EPIPHYTIC LICHENS

FROM THE FOREST-MARINE ECOTONE OF SOUTHEASTERN ALASKA

by

Karen Louise Dillman

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Karen L. Dillman

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_____,Chair

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Supervisory Committee

ACCEPTED:

_____

Director of the School

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Dean, Division of Graduate Studies

ABSTRACT

The forest-marine ecotone in southeastern Alaska contains a wide range of epiphytic lichen microhabitats presumably induced by climatic and structural characteristics where old-growth coastal forests meet the North Pacific. The forest-marine ecotone is described as the junction between two distinct habitats; old-growth coastal forests and maritime waters. Epiphytic lichens from this ecotone were sampled by this researcher from conifer branches and a spectrum of other woody substrates. Of the 143 lichens species found in 39 sample units, 17 were reported as new to Alaska, including *Bryoria pikei*, *Leioderma sorediatum*, *Pannaria rubiginella, Parmeliella parvula, Physciella chloantha, Pseudocyphellaria perpetua, Usnea arizonica, U. hesperina, U. madeirensis,* and *U. wirthii*. Lichen communities showed marked variation with respect to exposure to open ocean waters, latitude, and mean winter temperature at the forest-marine ecotone. Lichen species richness, total lichen abundance, and occurrence of rare lichens were most strongly related to sites exposed to the open ocean. Nineteen species were more frequent at locations considered exposed, including *Lobaria pulmonaria, L. scrobiculata, Parmelia saxatilis,* and *Parmotrema arnoldii*. Exposed edges of the forest-marine ecotone also hosted a diverse assemblage of both rare species ("*Dendriscocaulon "* sp., *Lobaria amplissima, Pseudocyphellaria. rainierensis*,) and forage lichens (*Ramalina menziesii*, *Usnea filipendula*, *U. longissima*), presumably abundant due to thallus fragmentation induced by the stronger winds associated with exposed locations. The forest-marine ecotone was described as a hotspot for lichen biodiversity, suggesting that the continued protection of the coastal forests of the immediate coastline will be important for maintaining biodiversity of the region.

Dedication

This thesis is dedicated to the memory of my father Jack V. Dillman III, and grandfather Arthur A. Kuebler; two much loved and sorely missed mentors in my life.

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INTRODUCTION

Epiphytic lichens represent a substantial portion of the biodiversity and biomass in temperate rainforests of the Pacific Northwest region of North America (McCune et al. 2000; Neitlich 1993; Pike 1981, Sillett et al. 2000). Research suggests that lichens in northern temperate rainforests: (1) require several hundred years to accumulate high epiphytic diversity and biomass (McCune 1993; Pike et al. 1977), (2) provide either food or shelter for many vertebrates and invertebrates (Rominger et al. 1994; McCune & Daly 1994; Rosentreter et al. 1997; Stevenson 1979; Maser et al. 1985; Pettersson et al. 1995), and (3) potentially make a sizeable contribution to the N budget through atmospheric nitrogen fixation in lichens associated with cyanobacteria (Becker 1980; Denison 1973; Nash 1996a). Nitrogen is transferred into the ecosystem for higher plant use through leaching and decomposition of lichen litterfall (Knops et al. 1996; Coxson & Nadkarni 1995; Pike 1978). The poikilohydric nature of lichens allows them to easily absorb atmospheric elements and be widely used as monitors of air quality (Geiser et al. 1994; Nash & Wirth 1988; Fenn et al. 2003; Smith et al 1993). Many lichens are generalists, but species that are indicators of specific habitats or ecological conditions have been used to detect climatic or other environmental changes (Neitlich et al. 2003, Nilsson et al. 1995; Kuusinen 1996; Sillett & Goward 1998).

Lichen research from the Pacific Northwest region has mainly concentrated on lichens from mid-elevation forests in the Oregon and Washington Cascades and Olympic ranges (Glew 1998; Sillett 1995; McCune et al. 1997a, 2002; Neitlich 1993; Peterson & McCune 2001; Pike et al. 1975; Rosso et al. 2000), the low elevation

Willamette valley oak savannas (Pike 1973, Stone 1989) and British Columbia (Goward 1999; Goward et al.1994; Brodo 1995; Noble 1982; Vitt et al. 1973). Comparatively, fewer studies describe the floristics and community ecology of lichens from southeastern Alaska (Derr 1994; Geiser et al. 1994 & 1998; Krog 1968; McCullough 1965; Degelius 1937; Herre 1919). The relatively pristine habitats of southeastern Alaska possess an abundant lichen flora due to the cool, moist hyper-maritime climate and the absence of fire as a large, catastrophic disturbance factor (Martin 1989; Nowacki et al. 2001). Over 500 lichen species are known to occur in southeastern Alaska, from rocky seashores to alpine habitats (Geiser et al. 1998).

The focus of this study was the epiphytic lichen communities from the forest-marine ecotone of southeastern Alaska's old-growth coastal forests. An ecotone is defined as a community junction where increased variety and density of species is characteristic of and often restricted to a specific ecotone, or edge (Odum 1971). I defined the forest-marine ecotone as the narrow band of trees and shrubs found along the marine shoreline where the saltwater margin ended and conifer forest began. This strip of vegetation is adapted to exposure to salt spray, wind, and surf, where different vascular plant communities exist compared to interior forests due to the amount of contact with these elements (Alaback & Pojar 1997). Although similarities exist between the epiphytic lichen communities of interior old-growth coastal forests and the forest-marine ecotone (Geiser et al. 1994), I have observed lichen communities exclusive to this edge habitat. Environmental conditions at this ecotone are differentially optimal for some lichen species and inhospitable for others. For example, some lichens are able to tolerate high nitrogen levels on substrates enriched with guano from shorebirds and certain small mammals that almost exclusively use the maritime coastline (Barkman 1958; Hansen 2000; Brodo et al. 2001; Nash 1996). Additionally, some lichens are

considered more adaptable than others to contact with sea- spray aerosols associated with the marine environment (Nash & Lange 1988, Fletcher 1976). Studies show that lichens on rocks and driftwood of the inter-tidal area display distinct zone preferences due to the amount of contact with saltwater splash, salt-spray, and the influence of freshwater from streams (O'Clair et al. 1996; Ryan 1988).

The objectives of this study of the lichens from the forest-marine ecotone were to: (1) compare total species richness of lichens (including crustose species) between two different habitats: the forest-marine ecotone and interior forests (described to be at least 300 m away from marine waters), (2) describe the epiphytic macrolichen communities of the forest-marine ecotone through ocular abundance estimates on all woody substrates (hereafter termed whole-plot abundance), (3) describe the epiphytic macrolichen communities of the forest-marine ecotone through percent cover estimates on conifer branches of *Picea sitchensis* and *Tsuga heterophylla* (hereafter termed branch-level abundance), (4) relate variation in species composition and abundance of lichen communities at the forest-marine ecotone to environmental variables, and (5) relate gradients in epiphytic lichen communities from the forest-marine ecotone to: (a) measured environmental variables, particularly the amount of exposure to marine conditions, (b) membership in functional groups of lichens (cyanolichens, forage, matrix or nitrophilous lichens), and (c) the occurrence of rare lichen species.

STUDY AREA

During the 2002 and 2003 field seasons, I surveyed sample units between 54°.5' to 58° N and 130° to 136°W (Fig. 1). Sample units were from the beaches, estuarine, or rocky headland landform classifications (USDA 1996). All sample units were without a recent history (less than approximately 150 years) of catastrophic disturbances such as windthrow, landslide or large-scale harvesting. I determined this with aerial photos, and by examining the forest along the shoreline for evidence such as large patches of second-growth trees and old tree stumps from past harvests. Aside from these criteria, sample units were arbitrarily selected within the study area without a preconceived bias (McCune & Grace 2002).

The cool summers, and the lack of summer drought periods along with ephemeral snow levels at sea level help characterize this region as a per-humid rain forest zone (Alaback 1996). Fire is generally considered to be of minor importance to the ecology of this region, thus distinguishing it ecologically from other forest types in North America (Alaback & Pojar 1997). Warm currents from the Pacific Ocean carry tremendous amounts of heat from tropical-origin waters to southeastern Alaska (Salmon 1997). The ocean water greatly moderates the seasonal temperature changes due to the intricate maze of seawater that permeates around the islands, providing sea to air warming in the winter and sea to air cooling in the summer (Nowacki et al. 2001). This moist maritime climate nurtures lush coniferous rain forests, wetland systems, and permanent icefields throughout the steep mountainous islands and mainland fjords. Distinct climatic gradients occur in the region from north to south and from east to west (Nowacki et al. 2001). Mean winter temperature decreases to below freezing closer to

the mainland and in the northern 1/3 of the region near Juneau (Nowacki et al. 2001). Mean annual precipitation varies within the region from ≤ 1500 millimeters in certain northern sections to 7600 millimeters in higher elevations on the mainland and some outer islands (Schwartz & Miller 1983). Elevations range from sea level to 1000 meters on islands and to over 3000 meters on the mainland.

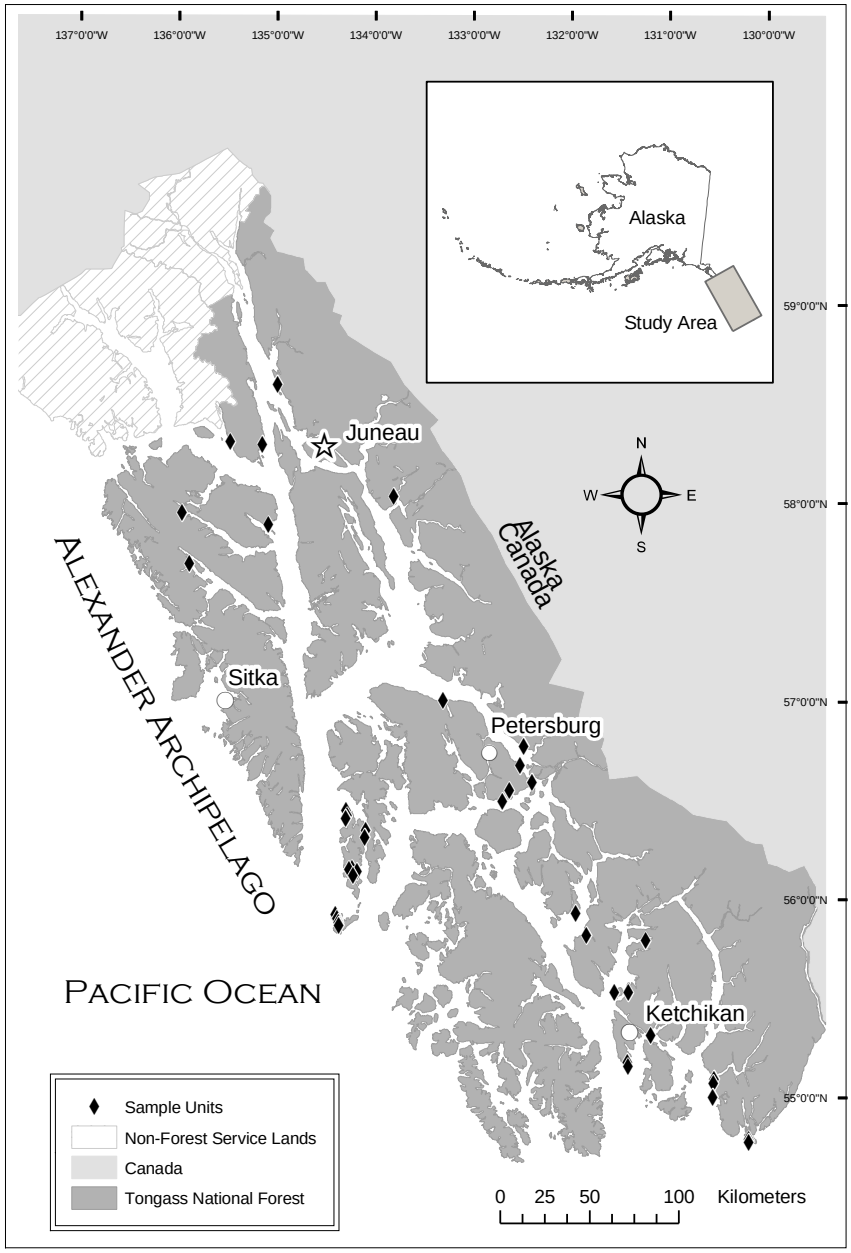


Figure 1. Location map of southeastern Alaska. Dark triangle symbols represent the general locations for 39 sample units from the forest-marine ecotone.

