (saplings vs. <70% live)	+	0.00063
<i>P. glauca</i> basal area	+	< 0.001
Mean canopy cover	-	0.00041
Distance to water	-	< 0.001
<i>Plot-scale Model - Occupancy</i>		
Study area (Coffee Cr. vs. others)	-	0.00014
<i>Plot-scale Model - Abundance</i>		
<i>P. glauca</i> density (log scale)	+	< 0.001
Shrub cover ≥ 200 cm	-	< 0.001
Deciduous basal area	-	0.00022

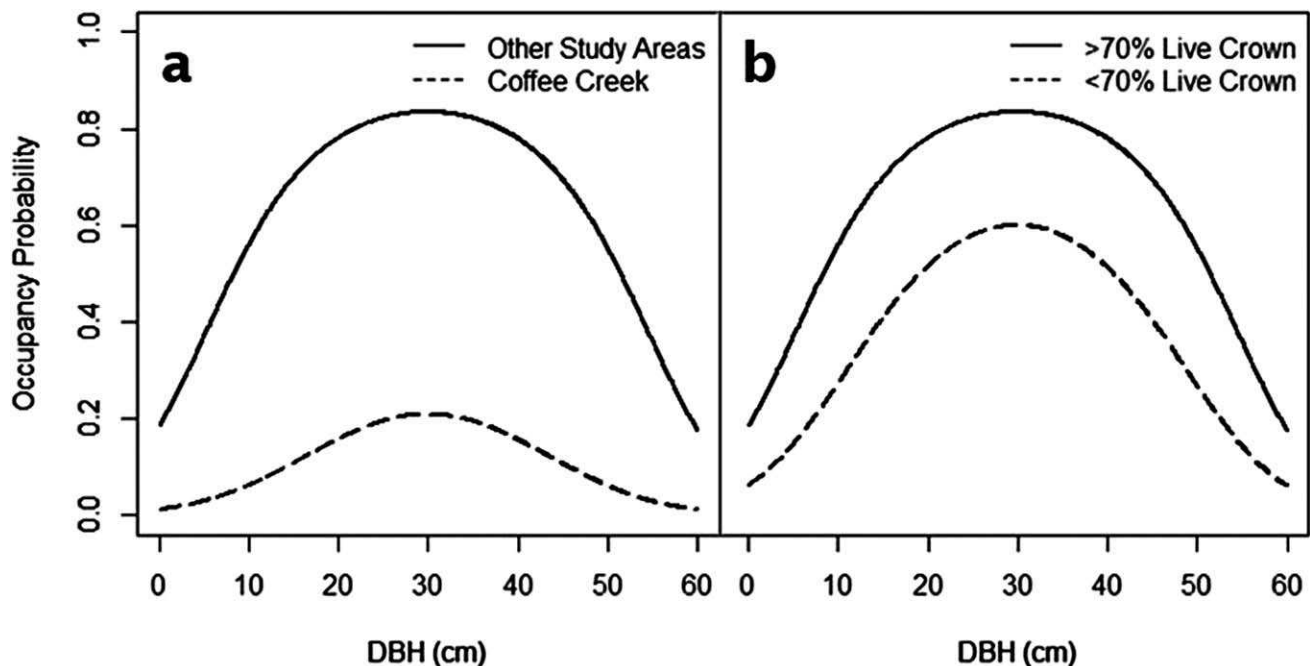


Figure 4. The occupancy probability of *Erioderma pedicellatum* across the sampled range of *Picea glauca* diameter at breast height values within (a) study areas and (b) percent live crown classes.

than our estimates which were based solely on our four study areas, and not the area in between.

DISCUSSION

Our study reports the first analysis of the habitat attributes and host preferences of the globally endangered epiphytic lichen, *Erioderma pedicellatum*, in a recently discovered population center in south-central Alaska. We also provide a population estimate of this imperiled species that indicates this region likely supports the world's largest extant population. Previous studies report a world population of approximately 8,100 *E. pedicellatum* thalli, based on actual observations and considered an estimation only because of the species rapid decline in those areas (Goudie et al. 2011). We report an additional 2,035 thalli observations, but are certain that the number of existing thalli in our study area is greater, since we sampled only a portion of the apparent suitable habitat, and because we observed additional thalli when travelling between sample points. Additionally, our survey methods included a search for *E. pedicellatum* only up to 2 m in height, even though it is likely that this species is found higher in the canopy, at least in small numbers (e.g., Liu et al. 2000).

Erioderma pedicellatum in DNPP occurred across a spectrum of relatively common forest types for this region, and thus it is likely to occur in other similar locations in south-central Alaska. Our results suggest that more surveys are required to establish the

geographic distribution of the species in Alaska and that research into the genetic, ecophysiological, and taxonomic status of these populations is warranted to determine how they are similar to, or different from, *E. pedicellatum* populations of Scandinavia and Atlantic Canada, where the species may be going extinct (Goudie et al. 2011; Holien et al. 1995).

