

# GIS-based modeling to assess ecological niche differentiation in four species of sympatric lichens at risk in Nova Scotia, Canada

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**ABSTRACT.** Species distribution models (SDMs) rely on the concept of niche theory that suggests that individual species live within definable ranges of environmental conditions. Comparisons of SDMs between species can help further the understanding of competitive exclusion and niche differentiation. SDMs were created for *Erioderma pedicellatum*, *E. mollissimum*, *Pectenaria plumbea* and *Pannaria lurida*, four sympatric species that occur in Nova Scotia, Canada. Logistic regression was used to create SDMs using nine environmental explanatory variables and presence of the modeled species as the response variable. There was significant overlap in environmental space between species, but each species tended to occupy a unique combination of environmental attributes. The *Erioderma pedicellatum* model from this study suggests this species occurs in cooler wet climate at mid-elevations in older closed canopy coniferous forest. Results from this study indicate *Erioderma mollissimum* occurs in old to mature deciduous forests at low to mid-elevation in warm, moderately wet climates. *Pectenaria plumbea* tended to be found at low to mid-elevations in areas with moderately cool temperature with mid to high mean annual precipitation. *Pannaria lurida* tended to occupy mature to old forests occurring in areas with mid-range mean annual precipitation at higher elevations. Since this study examined a relatively small number of environmental variables, further study at different scales and with more extensive datasets would likely reveal further insights into competitive exclusion among these four cyanolichens.

**KEYWORDS.** Species distributions model, sympatric cyanolichens, niche differentiation, Nova Scotia.



The advent of Geographical Information Systems (GIS) and increasing computing power has resulted in the proliferation of models to predict occurrence of species, often termed species distribution models (SDMs). The SDM approach has been used for a variety of purposes. As a contribution to increased knowledge and understanding of species and ecosystems, SDMs have been most often used to identify environmental variables that help explain species presence or abundance (Stauffer 2002). SDMs have also been used by geographers and ecologists to study how and why species are distributed across the landscape (Guisan & Thuiller 2005). In conservation planning, SDMs have been used to identify new areas of occupation or potential new locations for rare or at risk species (Rodriguez et al. 2007).

Species distribution is the geographic area in which a species occurs. The International Union for the Conservation of Nature (IUCN) define species distribution as the area bounded by all known or inferred occurrences with some exceptions (e.g., introductions outside the species natural range). This distribution area can also have within it significant areas of exclusion where the species does not occur (IUCN 2012). Species extent of occurrence (EOO), which is related to the spread of extinction risk, and area of occupancy (AOO), which is the occupied range area, are terms used by IUCN to assess species of conservation concern. EOO and AOO may not equate with species distribution (IUCN 2018). Distribution studies can include the entire range in which a species occurs or specific regions of interest. Modeling species distribution involves the use of techniques for interpolating and extrapolating the area a species could

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occupy based on quantitative or rule-based models (Zurell et al. 2020). The models relate environmental data to species abundance or occurrence locations and then project that onto a geographic space to predict where that species might occur.

Data used in modeling can be derived from random or systematic sampling for abundance, presence only or presence-absence (Guisan & Thuiller 2005). In practice, few SDMs are derived from random or systematic sampling. Researchers often take advantage of opportunistic data, such as from museum collections or conservation data centers (e.g., Reutter et al. 2003).

A variety of techniques have been used in the creation of SDMs. Regression analysis has been used with abundance data (e.g., multiple linear regression) and presence-absence data (e.g., logistic regression). Abundance data is often difficult or costly to acquire, thus a variety of techniques for model creation with presence-absence data have been proposed (e.g., Classification and Regression Tree). Sometimes data consists of presence only, such as from museum records, and a variety of techniques have been developed for modeling with these kinds of data (e.g., maximum entropy, Mahalanobis D statistic). New techniques include machine learning which use computer programs or algorithms that adapt or change from an experience (data) using certain performance measures. Examples of machine learning include Maximum Entropy, BIOCLIM, Random Forest and CLIMEX (Gobeyn et al. 2019).