METHODS

Lichen species richness of two different habitats.--- To investigate the differences I observed in lichen communities between interior forests and the forest-marine ecotone, I collected live *Tsuga heterophylla* branches from both habitats, and removed and identified all lichens present. Air temperature, light, and relative humidity at the beach only influence the microclimate of the forest edge to about 30 meters in from the beach, while oceanic winds may penetrate up to 120 meters into the forest (Concannon 1995). For this floristic study, interior forest was considered to be at least 120 meters inland from the beach. This distance was to help ensure that climatic conditions from the beach had negligible effects on the epiphytic lichens from interior forests.

The branches I collected were from sample units and other accessible beach locations that contained old-growth *Tsuga heterophylla* trees. I collected a total of twenty-two branches from the following locations: Neets Bay (four branches), Mountain Point (two branches), Settlers Cove (two branches), and Point Higgens (five branches) on Revillagigedo Island near Ketchikan; Mallard Slough (three branches) and Howard Bay (two branches) near Juneau; and Patterson Bay (two branches) and Goose Flats (two branches) on Chichagof Island. Between 30 and 100 meters elevation, I collected 22 interior forest branches from old-growth forests on Revillagigedo Island near Ketchikan, and from the Chilkat Peninsula near Juneau. All the interior forest locations were at least 300 meters from marine waters.

I collected branches rather than twigs and boles because branches were: (1) the most manageable to standardize by length and diameter, (2) relatively easy to bring in from the field without damage to the lichens compared to tree trunk sections or small twigs, (3) midway in successional age compared to twigs and tree trunks, and (4) where the bulk of epiphytic biomass occurred in the Pacific Northwest region (Pike et al. 1977).

Suitable *Tsuga heterophylla* branches were: (1) at least 5 cm diameter at the bole attachment, (2) alive, (3) from trees at least 10 m tall and 20 cm diameter DBH, (4) accessible from the ground (5) selected arbitrarily but without a preconceived bias (McCune & Grace 2002), and (6) from trees within old-growth structured forests (USDA 1992). I trimmed off the outermost lengths of each branch and sawed off the first one-meter section, wrapped it in plastic, and carried it out of the field. I examined the branches for lichens with a 20x hand lens and a dissecting scope. I removed the lichens and placed them in individual packets for identification. I did not include samples that were too small for identification to the genus level (approximately 25 samples total).

I calculated *alpha*, *beta*, and *gamma* diversity with presence/absence data of lichens. I calculated *gamma* -diversity for each habitat from the total number of species from 22 branches. I used the total number of species identified from each branch to calculate *alpha*- diversity for each habitat. I calculated *beta* –diversity as *gamma*/*alpha* ($B_{w,}$ McCune & Grace 2002; Whittaker 1972).

After lichens were removed from branches, I assigned each species to one of four groups (crustose, forage, matrix and cyanolichens) for comparisons between habitats. Crustose lichens were defined as flat or two-dimensional forms that were tightly adhered to their substrate such as *Pertusaria* and *Ochrolechia*. Forage lichens were defined as the pendulous hair-like species (also called fruticose growth form) that contained only green algae. Examples were species in the genera *Alectoria*, *Usnea*, *Bryoria*, and some *Ramalina*. Green-algal or matrix lichens were those with a green-algal photobiont that were mainly foliose but also included some of the smaller tufted fruticose species. Examples from this group are the genera *Parmelia*, *Platismatia*, *Sphaerophorus*, *Cladonia*, and *Hypogymnia*. Cyanolichens contained a cyanobacterium

as the primary photobiont or secondarily in small structures called cephalodia. Genera in this group included *Lobaria*, *Nephroma, Pseudocyphellaria*, and *Peltigera*.

Description of epiphytic lichen communities with whole plot and branch-level surveys.--- To address objectives 2 and 3 of this study, the total number of lichen species found in each sample unit, including the infrequent species, were used to calculate *alpha* diversity at the sample unit. Lichen *gamma* -diversity was calculated from the total number of species from sample units for both whole-plot and branch-level data. *Beta* -diversity was calculated in two ways: 1) as *gamma*/*alpha* (B_w, McCune & Grace 2002; Whittaker 1972); and 2) as the average half changes that corresponded to the average dissimilarity among sample units (B_D, McCune & Grace 2002, McCune & Mefford 1999). *Beta* diversity can be used as a descriptor of the amount of compositional change in a community in a multi-dimensional space (B_w, McCune & Grace 2002). As a rule of thumb, values of $B_w < 1$ are low and $B_w > 5$ are high. The larger the value, the more challenging the dataset is for ordination because some ordination techniques deal with high heterogeneity better than others (McCune & Grace 2002). The other beta measurement, B_D , calculates the average number of half changes corresponding to the average dissimilarity among sample units (McCune & Grace 2002). Two sample units separated by one half change have a 50 percent similarity of species (McCune & Grace 2002). B_w is only based on the presence-absence with no specific gradient, while B_D includes differences in abundance.

Variation in epiphytic lichen communities with whole-plot surveys. --- To address objective 4, I surveyed 39 sample units for epiphytic lichens from all woody substrates along the forest-marine ecotone of southeastern Alaska (Fig. 1, see Appendix I for sample unit information). The use of a single, large sample unit for whole-plot lichen abundance emphasized species capture while smaller sub-samples on conifer branches

(described below) permitted quantitative accuracy of lichen abundance (McCune & Lesica 1992). Macrolichens were defined as those that attained three dimensions and were relatively easy to remove from their woody substrates. Sample units ranged from 500 to 1800 m long by approximately 6 m wide and followed the natural contour of the forest-marine ecotone along the beach.

I accessed the beaches by boat, or floatplane from the nearest community or on foot from the nearest road. Sample unit length varied due to the availability of 20 conifer branches for branch-level abundance estimates within a stretch of shoreline (described below). The beginning point of a sample unit was the general location where I arrived at the beach after hiking from a nearby road or from a boat or plane on shore. The end point of a sample unit was reached when 20 branches were measured for branch-level lichen abundance.

I estimated whole-plot abundance of lichens during a timed- ocular survey of approximately 2.5 hours per sample unit. At the end of each survey, I assigned an abundance rating (1-5) to each lichen species encountered. This scale differed from that of McCune et al. (1997a) of 1-4 to include more information on species with greater than 10 individuals, but with patchy distribution less than 40 individuals. The scale used was based on the number of individuals sighted per sample unit on all woody substrates: 1= 1-3 individuals, 2=4-10, 3= 11-39, 4= greater than 40 but less than ½ the branches or boles, and 5= greater than 40 and greater than ½ the branches or boles. I surveyed the following tree species for lichen abundance across the study area: *Picea sitchensis*, *Tsuga heterophylla*, *Tsuga mertensiana*, *Thuja plicata*, *Chamaecyparis nootkatensis*, *Alnus rubra, A.sitchensis*, *Malus fusca,* and *Acer glabrum* var. *douglasii*. The dominant woody shrubs I surveyed for lichens were *Vaccinium* spp*., Menziesia ferruginea,*

Viburnum edule, *Ribes* sp. and *Salix* spp. I included snags in the surveys. Downed trees were not surveyed to eliminate the possibility of including terrestrial lichens.

Variation in epiphytic lichen communities with branch-level surveys.--- To address objective 4, I surveyed exclusively for branch lichens from 38 sample units. Rather than restricting this portion of the study to a single species substrate, I sampled the lower branches of both *Tsuga heterophylla* and *Picea sitchensis* trees greater than 20 cm DBH (1.5 m from the ground) according to availability. I have observed that epiphytic lichen species differed little between these two conifers. Epiphytic lichens from these two conifers varied little on older trees during a pilot study of lichens in Glacier Bay (Neitlich et al. 1993). Additionally, no host specificity was found for bryophytes or lichens on boles of both species from the Queen Charlotte Islands (Glime & Hong 2002). Both conifer species were present along the forest-marine ecotone throughout southeastern Alaska (Pojar & MacKinnon 1994), however *P. sitchensis* was generally more abundant on some beaches due to more recent isostatic rebound, and along estuaries and riparian land features (USDA 1992,1996).

I recorded branch–level abundances by lichen species relative to the area of the upper-half cylinder of a 100 cm branch segment beginning at the trunk and using the scale: 0= 0%, 1=0-1% (0-3 mm of branch length), 2= 1-5% (3-15 mm), 3= 5-25% (15-75 mm), 4 = 25-50% (75 – 150 mm), 5= 50-75% (150-225 mm), 6= 75-95% (225-285) mm), 7= 95-99% (285-299 mm), and 8= 99-100% (299-300 mm of branch length) (McCune 1990). I stratified branches for sampling (between 5-10 cm diameter) to help reduce the variation in lichen abundance due to branch age or size. Upon arrival to the next tree greater than 20 cm along the forest edge, I selected a branch for lichen estimates that met the above criteria.

Lichen community gradients in relation to environmental variables.--- To address objective 5, each sample unit was scored for 16 environmental variables. Lichen community characteristic variables for each sample unit were: (1) sum of abundance, (2) species richness, (3) rarity, and (4-7) lichen functional group membership (forage, matrix, cyano, and nitrophilous). Site variables for each sample unit were: (8) aspect, (9) latitude, (10) longitude, (11) percent of *Alnus sitchensis* (12) distance in kilometers from outer coast (13) length of sample unit in meters (14) annual precipitation, (15) mean winter temperature, and (16) topographic position (exposed or protected).

(1) Sum of abundance for each sample unit was defined as the added abundances for all species, excluding infrequent species. (2) Species richness was defined as the number of species in each sample unit (*alpha*-diversity), excluding infrequent species. I calculated sum of abundance and species richness from the summary statistics for both datasets (whole-plot and branch-level) in PCORD Version 4 (McCune & Mefford 1999). (3) I assigned a rarity score to each lichen species as follows: 4=species was either endemic to the PNW, or had a very limited distribution in North America and had been documented less than 20 times in North America -globally rare, 3= species had a range extension in southeastern Alaska and/or was exclusively from the coastal forest edge- regionally rare, 2= species had previously been documented in southeastern Alaska primarily with riparian forests along large mainland rivers, or other open habitats; regionally uncommon except in preferred habitat, 1= species was infrequent in the region and due to small size has possibly been overlooked- regionally infrequent, and 0= species was commonly found in most forest habitats of southeastern Alaska and the PNW (Geiser et al. 1994; 1998, Derr 1994; Brodo et al. 2001; Goward 1999; Goward et al. 1994; McCune & Geiser 1998).

(4-7) I assigned lichens to one of the four functional groups (forage, matrix, cyano, and nitrophilous). Forage, matrix, and cyanolichens are described above. Nitrophilous lichens were those that were commonly found associated with areas of high nitrogen from bird and mammal guano (van Herk 2001). The lichens I considered nitrophilous in this study were those in the genera: *Candelaria*, *Melanelia*, *Physcia,* and *Xanthoria*. Some lichens considered nitrophilous in Jovan & McCune (2004), such as *Parmelia hygrophila* and *Ramalina subleptocarpa*, were also species I considered nitrophilous in this study due to their greater abundance where shorebird use was high.

(8) I measured aspect as heat load index that rescaled aspect to a scale of zero to one; zero being the coolest and one being the warmest (McCune & Grace 2002). (9-10) Latitude and longitude were obtained by GPS (Global Positioning System) using the Alaska NAD 27 datum. (11) With aerial photographs and field notes, the percent of *Alnus sitchensis* along the forest-marine ecotone was estimated after a sample unit was surveyed. (12) I roughly calculated the distance in kilometers of each sample unit to the outer coast by drawing a straight line on a map from the southern portion of the region to the northern portion of the region and along the outside western edge of the outermost islands of the Archipelago. From each sample unit, I measured horizontally to the line drawn west of the outermost boundary of the Archipelago, and converted the measurement to kilometers. (13) Length of sample unit was calculated by GIS to the nearest meter (Geographic Information System). (14-15) Annual precipitation and mean winter temperature (in millimeters) were estimated from isotherm maps in Nowacki et al. (2001). (16) For topographic position, I assigned each sample unit a position score coarsely defined as: 1 = exposed, defined as a beach positioned on a large, open body of water, often on a prominent coastal feature or directly exposed to the Gulf of Alaska,

or 0 = protected, defined as a beach inside a deep bay or protected estuary, some distance from a larger, open body of water.