Perhaps the most noteworthy result of our study is the high frequency of occurrence of *Erioderma pedicellatum* overall, appearing in a relatively wide range of stands and forest communities within our sample. The species occurred across a continuum from open subalpine *Picea glauca* forest to closed lowland mixed conifer-broadleaf forest, and also in stands with varying understory composition. This finding is especially significant considering the global rarity of this taxon (Scheidegger 2003) because these forest types are common throughout south-central Alaska (Viereck et al. 1992). While *E. pedicellatum* occupied a variety of stand types, it was tightly associated with *P. glauca*. The species occurred almost exclusively on *P. glauca* twigs and branches, and at greatest frequency and abundance in sites with particularly high *P. glauca* BA and density. In general, thalli were small (< 2 cm across), fertile, and solitary.

The strong affinity with *Picea glauca* exhibited by Alaska populations of *Erioderma pedicellatum* differs from Scandinavian populations, which primarily occupy *Picea abies* twigs (Ahlner 1948), and Atlantic Canadian populations, which primarily occupy *Abies*

balsamea boles. Neither *P. abies* nor *A. balsamea* occur in Alaska, so it is unknown whether Alaskan *E. pedicellatum* populations would prefer members of those species as hosts in our area. Considering its global range, *E. pedicellatum* is clearly able to colonize and occupy several different coniferous phorophyte species although it favors certain species over others in each area that it occurs. We suspect physical characteristics of the different tree species (*Picea* vs. *Abies*) may alter important habitat attributes, such as stem flow, branch structure, and resultant light conditions, favoring *E. pedicellatum* occupancy on different phorophyte species. Also presumably important are the sites the different phorophyte species occupy, as *Picea glauca* is more tolerant of xeric conditions than *A. balsamea* (Larsen 1980) and when in direct competition may be displaced to drier sites. *Erioderma pedicellatum* only rarely occurs on *P. glauca* in Atlantic Canada (Maass & Yetman 2002), even though that species occurs there, perhaps because its location within the forest mosaic is limited to sites undesirable for *E. pedicellatum* establishment, or because the microclimate created by individual *P. glauca* phorophytes is less desirable for *E. pedicellatum* growth.

Tree-scale occupancy model. Our analyses suggest that both individual tree characteristics and stand characteristics influence the occupancy of *Erioderma pedicellatum* at the tree-scale. The species occurs in highest occupancy on relatively large trees of approximately 35 cm dbh, with occupancy declining on both smaller and the very largest individuals. Previous studies have indicated that large, old trees provide, on average, both a larger area (i.e., more branches) and a longer-duration target for epiphytic lichen colonization (Johansson & Ehrlén 2003; Lie et al. 2009; Neitlich 1993). While this is generally supported by our data, the decline in occupancy on very large trees in our model indicates that the relationship is somewhat more complex in our dataset. We suspect dbh is also acting as a surrogate correlate for other unmeasured variables such as the fine-scale within-tree conditions of canopy shape, branch quantity and quality. The decline in occupancy on very large trees may also reflect a lack of suitable branches within the 2 m search height, either from self-pruning in dense stands or because low branches on large trees hang above 2 m in height. Therefore, we may be underestimating *E. pedicellatum* occupancy on large trees or on trees in dense stands.

Epiphytic lichens, especially cyanolichens, are known to occupy and prosper on the lower branches of conifers (Liu et al. 2000; Sillett & Neitlich 1996), at least partially because they receive water-borne nutrients from the canopy above (e.g., Goward & Arsenault

2000). We observed that large *Picea glauca* with full canopies shed water down and away from the center of the tree. When this moisture flux reaches the lower canopy, it passes over the distal twigs and branches maintaining a particularly moist environment, especially in contrast to interior branches. Branches here tend to have little to no needle coverage, which provided better illumination and stable substrate. The combination of water dripping down through a large canopy and adequate light due to needleless branches appears to favor *Erioderma pedicellatum* occupancy, as this is where it frequently occurred in our sample. *Erioderma pedicellatum* populations in DNPP occurred with a relatively rich assemblage of epiphytic lichens, including the cyanolichens *Pseudocyphellaria crocata* and *Lobaria pulmonaria*, which are frequently associated with diverse epiphytic communities in humid, shady, old-growth forests (Gauslaa et al. 2007; McCune 1993; Neitlich 1993).

Picea glauca with longer crown lengths usually had more of the optimal low, dead branches within the portion of the tree we were able to search (within 2 m of the ground). Trees with shorter crown lengths generally lacked low dead branches in the lowest (accessible) regions of the tree's vertical profile, thus reducing sites available for colonization by *Erioderma pedicellatum*. Since we were not able to search higher in the canopy, we cannot be certain that *E. pedicellatum* did not occur higher in the canopy. Saplings, in contrast, almost always possessed branches within the 2 m search height. Thus suitable habitat, and *E. pedicellatum* occupancy, on saplings was greater than on trees with < 70% live crown. However, a sapling's position nearby to a larger tree may also help it achieve micro-habitat conditions supportive of *E. pedicellatum* occupancy. Overall, this suite of the best tree-scale characters for *E. pedicellatum* was exemplified in the subalpine forests of the Cascade Cr. study area, which supported the greatest number of thalli per stem. *Picea glauca* at Cascade Cr. were large and open grown individuals, producing full, wide canopies held low to the ground, perhaps representing the optimal trees for *E. pedicellatum* occupancy in the region.

Additional plot-scale measures, which appear to be related to a need by *Erioderma pedicellatum* thalli for humid and cool conditions with adequate light (Ahti & Jorgenson 1971; Maass 1980), were also important in predicting tree-scale occupancy. Plot-scale *Picea glauca* BA positively influenced occupancy on individual trees. Although this may reflect a need by *E. pedicellatum* thalli for an appropriate host, dense forests are also generally more humid and cool than open stands (Halonen et al. 1991). Additionally, plots

with low *P. glauca* BA often supported high deciduous BA. The presence of deciduous trees in the canopy has been documented to raise stand temperature (Leuzinger & Körner 2007; Ma et al. 2010), alter the distribution of light to the lower canopy (Canham and Burbank 1994) and change patterns of canopy throughfall (Campbell et al. 2010; Goward & Arsenault 2000), thereby influencing local humidity. Thus in the mixed coniferous-deciduous forest stands occupied by *E. pedicellatum* in DNPP, a balance between the quantity and quality (diameter, crown length, etc.) of phorophytes available for *E. pedicellatum* colonization, and the light and humidity conditions suitable for *E. pedicellatum* growth maintained in the lower canopy was necessary. Both high percent canopy closure and increased distance to water, discussed below, were negatively associated with *E. pedicellatum* occupancy on individual stems, further confirming the importance of overall stand conditions in determining *E. pedicellatum* occupancy at the tree-scale.

Plot-scale occupancy and abundance models. Our analyses suggested that the categorical variable of study area was the most important factor measured in determining *Erioderma pedicellatum* occupancy at the plot-scale. Occupancy was significantly lower in the Coffee R. study area, which had a less continuous forest mosaic and low mean BA of *Picea glauca*, as compared to the other three study areas. Abundance of *E. pedicellatum* was greatest in plots with high *P. glauca* density, as expected given that *P. glauca* is the main host in DNPP. Abundance of *E. pedicellatum* at the plot level was also negatively influenced by increasing deciduous BA and increasing cover of tall shrubs, variables we believe are related to microclimatic conditions in the lower canopy.

Our analyses indicated *Erioderma pedicellatum* occurs less frequently and in less abundance in areas with limited light transmission to the lower canopy caused by high canopy cover, deciduous BA, or cover of tall shrubs. In contrast, *E. pedicellatum* in Atlantic Canada has declined in part due to forest management practices that have reduced canopy coverage (Maass 1980). For Canadian *E. pedicellatum* populations, maintaining a deciduous canopy component is considered critical for the conservation of rare cyanolichens (Cameron & Neily 2008). These apparent differences could indicate that light is more limiting in the undisturbed forest mosaic of DNPP than in other population centers with longer histories of human disturbance. It could also be that other factors operating at a larger scale, such as the general climate differences among the distant areas that support *E. pedicellatum*, forest size, and/or the other impacts to

the populations already in effect (i.e., forestry practice or air quality) are more important than the plot-scale measurements in question.

Erioderma pedicellatum in Alaska showed an affinity for locations with high humidity, occurring more frequently on trees in plots that were closer to water. World-wide, forest stands inhabited by *E. pedicellatum* are frequently located near large glaciers, rivers, or wetland complexes that significantly affect local humidity, moisture, and temperature regimes. In Atlantic Canada, a heuristic model that included distance to wetlands and the coast was successful in identifying suitable habitat for *E. pedicellatum* (Cameron & Neily 2008), but it was indeterminable to what degree the model relied on that metric. Our analyses showed that forests closer to surface water had higher occupancy of *E. pedicellatum* at the tree-scale, but not at the plot-scale, suggesting that other stand or landscape features were more important in predicting occupancy and abundance at that larger scale. Alternatively, the absence of distance to water as an important predictor in the plot-scale model may simply be because it was removed due to its weak but significant correlation ($r = 0.27$, $p < 0.05$), with *Picea glauca* density, a variable positively associated with plot-scale abundance.