To calculate functional group membership (four variables) and rarity scores (one variable) for all species in both whole-plot and branch-level datasets, I created two new matrices of lichen species by the five variables. I assigned each sample unit a score, 1 or 0, for each of the four functional groups. A '1' identified a species belonging to a functional group; a '0' for not belonging to that functional group. For the rarity variable, I assigned each species a number indicating rarity, ranging from zero to four as described above. I multiplied each new matrix by the appropriate lichen abundance matrix. This produced a set of group and rareness scores for each species in environmental space for each matrix. I augmented both existing environmental matrices with this new information.

Lichen community gradients in relation to topographic position.--- To compare lichen abundances and communities between two groups of sample units, I tested the hypothesis that lichen species abundance and communities differ between exposed (n=24) and protected (n=15) sample units using non-metric Multi-response Permutation Procedures (MRPP) and Indicator Species Analysis (ISA) (McCune & Mefford 1999). MRPP is a non-parametric method used to describe multivariate differences among 'a priori' groups (Mielke & Berry 2001), while ISA (Dufrêne & Legendre 1997) describes how well each species differentiates among groups. Non-metric MRPP is the same as MRPP except that the distance matrix is converted to ranks before calculating the test statistic. The rank transformation can help correct the loss of sensitivity of distance measures as community heterogeneity increases and makes the results in theory more analogous to those from NMS (McCune & Grace 2002).

I used Sørensen distance to enhance the correspondence of the MRPP with NMS results (McCune & Grace 1999). Group differences are shown with the *A* statistic, the "chance-corrected average within-group agreement" ($A = 0$ is the expectation under the null model; $A = 1$ when all members of a group are identical and non-overlapping with other groups; negative values indicate groups are more similar than expected by chance). For community data $A < 0.1$ is common, even when differences between groups are apparent; $A > 0.3$ is quite high (McCune & Mefford 1999). For ISA, 1000 randomizations were used to test the hypothesis that the largest indicator value for a given species is no larger than expected by chance. A *p*-value < 0.05 was used for significance. I used whole-plot data only for this type of analysis.

Multivariate analysis of lichen communities.--- To address objectives 2-5, I used multivariate techniques to determine the natural range of variability for lichen communities at the forest-marine ecotone. I conducted all statistical analyses using PCORD Version 4 (McCune & Mefford 1999). First, I sought outlier sample units and species by examining distances among sample units in species space and species in sample unit space (McCune & Mefford 1999). I screened out two outlier sample units that did not contain late-successional or old-growth conditions from evidence of recent wind disturbance or landslides. These two sample units also contained the lowest total lichen abundance and *alpha*-diversity. No species were screened as outliers.

To analyze the abundance data for the variation in species composition and lichen communities, and relate these to environmental factors, I produced two matrices each for whole-plot and branch-level analyses. The matrices described lichen abundance and environmental variables from each of the sample units. Those infrequent species occurring in less than 5% of the sample units (35 species) were temporarily removed from the abundance dataset prior to the analysis (McCune & Grace

2002). The removal of infrequent species typically improves correlations between ordination axes and environmental variables (McCune & Grace 2002). This was appropriate for my goal of understanding the most important gradients in epiphytic lichen community composition.

The matrices of sample unit by species abundances contained: (1) 39 sample units with whole-plot abundances for 108 species, and (2) 38 sample units with branch-level abundances for 53 species. For whole-plot abundance, the coefficient of variation (CV) of species totals was 99 percent and no transformation was applied. For the branch-level abundance matrix, lichen cover was averaged by lichen species per branch and then divided by the number of branches (20) for each sample unit. For this portion of the analysis, I lumped together the members of the genus *Cladonia* because individual species may have been overlooked due to insufficient fertile material for proper identifications. The *Cladonia* species identified were retained for the diversity measures of that dataset. The resulting matrix was relativized by the maximum of species totals to avoid strong emphasis on dominant species and to equalize the peaks of species responses (McCune & Grace 2002). Relativization reduced the CV of species totals for branch-level data from 145 to 71percent.

I used non-metric multidimensional scaling ordination (NMS) (Kruskal 1964; McCune & Mefford 1999) on matrices of sample units by species abundances to detect prominent gradients in species composition. NMS is an ordination technique well suited for non-normal community data, and like other ordination techniques, the data are reduced to a few dimensions (McCune & Grace 2002). NMS is an iterative search for the best positions of n entities (sample units) on k dimensions (axes) that minimize the stress of the k-dimension configuration (McCune & Grace 2002). Stress is summarized as the measure of departure from monotonicity in the relationship between the

dissimilarity (distance) in the original n-dimensional space and distance in the ordination space (McCune & Grace 2001). The closer the points are to a monotonic line, the better the fit and the lower the stress (McCune & Grace 2001). The resulting axes can be interpreted by evaluating lichen species' responses along the gradients revealed, and by examining correlations between sample unit gradient scores and environmental data.

The "slow and thorough" autopilot mode of NMS used the best of 40 runs with the real data along with 50 runs with randomized data for a Monte Carlo test of significance. The Sørensen (Bray-Curtis) distance measure proportion coefficient was used to express community resemblances (shared abundance divided by total abundance). For both lichen abundance matrices (whole-plot and branch-level), a three-dimensional (3-D) solution was recommended. I selected the lowest stress 3-D solution out of 100 trials with randomized starting configurations. Rules of thumb for evaluating final stress by Clark (1993) were used as a guide to determine if the stress values were satisfactory for this dataset. Stress values between 10 and 20 are common for most ecological community data (McCune & Grace 2002). Randomization tests of the final stress, based on Monte Carlo 100 randomized runs, revealed stronger patterns than expected by chance in the 3-D solution.

Using PCORD, I calculated coefficients of determination (r^2) between original sample unit distances and the distances in the final ordination solution to assess how much variability in lichen community composition was represented by the NMS axes (McCune & Grace 2002). For both whole-plot and branch-level ordinations, I maximized the correlations between environmental variables and the ordination solution using orthogonal rotation. Most of the variables were loaded on two axes (1 and 3) for visual clarity. The rotation of the 3D configuration can often result in the factors of interest being displayed in a convenient 2D representation, putting less interesting or minor

variation onto a third axis that is not displayed. Environmental variables were related to the strongest gradients (axes) in species composition using joint plot and correlation coefficients (McCune & Mefford 1999).

Specimen identification and voucher location.--- Lichen vouchers for all specimens are located in the Arizona State University lichen herbarium and the Tongass National Forest lichen herbarium in Petersburg, Alaska. Exceptions are *Pannaria rubiginella* and *Santessoniella grisea* at University of Bergen (UB). I followed the keys of McCune & Geiser (1997) and Brodo et al. (2001) for most identifications. For *Xanthoria* identifications, I followed the taxonomy of Lindblom (1997). I used the keys of Halonen et al. (1998) and Brodo et al. (2001) for *Usnea* identifications. For the lichens in the Panneriaceae, I used Jørgenson (2000). I followed Tønsberg (1992) for *Lepraria* identifications. I identified other crustose with Purvis et al.1992; Brodo et al. 2001; and Dibben 1980. I performed thin-layer chromatography to aid identifications (Culberson 1972; Culberson & Johnson 1982). I followed the taxonomy and nomenclature of Esslinger (1997).

RESULTS

Lichens new to Alaska.---Lichen species reported new to Alaska from this study are: *Arthonia didyma, Bryoria pikei*, *Evernia prunastri, Leioderma sorediatum*, *Pannaria rubiginella* , *Parmeliella parvula*, *Parmotrema crinitum*, *Physconia isidiigera*, *Physciella chloantha*, *Pseudocyphellaria perpetua, Ramalina subleptocarpha*, *Santessoniella grisea*, *Usnea arizonica*, *U. hesperina*, *U. madeirensis*, *U. wirthii* and *Vermilicinia cephalota***.**

Lichen species richness of two different habitats.--- Lichen *gamma* -diversity from 22 branches at the forest-marine ecotone was 70 species, and 37 species from 22 interior forest branches (Appendix II). Forty-nine of the 70 species (71 percent) were found exclusive to this ecotone, and were mainly crustose (Appendix II). Thirteen of the 37 species (35 percent) were found exclusive to interior forest branches and were mainly crustose (Appendix II). However, 69 percent of the 13 lichen species apparently exclusive to the interior forest branches were previously recorded from the forest-marine ecotone in other portions of this study.

Alpha-diversity of epiphytic lichens per branch was 11.2 species (sd 4.8) at the forest-marine ecotone, and 4.8 (sd 2.2) for interior forest branches. *Beta*- diversity was high for both habitats; B_w = 6.2 and 7.7 for forest-marine ecotone branches and interior forest branches, respectively. The two most frequently occurring lichens on branches from the forest-marine ecotone were *Platismatia glauca* (66 percent) and *Parmelia saxatilis* (54 percent). *Plastimatia glauca* occurred less frequently (12 percent) on interior forest branches, while *P. saxatilis* was absent. The most frequently occurring macrolichens on interior forest branches were *Cladonia chlorophaea* (38 percent) and *Sphaerophorus globosus* (88 percent).

Forage lichens were more common, and with greater number of species on branches from the forest-marine ecotone (twelve species) than on interior forest branches (one species). The few matrix lichens that were common to both habitats were four species of *Cladonia*, *Platismatia glauca,* and *P. norvergica* (Appendix II). Branches from the forest-marine ecotone contained three cyanolichen species from the genus *Lobaria*, while interior forest branches contained six species within several cyanolichen genera, including the cyanomorph of *Peltigera britannica* (Appendix II).

Interior forest branches contained 13 crustose species compared to 30 crustose species at the forest-marine ecotone. The most frequently occurring crustose lichens from branches of the forest-marine ecotone were *Chrysothrix candelaris* (36 percent) and *Pertusaria ophthalmiza* (40 percent). On interior forest branches, *Lepraria rigidula* (63 percent) and *Loxosporopsis correlifera* (29 percent) were the most frequent. Present in both habitats were the following crustose species: *Lopadium disciforme*, *Loxosporopsis corralifera*, *Lecidea nylanderi*, *Mycoblastus affinus*, *M. caesius*, *Ochrolechia androgyna*, *Pertusaria borealis*, *P. ophthalmiza*, and *Thelotrema lepadinum*.

Description of epiphytic lichen communities from whole plot and branch-level surveys.--- From 39 sample units, a total of 143 epiphytic macrolichens (*gamma*-diversity) were found on all woody substrates at the forest-marine ecotone (Table 1). Cyanolichens represented 34 percent of the lichen species, while 61 percent were of forage and matrix groups combined. Nitrophiles were the least represented, with roughly 5 percent of the species.

From 38 sample units, a total of 53 epiphytic macrolichen species (*gamma*-diversity) were found on *Tsuga heterophylla* and *Picea sitchensis* branches at the forest-marine ecotone. Approximately 63 percent of the epiphytic lichens from whole-plot data were not found during the branch-level data. Cyanolichens represented 41percent of the lichen species found during branch-level surveys. Matrix lichens represented approximately 47 percent, and forage lichens 10 percent of the lichen species. Nitrophilous lichens were least represented with 2 percent of the species.

Alpha-diversity for epiphytic lichens from whole-plot surveys varied between 19 and 75 species per sample unit (mean 45.0, sd 11.1) and 3 to 30 species per sample unit for branch-level surveys (mean 18.3, sd 6.0) (Table 2). *Beta* -diversity (B_w) appeared nearly equal for both surveys (Table 2). The number of half changes (B_D =1.0

and 1.3 for whole plot and branch-level data, respectively) indicated that the data were relatively homogenous for a community data set (Table 2). The similarity of lichen communities was approximately 50 percent within the sample units from the forest-marine ecotone.

Species- rich lichen genera at the forest-marine ecotone were: *Bryoria* (13 species), *Cladonia* (12 species), *Hypogymnia* (8 species), *Peltigera* (10 species and one cyanomorph), *Pseudocyphellaria* (6 species), *Ramalina* (6 species), and *Usnea* (15 species) (Table 1). The lichen *Vermilicinia cephalota,* reported as new to Alaska from the forest-marine ecotone, was found just outside the boundary of a sample unit. Therefore, it was not included in the species diversity measures. Other rare lichens found outside sample units at the forest-maritime ecotone were *Lobaria retigera* and *Nephroma occultum*.

Table 1. Summary of lichens found on 39 sample units from forest-marine ecotone of southeastern Alaska. Lichen species in boldface were statistically significant indicators of exposed sites ($p<0.05$). Total % freq is percentage of sample units where species occurred. Associated indicator values (IV) are reported for species. Indicator species % Freq is percentage of sample units where the indicator lichen occurred at exposed sites. Rareness scores: 0=common; 1=infrequent; 2=infrequent in restricted habitats; 3=rare in restricted habitats; 4= rare endemic to North America or with very limited distribution. The ---- indicates a species is not applicable to the column.

Lichen	Total % Freq (n=39)	IV	Indicator species % Freq exposed sites (n=24)	Rareness score
Alectoria sarmentosa	92.30	-----	-----	0

Bryocaulon pseudosatonanum	5.12	-----	-----	0
Bryoria bicolor	38.46	-----	-----	0
Bryoria capillaris	87.17	-----	-----	0
Bryoria carlottae	43.58	-----	-----	1
Bryoria cervinula	17.94	-----	-----	1
Bryoria friabilis	5.12	-----	-----	1
Bryoria fuscescens	2.56	-----	-----	1
Bryoria glabra	23.07	-----	-----	0
Bryoria lanestris	2.56	-----	-----	1
Bryoria pikei	5.12	-----	-----	3
Bryoria simplicior	2.56	-----	-----	1
Bryoria tenuis	38.46	-----	-----	0
Bryoria trichodes subsp.*americana*	41.02	-----	-----	0
Bryoria trichodes subsp.*trichodes*	38.46	-----	-----	0
Bunodophorun melanocarpum	15.38	-----	-----	1
Candelaria concolor	7.69	-----	-----	1
Cavernularia hultenii	100.00	-----	-----	0
Cavernularia lophyrea	53.84	-----	-----	0
Cetrelia cetrarioides	46.15	-----	-----	2
Cladonia albonigra	2.56	-----	-----	0
Cladonia bellidiflora	15.38	-----	-----	0
Cladonia carneola	2.56	-----	-----	0
Cladonia cenotea	5.12	-----	-----	0
Cladonia chlorophaea	17.94	-----	-----	0
Cladonia coniocraea	35.89	-----	-----	0
Cladonia fimbriata	2.56	-----	-----	0
Cladonia macilenta	2.56	-----	-----	1
Cladonia ochrochlora	41.02	-----	-----	0
Cladonia scabriuscula	17.94	-----	-----	0

Table 2. Continued.

Lichen	Total % Freq (n=39)	IV	% Freq exposed sites (n=24)	Rareness score
Cladonia squamosa	30.76	-----	-----	0
Cladonia umbricola	2.54	-----	-----	0
Collema furfuraceum	7.69	-----	-----	2
Collema subflaccidum	2.56	-----	-----	2
***Dendriscocaulon* sp.**	23.07	37.50	37.50	2
Erioderma sorediatum	12.82	-----	-----	3
Evernia prunastri	2.56	-----	-----	3
Fuscopannaria ahlneri	7.69	-----	-----	2
Fuscopannaria laceratula	53.84	-----	-----	1
Fuscopannaria leucosticta	10.25	-----	-----	1
Fuscopannaria leucostictoides	35.89	-----	-----	1
Heterodermia speciosa	2.56	-----	-----	2
Hypogymnia apinnata	71.79	61.70	100.00	0
Hypogymnia duplicata	48.71	-----	-----	0

Hypogymnia enteromorpha	76.92	-----	-----	0
Hypogymnia occidentalis	2.56	-----	-----	3
Hypogymnia oceanica	20.51	-----	-----	0
Hypogymnia physodes	46.15	-----	-----	0
Hypogymnia tubulosa	25.64	-----	-----	0
Hypogymnia vittata	30.76	-----	-----	0
Hypotrachyna sinuosa	51.53	-----	-----	2
Leioderma sorediatum	7.69	-----	-----	4
Leptogium brebissonii	30.76	-----	-----	2
Leptogium corniculatum	7.69	-----	-----	0
Leptogium cyanescens	7.69	-----	-----	2
Lobaria amplissima	28.20	37.40	45.83	4
Lobaria linita	84.61	-----	-----	0
Lobaria oregana	84.61	-----	-----	0
Lobaria pulmonaria	69.23	71.0	100.00	2
Lobaria scrobiculata	53.84	55.6	87.50	2
Melanelia exasperatula	35.89	-----	-----	2
Melanelia fuliginosa	2.56	-----	-----	2
Melanelia multispora	5.12	-----	-----	3
Melanelia sorediata	2.54	-----	-----	2
Melanelia subaurifera	7.69	-----	-----	1
Menegazzia terrebrata	12.82	-----	-----	2
Nephroma arcticum	2.56	-----	-----	1
Nephroma bellum	76.92	-----	-----	0
Nephroma helveticum	76.92	-----	-----	2
Nephroma laevigatum	23.07	-----	-----	2
Nephroma parile	46.15	-----	-----	2
Nephroma resupinatum	23.07	-----	-----	0
Pannaria rubiginella	2.56	-----	-----	4
Parmelia hygrophila	58.97	48.9	71.00	0

Table 2. Continued.

Lichen	Total % Freq (n=39)	IV	% Freq exposed sites n=(24)	Rareness score
Parmelia pseudosulcata	5.12	-----	-----	1
Parmelia saxatilis	82.05	59.1	100.00	0
Parmelia squarrosa	71.79	-----	-----	0
Parmelia sulcata	84.61	-----	-----	0
Parmeliella parvula	23.07	-----	-----	3
Parmeliella triptophylla	12.82	-----	-----	0
Parmeliopsis hyperopta	7.69	-----	-----	0
Parmotrema arnoldii	43.58	57.1	70.83	2
Parmotrema chinense	2.54	-----	-----	3
Parmotrema crinitum	7.69	-----	-----	3
Peltigera aphthosa	7.69	-----	-----	0
Peltigera britannica	79.48	-----	-----	0
Peltigera britannica cyanomorph	28.20	-----	-----	1
Peltigera collina	84.61	59.2	92.00	0
Peltigera malacea	2.54	-----	-----	0
Peltigera membranacea	46.15	-----	-----	0

Peltigera neopolydactyla	12.82	-----	-----	0
Peltigera pacifica	12.82	-----	-----	1
Peltigera polydactylon	15.38	-----	-----	0
Peltigera praetextata	12.82	-----	-----	0
Peltigera scabrosa	20.51	-----	-----	0
Phaeophyscia sp.	2.54	-----	-----	-----
Physcia adscendens	17.94	-----	-----	*3*
Physcia aipolia	2.54	-----	-----	3
Physcia caesia	5.12	-----	-----	3
Physcia tenella	20.51	-----	-----	3
Physciella chloantha	2.54	-----	-----	3
Physconia isidiigera	7.69	-----	-----	3
Platismatia glauca	92.30	-----	-----	0
Platismatia herrei	71.79	-----	-----	0
Platismatia lacunosa	66.66	-----	-----	0
Platismatia norvegica	84.61	-----	-----	0
Polychidium contortum	66.66	-----	-----	1
Protopannaria pezizoides	20.51	-----	-----	1
Pseudocyphellaria anomala	66.66	-----	-----	2
Pseudocyphellaria anthraspis	38.46	47.5	62.50	2
Pseudocyphellaria crocata	76.92	-----	-----	2

Table 2. Continued.

Lichen	Total % Freq (n=39)	IV	% Freq exposed sites (n=24)	Rareness score
Pseudocyphellaria mallota	12.82	-----	-----	3
Pseudocyphellaria perpetua	2.54	-----	-----	4
Pseudocyphellaria rainierensis	48.71	52.1	79.16	2
Psoroma hypnorum	17.94	-----	-----	0
Ramalina dilacerata	20.51	33.3	33.33	2
Ramalina farinacea	89.74	74.4	100.00	2
Ramalina menziesii	33.33	59.1	54.16	3
Ramalina roesleri	74.35	53.5	100.00	2
Ramalina subleptocarpa	10.25	-----	-----	3
Ramalina thrausta	38.46	-----	-----	3
Santessoniella grisea	2.56	-----	-----	4
Sphaerophorus globosus	97.43	-----	-----	0
Sticta fuliginosa	76.92	-----	-----	0
Sticta limbata	48.71	56.7	79.16	2
Sticta weigelli	33.33	46.6	33.33	2
Sticta wrightii	2.56	-----	-----	3
Tuckermannopsis chlorophylla	100.00	-----	-----	0
Usnea arizonica	2.56	-----	-----	4

Usnea cavernosa	2.56	-----	-----	1
Usnea chaetophora	25.64	-----	-----	2
Usnea cornuta	46.15	-----	-----	2
Usnea filipendula	66.66	52.0	100.00	2
Usnea fragilescens var. *mollis*	12.82	-----	-----	2
Usnea glabrescens	2.56	-----	-----	3
Usnea hesperina	2.56	-----	-----	3
Usnea hirta	2.56	-----	-----	3
Usnea longissima	97.43	-----	-----	2
Usnea madeirensis	38.46	-----	-----	3
Usnea scabrata	5.12	-----	-----	2
Usnea subfloridana	5.12	-----	-----	2
Usnea substerilis	25.64	-----	-----	2
Usnea wirthii	7.69	-----	-----	3
Xanthoria candelaria	51.28	-----	-----	2
Xanthoria polycarpa	10.25	-----	-----	2

Table 2. Total species diversity for all lichens encountered at the forest-marine ecotone.

	Diversity Measure			
	alpha	*gamma*	B_w *beta*	B_D (half –changes)
Whole-plot (n=39)	45.0	143	3.3	1.0
Branch-level (n=38)	18.3	53	2.9	1.3

Variation in epiphytic lichen communities with whole-plot surveys.--- A Monte Carlo test of 100 runs with randomized data indicated the minimum stress of a 3-D solution was lower than would be expected by chance (p = 0.009). The final stress and instability of the 3-D solutions for were 15.4 and 0.00048, respectively (see Appendix III for stress plot). Forty percent of the variation in lichen abundances was explained by axis 1, 17 percent by axis 2 , and 25 percent by axis 3 (coefficients of determination r^2 for the correlations between ordination distances and distances in original n-dimensional

space were 0.41, 0.17, and 0.25 respectively). The three axes combined represented 83 percent of the variation in whole-plot lichen abundance (cumulative $r^2 = 0.83$).

Whole-plot lichen community gradients in relation to environmental variables.---Variation in lichen community composition reflected macroclimatic and topographic gradients. Axis 1 described a topographic position gradient and axis 3, a latitude-temperature gradient (Fig. 2.). The observed ordination trends are not artifacts resulting from the variable sample unit length, since ordination axes were not strongly associated to length of sample unit (Table 3). Exposed forest edges were highly correlated with axis 1(r = 0.76) (Table 3), defining the positive end of a topographic position gradient, while the percent of *Alnus sitchensis* and protected beaches were negatively correlated (r = -0.50) (Table 3). Species richness (r = 0.66), rareness scores (r = 0.75) sum of abundance (r = 0.70) and forage lichens (r = 0. 75) were all highly correlated with exposed topographic position (axis 1) (Table 3, Fig.2). Cyanolichens (r =0.45) and matrix lichens (r =0.49) were correlated less positively with exposed topographic position (Table 3). Lichen species whose abundances were strongly positively associated with exposed topographic position (axis 1) were (r > 0.40): *Bryoria capillaris*, *Hypogymnia apinnata*, *Lobaria pulmonaria*, *Parmelia saxatilis*, *Parmotrema arnoldii*, *Pseudocyphellaria anomala*, *Ramalina farinacea* (Fig. 3), *R. menziesii*, *R. roesleri*, *Sticta limbata*, *Usnea cornuta*, and *U. filipendula*. Nine of these species were also identified as indicator species for exposed forest edges with ISA (Table 1). Several species were weakly associated with the negative end of the topographic gradient (protected forest edges) and increasing *Alnus sitchensis (*r < -0.27*)*: *Cladonia chlorophaea*, *Cladonia ochrochlora*, and *Parmeliella parvula*.