Maass & Yetman (2002) suggested that the presence of certain understory plants, including ferns and *Sphagnum* spp., may act to buffer humidity in sites where *Erioderma pedicellatum* occurs. However, our results suggested that *E. pedicellatum* occurred in sites with a broad spectrum of understory composition and structure. For example, fern cover, although high at three of the study areas, was low at Kahiltna, which had the highest density of *E. pedicellatum* thalli of all of the study areas. Similarly, *Sphagnum* spp. were not a particularly important component of the terricolous moss flora in our plots, comprising at most 5.6% of the average moss cover (Cascade Cr.) compared to the average of 60% moss cover reported in Atlantic Canada (Cameron & Neily 2008). Both the Cascade Cr. and Ruth Gl. study areas supported similarly dense *E. pedicellatum* populations, but had significantly different canopy closure, shrub and terricolous moss cover. Cover of tall shrubs was negatively related to plot-scale *E. pedicellatum* occupancy, despite the highest shrub cover occurring in the Kahiltna study area, which also supported the greatest number of thalli per plot. Thus, it appears there are many ways to satisfy the habitat requirements for *E. pedicellatum*, and the influence of the understory is only important insofar as it detracts from available light or adds to humidity amongst low-lying *P. glauca* branches.

CONCLUSIONS

Our study is the first to statistically investigate the factors governing occupancy of the globally rare and endangered lichen species, *Erioderma pedicellatum*. Thalli were relatively common within a variety of spruce forest types in the Cook Inlet Basin of DNPP. Our work suggests that the species prefers distal twigs and branches on large *Picea glauca* with full crowns close to water bodies in sites with high *P. glauca* density, but it is negatively influenced by increasing canopy cover, and particularly by shading from deciduous trees and tall (> 2m) shrubs. Additionally, although it occurs across a wide range of forest types, we found that in one study area (Coffee Cr.), *E. pedicellatum* thallus occupancy was significantly reduced relative to other areas.

Our conservative estimate of thalli present within the study area likely increases the previously known world population by over ten times, from approximately 8,100 thalli to nearer to 100,000 thalli. Locations within DNPP can be considered safe from forest management threats, as timber harvest is generally prohibited there, and naturally occurring forest fires are rare in this region. However, changes in regional air quality and climate have the potential to impact *Erioderma pedicellatum* populations that occur within DNPP (e.g., Maass & Yetman 2002). Additional *E. pedicellatum* locations outside the park (see Nelson et al. 2009), some of which are yet to be discovered, are likely less safe from these threats.

The discovery of what appears to be a large and intact population of this species stimulates many new questions that can be addressed with additional research, including the following:

- 1) What is the overall geographic distribution of *Erioderma pedicellatum* in Alaska, and what factors govern the range extent for the species there?
- 2) What is the degree of genetic similarity between Alaska populations of *E. pedicellatum* and those elsewhere? Are thalli all members of a single species?
- 3) Are the Alaska populations the result of long distance dispersal event(s) from other population centers or is the interrupted global range of this species the result of the contraction of a once more continuous distribution?
- 4) How does the new information from Alaska affect the global conservation status for the species?

In future, detailed direct measurements of variation in microclimatic conditions and canopy through-fall chemistry and volume (e.g., Campbell et al. 2010)

could yield valuable information for identifying specific controls over the species distribution and abundance within and among sites of varying occupancy and abundance. In addition, observations of *E. pedicellatum* distribution within the canopy, including searches for thalli in the vertical strata above 2 m would yield more complete estimates of total population size within a given area. These new studies would optimally be conducted in more accessible sites where *E. pedicellatum* occurs (e.g., the Parks Highway corridor outside of DNPP) that would be logistically less complicated and expensive to visit, thus allowing for instrumentation that may require more frequent monitoring.

ACKNOWLEDGMENTS

The authors would like to dedicate this work to our good friend and colleague Tom Meier, who shared our enthusiasm about the discovery of *E. pedicellatum* in Alaska. We thank James Walton for his work on the Denali National Park and Preserve cryptogam inventory, which set the stage for this project. We also thank Duke Brady, Eric Groth, Matt Macander, Rory Nichols and Janet Prevey for their field assistance, and Joshua Schmidt for his guidance with statistical analysis. Tree ring analysis was graciously provided by Dr. Andrea Lloyd's tree lab at Middlebury College. The project was supported and funded by the National Park Service and Denali National Park and Preserve.

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manuscript received November 28, 2012; accepted December 6, 2012.

Supplementary documents online: Table S1. Mean abundances and plot frequencies of epiphytic lichen species in four study areas.