Axis 2 (not illustrated) represented a minor gradient in lichen species composition when the correlation coefficients of the species were examined for the ordination.

Weakly correlated with this axis were matrix and nitrophilous lichens (r = 0.44 and 0.43 respectively) (Table 3). The gradient of species composition was from forage, matrix, and nitrophilous lichens such as *Alectoria sarmentosa (*r = -0.45*), Hypogymnia apinnata (*r = -0.41*), Platismatia glauca (*r = -0.72*), and Parmelia hygrophila (*r = -0.40*)* to a weaker association with cyanolichens such as *Nephroma resupinatum (*r = 0.39*),* and *Peltigera neopolydactyla* (r = 0.39).

Axis 3 (25 percent of the variance) was positively correlated with latitude (r = 0.50) and was negatively correlated with mean winter temperature (r = -0.66) (Table 3). The lichen species positively associated with axis 3 (climatic gradient of increasing latitude) were (r = > 0.40): *Hypogymnia oceanica*, *Lobaria oregana, Melanelia exasperatula, Parmeliella parvula,* and *Xanthoria candelaria*. Species abundances associated with warm winter temperatures were (r = <-0.40): *Fuscopannaria laceratula*, *Platismatia lacunosa*, and *Usnea cornuta*. Topographic position, sum of abundance, and rareness variables were independent from climatic variables due to the near perpendicular arrangement of joint plot overlays (Fig. 2). Nitrophilous and matrix lichens were weakly associated with climatic variables (r = 0.41 and 0.33, respectively) and are displayed between axes 1 and 3 in the ordination (Table 3, Fig.2).

Table 3. Correlations between lichen community and site variables and the ordination axes for whole plot and branch-level analyses. Variables with IrI > 0.40 were considered to be correlated with an axis. Percentages shown below axes numbers represent variation explained for that axis in the NMS ordination.

	Whole-plot Abundance			Branch-level Abundance		
	Axis1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
	40%	17%	25%	45%	15%	21%
Lichen variables						

Sum of abundance	0.70	-0.19	0.17	0.66	-0.44	-0.33
Forage	0.75	-0.28	-0.08	0.66	-0.26	0.23
Matrix	0.49	-0.44	0.33	0.61	0.05	0.25
Cyano	0.45	0.23	0.08	0.01	-0.40	-0.76
Nitrophilous	0.44	-0.33	0.41	0.53	-0.26	-0.04
Rareness score	0.75	-0.05	-0.05	0.79	-0.38	-0.04
Species richness	0.66	-0.12	0.12	0.62	-0.40	-0.03
Site variables						
Aspect of beach	0.33	0.04	0.24	0.32	0.22	0.03
Latitude	-0.28	0.05	0.50	-0.05	0.36	-0.11
Longitude	-0.35	0.15	0.09	-0.02	0.33	-0.21
% *Alnus*	-0.50	0.20	0.19	-0.30	0.20	0.13
Distance from outer coast	0.24	-0.19	0.36	-0.03	-0.17	0.24
Length (m)	-0.25	0.14	0.32	-0.11	0.11	-0.10
Precipitation	- 0.34	-0.11	-0.36	-0.17	0.06	0.19
Mean winter temperature	0.07	0.11	-0.66	0.04	-0.13	0.07
Position	0.76	-0.09	0.15	0.61	-0.22	-0.17

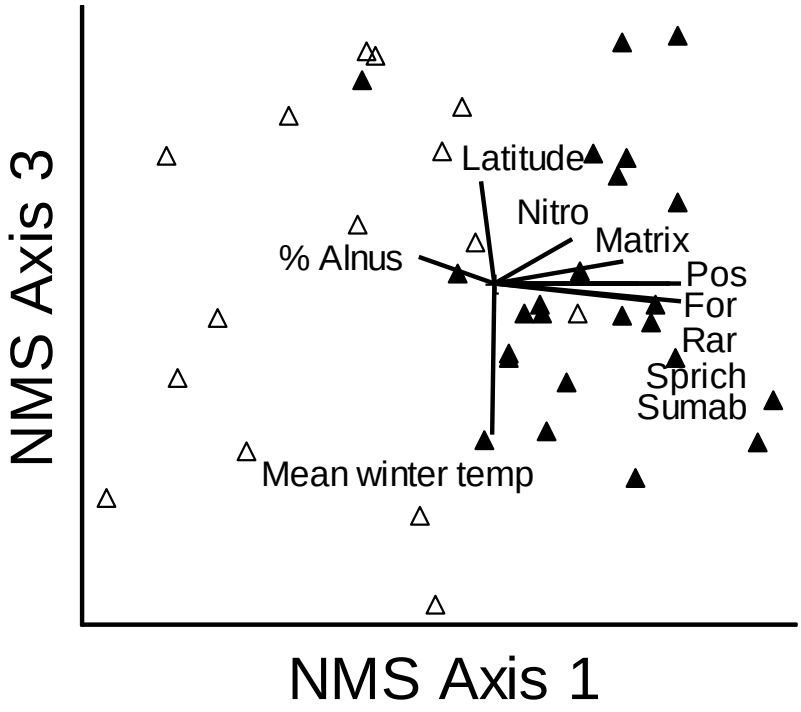


Figure 2. NMS ordination of sample units in epiphytic lichen species space for whole-plot data (n=39) with the joint plot overlays. Vector length and direction indicates the strength of the variables' correlation with the ordination axes. Only vectors with I r I > 0.30 for one axis are shown for clarity. Several vectors positively associated with axis 1 are overlapping and therefore are not clearly separated in the ordination: sum of abundance= Sumab; topographic position= Pos; forage = For; rarity = Rar; and species richness =Sprich). Open triangles represent protected sample units and solid triangles represent exposed sample units.

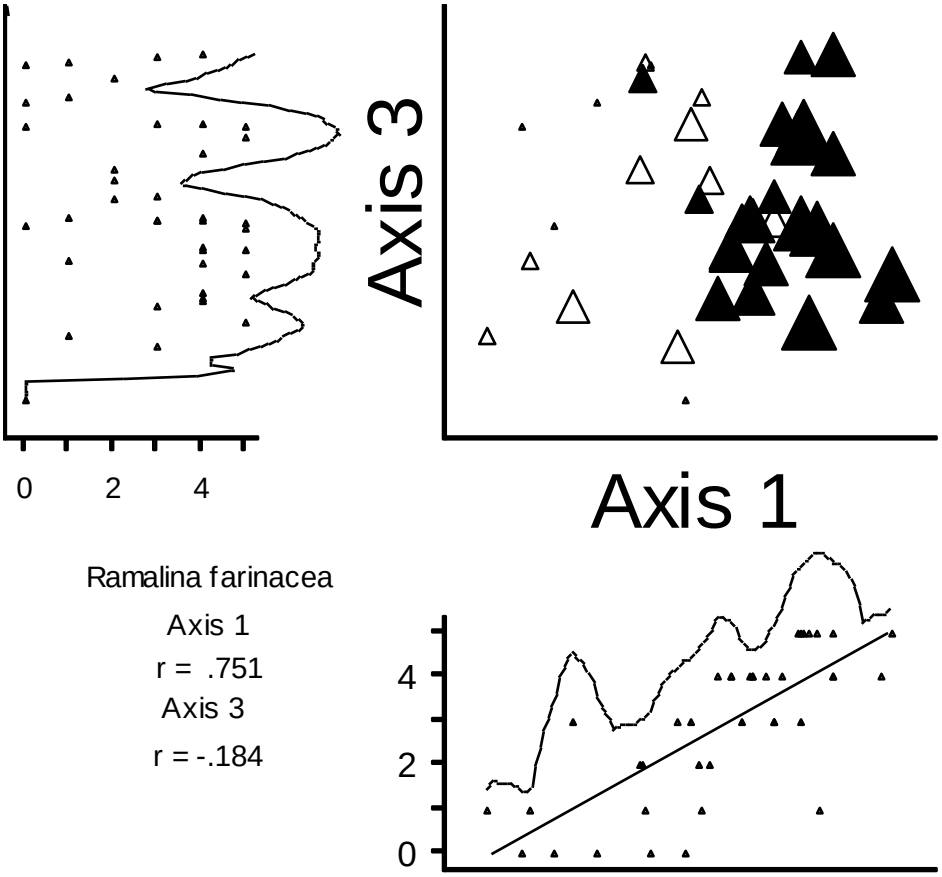


Figure 3. Scatterplot of abundance for *Ramalina farinacea* on axes 1 and 3 of an NMS 3-D ordination for whole-plot data. Symbol size is proportional to species abundance.

Solid triangles are exposed sample units. Upper right: 3-D ordination of species occurrence across sample units. Lower right: scatterplot of abundance of species against score on axis 1 where a relationship with position was found (r = 0.75). Upper left: scatterplot of abundance of species against axis 3 where a strong relationship was not found. Superimposed on the abundance scatterplots are the least squares regression lines. The envelope line was fitted by PC-ORD as a smoothed line to include points falling within two standard deviations of a running mean of *Ramalina farinacea* abundance along a gradient. Values on the axes with numbers represent lichen abundances.

Variation in epiphytic lichen communities with branch-level surveys.--- A Monte Carlo test of 100 runs with randomized data indicated the minimum stress of a 3-D solution was lower than would be expected by chance (p = 0.009). The final stress and instability of the 3-D solution were 14.33 and 0.00005 respectively. Forty-five percent of the variation was explained by axis 1, 15 percent by axis 2, and 21 percent by axis 3 (coefficients of determination r^2 for the correlations between ordination distances and distances in original n-dimensional space were 0.45, 0.15 and 0.21 respectively). The three axes combined represented 81 percent of the variation in branch-level abundances (cumulative r^2 = 0.81).

Branch-level lichen community gradients in relation to environmental variables.--- Exposed and protected sample units were not as clearly separated in the branch-level ordination as in the whole-plot ordination (Figs.2-4). However, similar to whole plot ordination, axis 1 (representing 45 percent of the variation on conifer branches) was strongly associated (r = 0.61) with the sample units defining the positive end of a topographic position gradient (Table 3). The observed ordination trends were not artifacts resulting from the variable sample unit length, since branch–level lichen

abundances were not strongly associated with length of sample unit (Table 3). The lichen community variables: sum of abundance (r = 0.66), species richness (r = 0.62), rareness (r = 0.79), and forage (r = 0.66), matrix (r = 0.61) and nitrophilous (r = 0.53) lichens were positively associated with topographic position (Table 3, Fig. 4). The percent of *Alnus sitchensis* at the forest edge was not as strongly related to lichen abundance (r = -0.30) compared to the whole-plot ordination (Table 3), and thus did not appear as a vector in the joint plot overlay (Fig. 4). Species abundances that were strongly positively associated with axis 1 on conifer branches were (r = > 0.40): *Hypogymnia apinnata*, *Lobaria scrobiculata*, *Parmelia saxatilis*, *P. squarrosa*, *P. sulcata* (Fig.5) *Platismatia norvegica*, *Ramalina farinacea*, *R. menziesii*, *R. roesleri*, and *Tuckermannopsis chlorophylla*. Although not strongly associated with the negative end of the topographic gradient with abundant *Alnus*, several lichens were associated with protected forest edges: *Cladonia* spp. (r = -0.59), and *Peltigera britannica* (r = -0.50).

Axis 2 (not illustrated) described a weak gradient negatively associated with cyanolichen species such as *Fuscopannaria laceratula* (r = -0.40), to the positively associated matrix lichens such as *Platismatia glauca* (r = 0.45) and *P. herrei* (r = 0.48).

Axis 3 represented approximately one-quarter of the variation in lichen communities from conifer branches. Axis 3 represented a gradient in lichen communities with greater abundance of cyanolichens (r = -0.76) (Table 3, Fig.4). The cyanolichens negatively associated (or positively associated with lower latitudes) (r = < -0.38) with axis 3 were; *Fuscopannaria laceratula, Lobaria linita*, *Lobaria pulmonaria, Peltigera collina*, *Peltigera membranacea* (Fig.6), *Pseudocyphellaria anthraspis, Pseudocyphellaria rainierensis,* and *Sticta fuliginosa*.

Mean winter temperature was associated with axis 3 in the whole-plot ordination (Fig. 3). To help understand the cyanolichen relationship to the environmental gradients

displayed in Figure 2 of branch-level ordination, I overlaid the cyanolichen scores from sample units of the branch-level environmental matrix on the ordination of whole-plot data. The resulting ordination graph displayed the branch-level cyanolichen vector weakly associated with the temperature gradient on axis 3 of the whole-plot ordination (r = -0.43, Appendix 5).

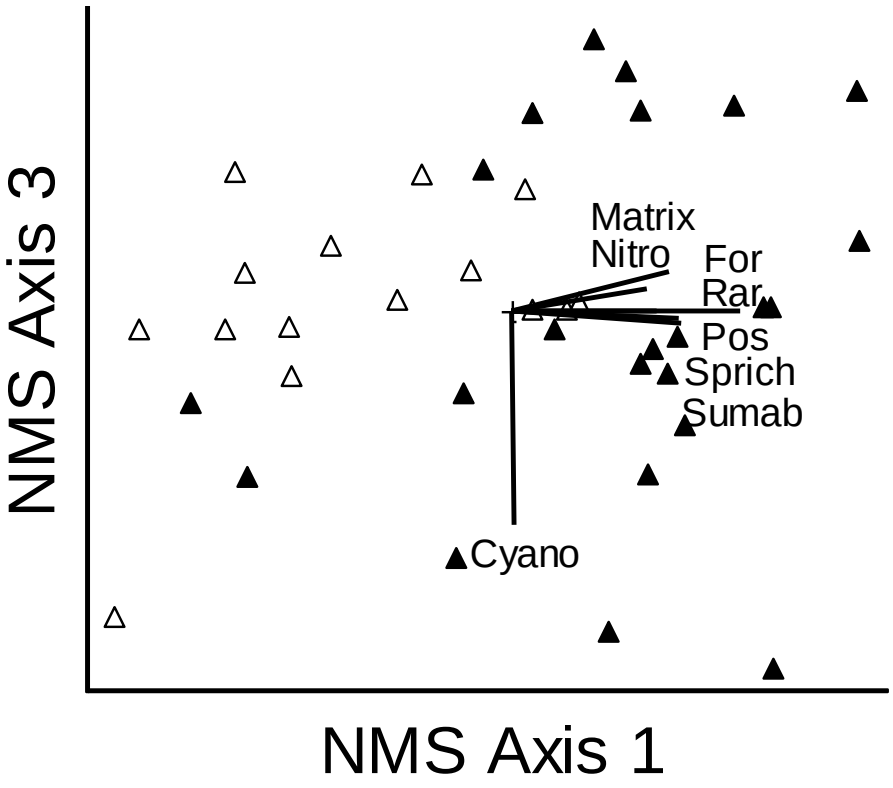


Figure 4. NMS ordination of sample units in epiphytic lichen species space for branch-level data (n=38) with the joint plot overlays. Vector length and direction indicates the strength of the variables' correlation with the ordination axes. Only vectors with I r I > 0.50 for one axis are shown for clarity. Several vectors with similar strength are positively associated with axis 1 and are overlapping and therefore are not clearly separated in the ordination: topographic position = Pos; species richness = Sprich;

Rarity = Rar; sum of abundance = Sumab. Open triangles represent sample units from protected forest edges and solid triangles represent sample units from exposed forest edges.

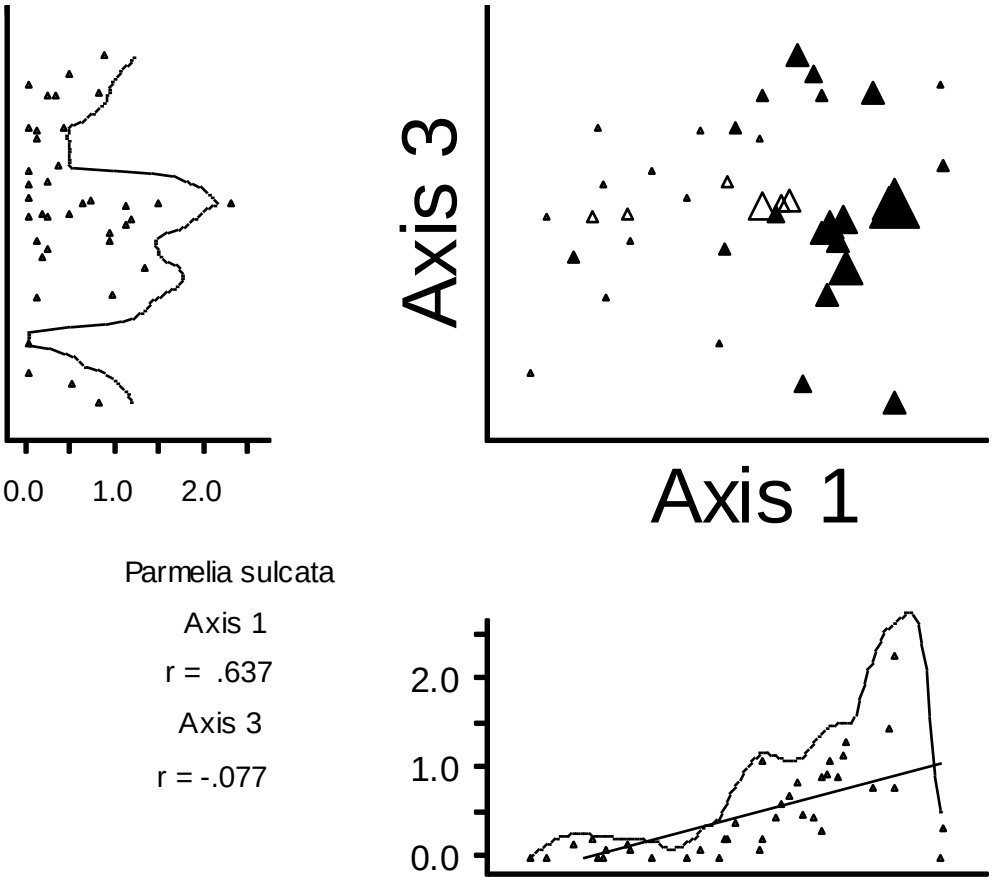


Figure 5. Scatterplot of abundance for *Parmelia sulcata* (matrix lichen) on axes 1 and 3 of an NMS 3-D ordination for branch-level abundance data. Symbol size is proportional to species abundance. Solid triangles are exposed sample units. Upper right: 3-D ordination of species occurrence across sample units. Lower right: scatterplot of abundance of species against score on axis 1 where a relationship with “position” was found (r = 0.64). Upper left: scatterplot of abundance of species against axis 3 (cyanolichen gradient) where a strong relationship was not found for this species. Superimposed on the abundance scatterplots are the least squares regression lines. The envelope line was fitted by PC-ORD as a smoothed line to include points falling

within two standard deviations of a running mean of *Parmelia sulcata* abundance along a gradient. Values on the axes with numbers represent lichen abundances.

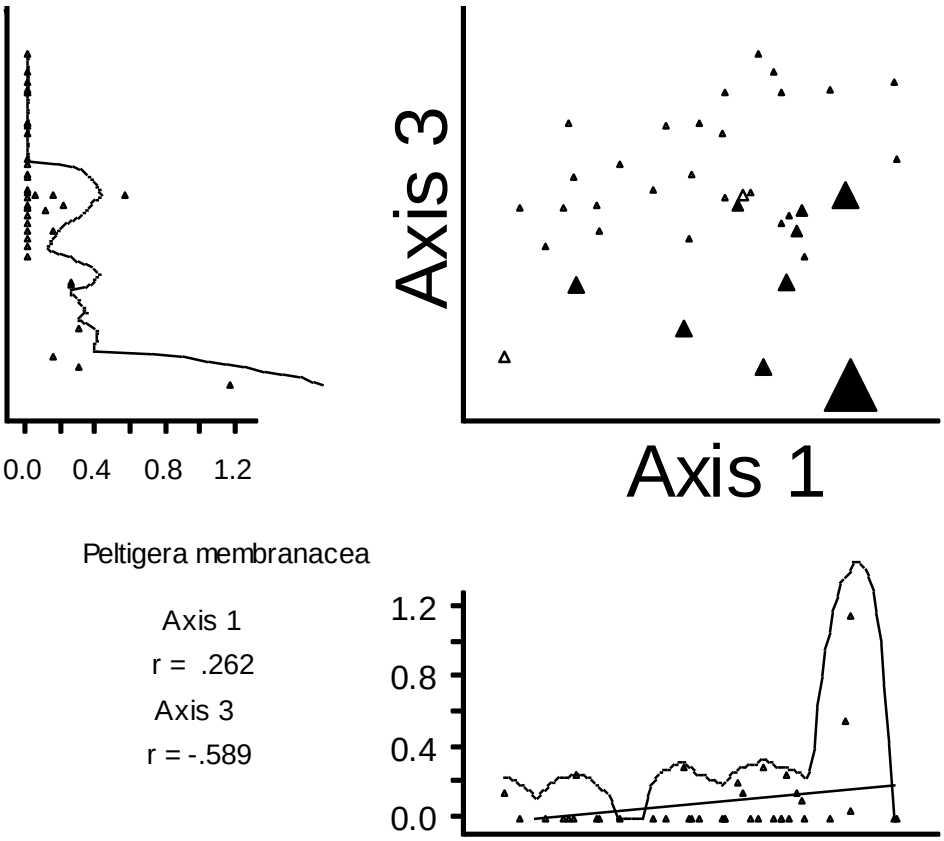


Figure 6. Scatterplots of abundance for *Peltigera membranacea* (cyanolichen) on axes 1and 3 of an NMS 3-D ordination for branch-level abundance data. Symbol size is proportional to species abundance. Solid triangles are exposed sample units. Upper right: 3-D ordination of species occurrence across sample units. Lower right: scatterplot of species abundance against score on axis 1 where a relationship with “position” was not found. Upper left: scatterplot of abundance of species against axis 3 (cyanolichen gradient), where a strong relationship was found (r = -0.51). Superimposed on the abundance scatterplots are the least squares regression lines. The envelope line was fitted by PC-ORD as a smoothed line to include points falling within two standard

deviations of a running mean of *Peltigera membranacea* abundance along a gradient. Values on the axes with numbers represent lichen abundances**.**

Lichen community gradients in relation to topographic position.--- Two topographic positions, exposed and protected, contained different lichen communities (non-metric MRPP: A=0.116, $p < 0.0001$) from whole-plot data. Eighteen lichen species were identified as indicator species for exposed forest edges of the forest-marine ecotone (ISA; $p < 0.05$) (Table 1). The strongest indicators of exposed forest edges were *Lobaria pulmonaria*, *Ramalina farinacea,* and *Usnea filipendula* (Table 1). These species occurred in all sample units considered exposed. Several rare cyanolichens were also indicators of exposed edges of the forest-marine ecotone (Table 1).

DISCUSSION

Lichen species richness of two different habitats.--- Ecosystem productivity and species richness are assumed to increase together (Huston 1994). However, these factors do not always go together in coastal rain forests, where productive Western Hemlock forests produce large amount of wood fiber per hectare, but often have low species richness (Alaback & Pojar 1997). This is due to the limited solar radiation and heavy rain that shade out the sun in dense forested areas. Lichen communities from this portion of the study appear to follow this observation; lower species richness from interior forest branches compared to the more open areas of the forest-marine ecotone. The forest-marine ecotone also contains greater habitat heterogeneity due to disturbance regimes induced by the maritime climate that encourages species richness by providing a richer complex of microhabitats and greater penetration of solar radiation.

Although this portion of the study contained a small sample size, results indicated that more crustose and forage lichens were habitat-exclusive to branches of the forest-

marine ecotone than matrix or cyanolichens (Appendix II). The larger number of crustose species exclusive to the branches at the forest-marine ecotone compared to matrix and cyanolichens could be due to more abundant bryophyte mats (and less bare bark) observed on interior forest branches. Matrix and cyanolichens were mainly found on the thick bryophyte mats on interior forest branches, while the crustose species were on the small patches of bare bark and on the undersides of the branches where bryophytes did not grow. Similar to the results of this study, Ellyson and Sillett (2003) found the lichen genera *Cladonia* (matrix) and *Lepraria* (crustose) (Appendix II) frequent the lower, bryophyte-covered branches of old-growth *Picea sitchensis* in northern California, possibly indicating a habitat preference of the lower canopy of interior forests.

Most of the forage lichens were also exclusive to the forest-marine ecotone, indicating that dispersal mechanisms such as strong winds and animals were less prevalent near the lower branches of interior forests. Forage lichen species can tolerate high light intensities (Gauslaa & Solhaug 1996), which may explain their more frequent occurrence at the forest-marine ecotone compared to interior forest branches.

Lichen communities at the forest-marine ecotone.--- Natural edge studies (as opposed to edges along clear-cuts or other man-made transition zones) have traditionally been avoided in ecology due to the difficulty of characterizing the rates of micro-disturbances across a particular landscape and relating these to communities of species (Noss 1987). In this study, it was difficult to quantify micro-disturbances that introduced substrate variability and therefore affected the lichen communities at the forest-marine ecotone. The lichen communities from this ecotone result from biotic and abiotic events over hundreds of years relatively unaltered by humans. This study found that the forest-marine ecotone support many lichens species that are poorly

represented or absent from interior old-growth *Tsuga heterophylla* and *Picea sitchensis* coastal forests of southeastern Alaska. The forest-marine ecotone, especially at exposed locations, is a central hotspot for epiphytic lichen diversity in southeastern Alaska. This is largely because of the number of species that were found to occur there and the key linkages between the physical and biotic process that take place in this ecotone.

The close proximity to the marine environment appeared to positively affect lichen species richness to a greater extent than other forested habitats away from the marine environment. This is supported by the apparent differences in lichen species richness found at the forest-marine ecotone, in riparian forests, and in other forested habitats in southeastern Alaska. Lichen communities of the forest-marine ecotone contained 63 percent more epiphytic lichen species than were found in the more open forests of the *Pinus contorta* peatlands of the region (Derr 1994). Roughly 62 percent more species were found at the marine-forest ecotone than were found in mainland riparian forests of predominantly *Picea sitchensis* and *Alnus rubra* (Geiser et al. 1994). Seventy-seven percent more lichen species were found at the forest-marine ecotone than in other old-growth forest habitats dominated by *Tsuga heterophylla*, *Picea sitchensis,* and *Chamaecyparis nootkatensis* (Geiser et al. 1994). Lichen data from these old-growth forest habitats were from relatively closed forests. More surveys are needed along large mainland riparian forest edges or along the forested edges of freshwater lakes to better contrast lichen species richness from old-growth forests habitats with similar incidences of solar radiation.

Lichen surveys from all woody substrates (whole-plot) contained nearly three times the number of lichen species that were found during branch-level surveys from the same locations. This suggests that lichen communities of the forest-marine ecotone are

species rich, in part, due to the different species and ages of woody substrates at the forest edge. This concurs with a study from Oregon by Peterson & McCune (2003); greater lichen diversity occurred where more hardwoods versus conifers existed compared to other old-growth forests with lesser amounts of hardwoods. In varying amounts, the forest-marine ecotone contains most of the hardwood species that occur in southeastern Alaska. The riparian forests of southeastern Alaska do have a hardwood component, but the interior swaths of old-growth forests contain virtually none. The study in Oregon also found that varying tree size, and a discontinuous forest canopy also promoted greater lichen diversity (Peterson & McCune 2003). Similar features exist at the forest-marine ecotone compared to interior forests; more light due to being an edge habitat and greater variation in forest structure due more direct contact with wind disturbance events influenced by oceanic weather conditions. For future surveys of biodiversity at the forest-marine ecotone, whole-plot surveys as opposed to branch-level surveys, will provide more information about species richness of epiphytic lichen communities.

Lichen community gradients in relation to environmental variables.--- Precipitation was not strongly associated with lichen abundance (Table 3), but this did not include the humidity gathered from fog. Many of the exposed forest edges were adjacent to large bodies of ocean, such as the Gulf of Alaska, where year-round fog is certain to be frequent and variable. Fog can be very important as a water source for epiphytic lichens (Stoutjesdijk & Barkman 1992; Matthes-Sears & Nash 1986). Daytime fog is actually more favorable to lichens than rain, because lichens require sufficient light, and moist, but not completely saturated conditions for photosynthesis (Stoutjesdijk & Barkman 1992). Differences in microclimate conditions concerning fog and wind velocities may have affected the sensitive wetting and drying cycles of lichens, which are

very important to their establishment and growth (Barkman 1958; Matthes-Sears et al. 1986).

Lichen community gradients in relation to topographic position.--- Forest-marine ecotones with exposed positions contained different lichen communities, greater species richness, and more rare lichens than protected edges. This suggests that certain environmental factors at exposed edges played a role in lichen establishment and growth. Roughly 18 percent of the lichen species were sufficiently frequent at exposed forest edges to show a significant difference between the two topographic positions (Table 1). Almost half of the 19 indicator lichens of exposed edges were also found along large mainland riparian areas of the region, while another 40 percent were only known from the forest-marine ecotone in southeastern Alaska (Geiser et al. 1994; Tønsberg & Goward 2001). Some indicator species of exposed forest edges are extremely rare in North America, such as *Lobaria amplissima* and *Pseudocyphellaira rainierensis* (Sillet & Goward 1998; Tønsberg & Goward 2001).

Approximately 25 percent of the indicator species of exposed topographic positions were forage lichens, and 47 percent were cyanolichens. Stronger winds expected at exposed sites may help fragment the lichens, thus explaining the greater abundance of forage lichens at this habitat. A study from coastal Canada found that cyanolichens were more abundant in forests closer to the open ocean (Price and Hochachka 2001). They hypothesized that cyanolichens may have been subjected to optimal wetting and drying cycles in exposed forests, while protected forests remained wet too long for cyanolichen development (Lange et al. 1993). Favorable climatic factors are possible reasons for such a large percentage of cyanolichens at exposed edges.

Protected forest edges of the forest-marine ecotone also contained rare lichens. Two very rare cyanolichens, *Nephroma occultum* and *Lobaria retigera* were found

outside sample units on protected forest edges. *Nephroma occultum* is thought to be exclusively an old-growth associated species (Sillet 1995). These occurrences were only the second for *Nephroma occultum* and the fourth for *Lobaria retigera* in southeastern Alaska (Geiser et al. 1998).

Protected forest edges contained large thickets of *Alnus sitchensis* (Sitka alder), especially where freshwater streams emptied into estuaries. Alder thickets may function as buffers that ameliorate the full impact of forest edge microclimate on the lower conifer branches and shrub layer where the surveys were conducted. Alder is deciduous, and has a low-profile with a contorted growth form that creates a shady microhabitat favored by bryophytes. Bryophyte competition may have influenced the abundance of epiphytic lichens that grew on the alder and on other woody substrates under the alder canopy.

Lichen community gradients in relation to functional groups.--- The lack of separation between cyanolichens and nitrophilous lichens at exposed edges (Table 3) appeared contradictory to what is well known about these two functional groups. Cyanolichens generally inhabit nitrogen-poor habitats because they produce their own nitrogen required for metabolic functions, while nitrophilous lichens tolerate nitrogen-rich substrates. However, the abundant microhabitats along the forest edge allowed for both functional groups to occur within the same sample unit. The nitrophilous lichens tended to be on twigs and branches where bird and mammal use concentrate. Due to different nutrient requirements, many of the cyanolichens were on the boles, or on other woody substrates that were probably more nitrogen-poor.

In the branch-level surveys, I observed that cyanolichens tended not to be as abundant on branches that contained nitrophilous species. This is expressed by their perpendicular arrangement in the branch-level ordination (Fig. 4). For the branch-level ordination, cyanolichens were strongly related to axes 3 (cyanolichen gradient) (Fig. 4),

and when overlaid on the whole-plot ordination were weakly related to axis 3 (temperature gradient) (Appendix IV). These differences could be due to the different substrates surveyed; conifer branches versus all woody substrates. Cyanolichen abundance relating to warmer winter temperatures (Appendix IV, Fig. 4) and not to exposed forest edges suggested that some species, such as the rare cyanolichens *Lobaria amplissima* and *Pseudocyphellaria rainierensis*, may reach their northern limit along the coast of southeastern Alaska.

Conservation implications for rare lichens and biodiveristy.---In the Pacific Northwest, conservation issues for lichen biodiversity have mainly focused on old-growth forests, riparian areas, and remnant trees (Peck & McCune 1997; Peterson & McCune 2001; McCune et al. 2002). This interest is markedly less on National Forest lands in Alaska due to the Region following different management directives than National Forests in the other western states (USDA & USDI 1994; USDA 1997; Derr et al. 2003). Worldwide threats to the biodiversity of lichens include loss of habitat due to disturbances from fire and timber harvesting, air pollution, climate change, agriculture, and tourism (Wolseley 1995). Lichen conservation requires habitat protection, which becomes a political situation in areas where lichens have no specifically mandated federal protection.

Aside from preserving biodiversity and rare species, lichen conservation is especially important for those species associated with old-growth forests, such as the pendulous forage species, which provide food and nesting material for a variety of wildlife (Rosentreter et al. 1997; Rominger et al. 1994; Stevenson & Enns 1993; Thomas & Rosentreter 1992), and cyanolichens such as *Lobaria oregana*, an ecologically important nitrogen fixer (McCune 1993; Pike 1978). Lichens are known for harboring arthropods, and thus form an important link in the food supply of branch-feeding birds

(Pettersson et al. 1995; Andre 1985; Gerson 1973). Therefore, lichens provide important ecosystem functions, and their decline worldwide validly raises an alarm and warrants conservation of habitats with greatest lichen biodiversity.

This forest-marine ecotone in much of southeastern Alaska is currently protected from large- scale timber harvesting under the Tongass National Forest Management Plan, however, small-scale tree removal is permitted for a variety of uses (USFS 1997). Current forest protection extends approximately 330 meters slope distance into the forest from the forest-marine ecotone. This protection measure was initially implemented to maintain the ecological integrity of the biologically rich tidal and intertidal zone, emphasizing habitats for bald eagles, waterfowl, shorebirds and other marine associated, terrestrial species (USFS 1997). With the addition of rare lichen habitat that is species-rich to this list of resources, continued protection of coastal forest buffers that include the forest-marine ecotone is important for maintaining biodiversity of lesser known organisms associated with this habitat.

Rare lichen distribution along this ecotone may be more than just random occurrences at exposed locations. Rare lichens may be related to specific temporal and spatial factors that should be analyzed at the species level to better understand their requirements. Some rare lichens are considered indicators of long ecological continuity in forests of the Pacific Northwest (McCune 1993), and could be used as indicator species for old-growth forest conditions (Tibell 1992). A larger sampling effort of lichens from the forest-marine ecotone that include more precise climate measurements, both macroclimatic and microclimatic (Stoutjesdijk & Barkman 1992) will help to further understand these emerging patterns of rare lichen distribution and lichen biodiversity of this ecotone.

APPENDIX I

DESCRIPTION OF SAMPLE UNITS INCLUDING, LOCATION, POSITION, LATITUDE, LONGITUDE, AND NUMBER OF LICHEN SPECIES.

Location	Position	Lat/Long	# lichen species	Location	Position	Lat/Long	# lichen species
Neets Bay, Revillagigedo Is.	protected	55°46'N 131°32'W	38	Dall Bay, Gravina Is.	exposed	55º 09'N 131º 44' W	48
Settlers Cove, Revillagigedo Is.	exposed	55°30'N 131°44'W	41	Dall Head Gravina Is.	exposed	55º 07'N 131º 44' W	47
Bridget Cove, Mainland, Juneau	exposed	58°37'N 134°55'W	40	Delong Is. Misty Fiords	exposed	54º 58'N 131º 00' W	75
Homeshore, Chilkat Pen.	exposed	58°18'N 135°22'W	36	W Kanagunut Is. Misty Fiords	exposed	54º 44'N 130º 42'W	63
Mallard Cove, Port Snetisham	protected	58°05'N 133°50'W	44	Lincoln Channel, Misty Fiords	protected	54º 44'N 130º 42'W	46
Iyoukeen Pen., Chichgof Is.	exposed	57°53'N 135°00'W	36	Kah Sheets Is. Misty Fiords	exposed	55º 02'N 131º 00'W	70
Betton Is., Behm Canal	exposed	55°30'N 131°50'W	38	Kah Sheets Pt. Misty Fiords	exposed	55º 03' N 130º 59'W	59
Mountain Point, Revillagigedo Is.	exposed	55°17'N 131°32'W	49	S. of Brownly Ernst Sound	exposed	55º55'N 132º10'W	45
Vixen Inlet, Cleveland Pen.	protected	55°47'N 132°05'W	33	Pt. Howe, Mitkof Is.	exposed	56º29'N 132º49'W	58
Howard Bay, Lynn Canal	exposed	58°18'N 135°04'W	40	Ideal Cove, Mitkof Is.	exposed	56º40'N 132º38'W	64
Patterson Bay, Chichagof Is.	protected	57°41'N 135°44'W	43	Windy Bay S. Coronation Is.	protected	55º52'N 134º17'W	36
Goose Flats, Chichagof Is.	protected	57°56'N 135°45'W	44	Windy Bay N. Coronation Is.	exposed	55º53'N 134º18'W	41
Jap Creek, Mainland, Petersburg	exposed	56º 46'N 132º 36' W	34	Egg Harbor, Nation Pt. Coronation Is.	exposed	55º55'N 134º19'W	34
S. Blind Slough Mitkof Is.	protected	56º 32'N 132º 45' W	45	Egg Harbor, Coronation Is.	exposed	55º54'N 134º18'W	49
West Point, Frederick Sound Kupreanof Is.	protected	57º 00' N 133º 20'W		Table Bay, Kuiu Is.	protected	56º08'N 134º12'W	32
Explorer Basin Kuiu Is.	protected	56º 25'N 134º 13' W	60	Kell Bay N. Kuiu Is.	protected	56º09'N 134º11'W	42
Whale Bone Cove, Kuiu Is.	exposed	56º 25' N 134º 14'W	44	Kell Bay S. Kuiu Is.	protected	56º08'N 134º08'W	19
Windfall Is. Tebenkof Wilderness	exposed	56º 27'N 134º 14'W	47	Kell Bay S. Arm Kuiu Is.	protected	56º07'N 134º10'W	25
Affleck Canal Kuiu Is.	protected	56º 19' N 134º 04'W	32	S. Mitkof Is. Stikine flats	exposed	56º35'N 132º32'W	68
Petrof Bay, Kuiu Is.	protected	56º 20' N 134º 03"W	24				

APPENDIX II

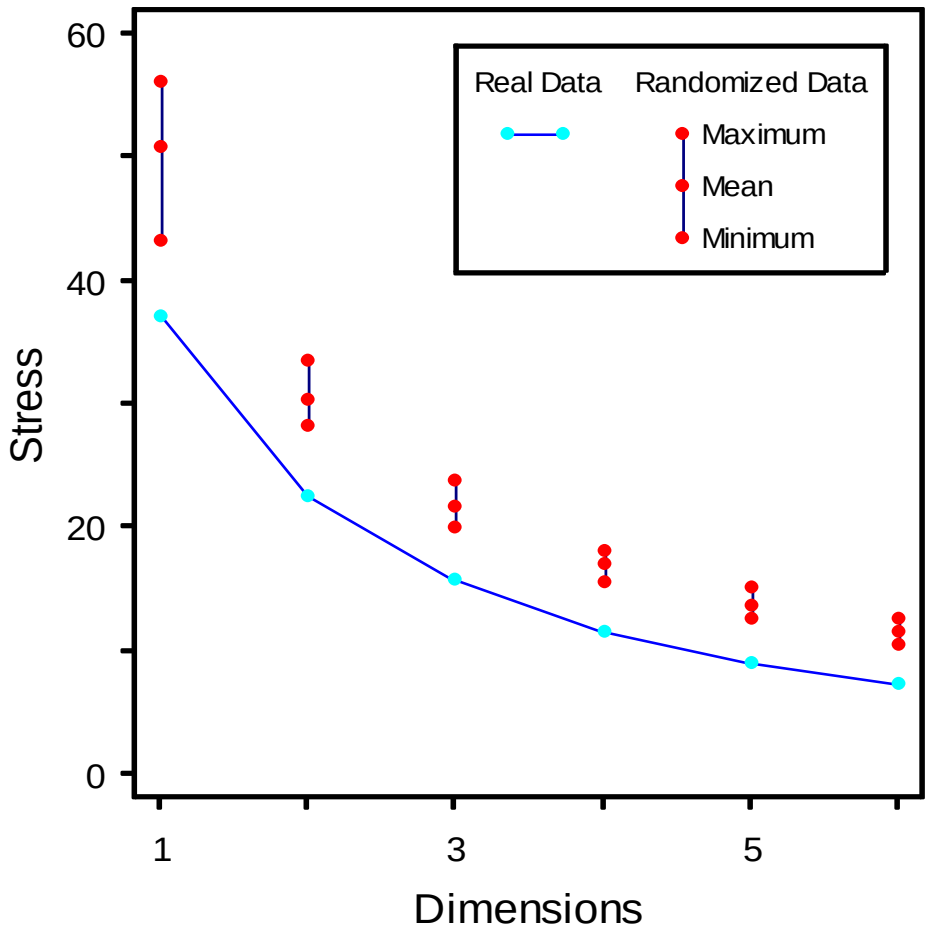
LIST OF LICHENS FROM *TSUGA HETEROPHYLLA* BRANCHES FROM THE FOREST-MARINE ECOTONE AND INTERIOR FORESTS OF SOUTHEASTERN ALASKA.

Forage	Crustose	Matrix	Cyano
Alectoria sarmentosa B	*Arthonia didyma* B	*Cavernularia hulteni* B	*Fuscopannaria laceratula* I
Bryoria capillaries B	*Arthonia punctiformis* B	*Cladonia chlorophaea* I	*Lobaria linita* BI
Bryoria carlottae B	*Buellia grisioverens* B	*Cladonia coniocraea* BI	*Lobaria oregana* BI
Bryoria cervinula I	*Buellia muriformis* B	*Cladonia norvegica* I	*Lobaria pulmonaria* B
Bryoria friabilis B	*Buellia* sp. I	*Cladonia ochrochlora* BI	*Nephroma laevigatum* I
Bryoria lanestris B	*Chrysothrix candelaris* B	*Cladonia scabriuscula* BI	*Parmeliella parvula* I
Bryoria trichodes ssp. *americana* B	*Cliostomum griffithi* B	*Cladonia squamosa* B	*Peltigera britannica* I
Ramalina farinacea B	*Cliostomum* sp. B	*Cladonia subfurcata* BI	*Peltigera britannica* cyanomorph I
Ramalina menzeisii B	*Cocotrema pocillarium* B	*Hypogymnia apinnata* B	*Peltigera collina* B
*Ramalina roesleri*B	*Japewia tornoensis* B	*Hypogymnia duplicata* I	*Peltigera scabruscula* B
Usnea chaetophora B	*Lecanora expallens* B	*Hypogymnia enteromorpha* B	
Usnea fragilis var. *mollis* B	*Lecidia nylanderi* BI	*Parmelia hygrophila* B	
Usnea longissima B	*Lecidella euphora* B	*Parmelia saxatilis* B	
	Lepraria incana B	*Parmelia squarrosa* B	
	Lepraria rigidula L	*Parmelia sulcata* B	
	Lepraria sp. 1 I	*Parmotrema arnoldii* B	
	Lepraria sp. 2 B	*Platismatia glauca* BI	
	Lopadium disciforme BI	*Platismatia herri* B	
	Loxosporopsis corralifera BI	*Platismatia lacunosa* B	
	Mycoblastus affinus BI	*Platismatia norvegica* BI	
	Mycoblastus caesius BI	*Sphaerophorus globosus* BI	
	Mycoblastus sanguinarius B	*Tuckermannopsis chlorophylla* B	
	Ochrolechia androgyna BI		
	Ochrolechia juvenalis B		
	Ochrolechia oregonensis B		
	Ochrolechia subpallescens B		
	Ochrolechia szatalaensis B		
	Opegrapha varia B		
	Pertusaria albescens I		
	Pertusaria amara B		
	Pertusaria borealis BI		
	Pertusaria dactylina B		
	Pertusaria *ophthalmiza* BI		
	Phlyctis argena B		
	Pyrrhospora quernea B		
	Thelotrema lepadinum BI		
	Trapelia corticola I		

B indicates found at the forest-marine ecotone
I indicates found on interior forest branches

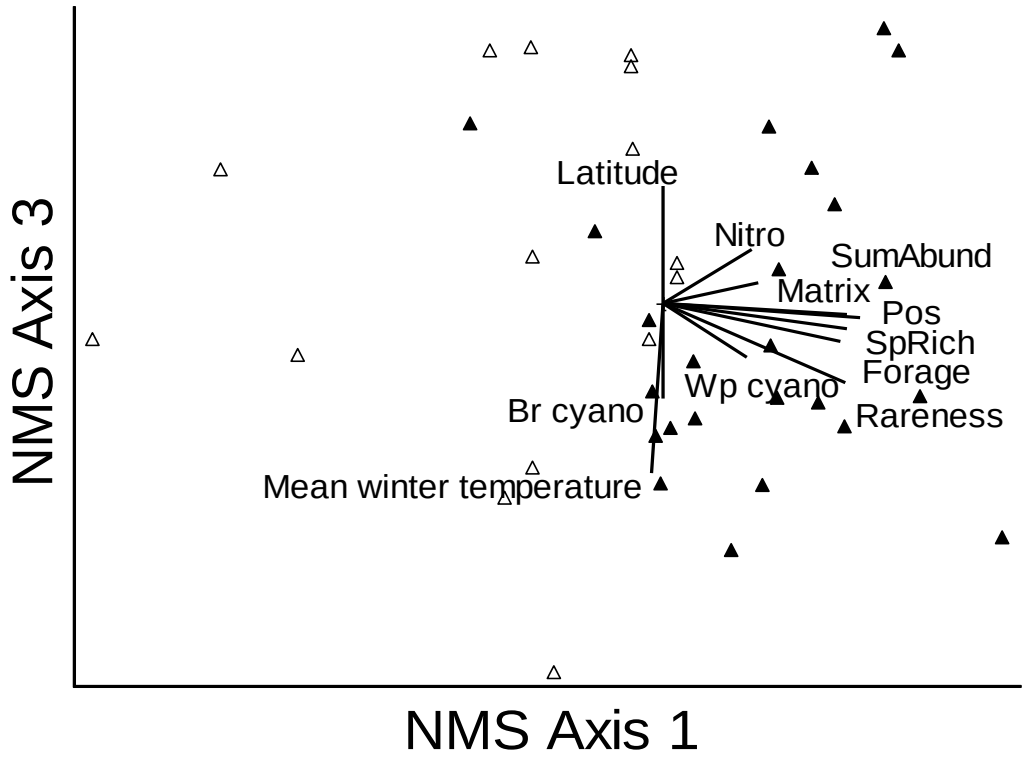
APPENDIX III

STRESS PLOT FOR WHOLE-PLOT DATA



APPENDIX IV

NMS ORDINATION OF SAMPLE UNITS IN EPIPHYTIC LICHEN SPECIES SPACE FOR WHOLE-PLOT DATA WITH BRANCH-LEVEL CYANOLICHEN SCORES INCLUDED. VECTORS RADIATING FROM THE CENTROIDS SHOW CORRELATIONS ($r^2 \geq 0.25$) WITH VARIOUS ENVIRONMENTAL VARIABLES. LENGTH OF THE CORRELATION VECTORS REPRESENTS THE RELATIVE STRENGTH AND DIRECTION OF THE VARIABLES WITH THE ORDINATION. RELATED VARIABLES WITH OVERLAPPING VECTORS OF SIMILAR STRENGTH ARE ABBREVIATED : “POS” (TOPOGRAPHIC POSITION), “SPRICH” (SPECIES RICHNESS), “SUMABUND” (SUM OF ABUNDANCE), NITRO (NITROPHILOUS LICHENS), WP CYANO (WHOLE-PLOT CYANOLICHENS), AND BR CYANO (BRANCH-LEVEL CYANOLICHENS).


NMS Axis 3
NMS Axis 1
Latitude
Nitro
SumAbund
Matrix
Pos
SpRich
Forage
Wp cyano
Br cyano
Rareness
Mean winter temperature

LITERATURE CITED

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