Regardless of model development method or data type, the underlying principle that supports this type of analysis is niche theory. Niche theory suggests that individual species live within definable ranges of environmental conditions (Chase & Leibold 2003). Thus it is possible to predict locations of occurrences of species if it is possible to define the environmental variables that describe that species niche and plot those environmental variables in space (Hirzel & Le Lay 2008). Describing and plotting environmental variables in space to predict species occurrences largely relies on the Grinnellian concept of niche (Grinnell 1917). Eltonian niche relates to the species relationship to other species (predation, competition, mutualism, etc.) (Elton 1927). It is possible to model both types of niches using the same methods and even within the same model. However, few SDMs have incor-

porated both Grinnellian and Eltonian niches. The vast majority of SDMs rely on the Grinnellian concept, which may be because spatially mapping relationships with other species is more challenging (Hirzel & Le Lay 2008). Both the Grinnellian and Eltonian concept of niche would be included within Grubb's definition of habitat niche for plants (Grubb 1977). Habitat niche is simply defined as the physical and chemical limits tolerated by the mature plant in nature. Other types of niches outlined by Grubb are life form, regeneration and phenological niche. For the purposes of this paper, habitat, niche and habitat niche are used interchangeably and follow the definition described by Grubb for plants.

Relying solely on the Grinnellian concept of niche has been one of the criticisms of SDMs, along with a number of other issues. The largest criticism has been that often the set of environmental variables available for modeling may be an incomplete explanation of niche. Variable selection has also been problematic and is often driven by which data is available for modeling (Hirzel & Le Lay 2008). Model selection requires careful consideration and there have been a greater number of recent studies comparing different modeling methods (e.g., Guillera-Arroita et al. 2015; Meynard & Quinn 2007).

Despite these shortcomings, SDMs have been quite successful in many instances. SDMs have helped explain which environmental variables are important in explaining distribution across the landscape for many species. SDMs have also been helpful in predicting where species occur, thus aiding in conservation for many at risk species (Guisan & Thuiller 2005).

One area of study using SDMs that has seen little research is competitive exclusion by niche comparisons (Anderson et al. 2002). It is possible to compare SDMs of two or more sympatric species to better understand how the species differentiate in niche space. One could model habitat of two or more species independently in the same area and simply compare their characteristics (Hirzel & Le Lay 2008). The main problem with this approach is that it can only show correlation, while only an experimental approach can test whether a causal link exists. However, Anderson et al. (2002) suggest that SDM comparison studies can, in some cases, come close to experimental design if the study meets the following

conditions: (i) the species occur in distinct areas so that the study provides a 'natural, removal experiment'; (ii) the species have partially overlapping niches; and (iii) there are some areas where the species are sympatric.

Numerous SDMs have been created for lichens at various scales using many different data sources. A few of the more recent examples from North America include Glavich et al. (2005) and Shrestha et al. (2012). From Europe, lichen SDMs include Dymytrova et al. (2013), Johansson & Ehrlén (2003) and Jürriado & Liir (2012). However, there have been few studies comparing models between species to assess niche separation. For the present study, SDMs were created for four sympatric lichen species at risk that occur in Nova Scotia, Canada. These species are often suggested as occurring together in similar habitats in Nova Scotia (Cameron & Neily 2008; Cameron & Richardson 2006; Cameron et al. 2011). At the same time, these species can be found alone or in combination with any of the other species. This trend could be explained by their rarity or by partially overlapping niches. Insufficient study has been completed on these species to fully understand if they meet the three criteria suggested by Anderson et al. (2002) listed above. However, what is known is suggestive that it is possible that these four species meet some or all the criteria.

*Pectenia plumbea* is a rare epiphytic cyanolichen which likely has the largest North American population centered in Nova Scotia, Canada. This species is reported to be found on deciduous trees mostly in older forests close to the Atlantic coast (Richardson et al. 2010). *Erioderma pedicellatum* is a globally listed endangered cyanolichen with a small population at the southern extent of its range in Nova Scotia, Canada. It occurs mostly on coniferous trees in forests near wetlands along the Atlantic coast (Cameron et al. 2015). *Erioderma mollissimum* is listed as endangered in Canada and is near the northern extent of its range in Nova Scotia. *Erioderma mollissimum* is a cyanolichen and epiphytic on both conifers and deciduous trees in older forests close the coast (Cameron et al. 2011). *Pannaria lurida* is listed in Canada as threatened, also a cyanolichen usually found on deciduous trees (COSEWIC 2016).

## METHODS

A species occurrence records database, developed by Mersey Tobetic Research Institute and

later warehoused at the Atlantic Canada Conservation Data Centre, was used to create the dependent variables in the models. Four species of at-risk cyanolichens were chosen and extracted from the database for study on the basis of rarity or threatened status (Anderson 2007; Cameron & Neily 2008; Cameron & Richardson 2006; COSEWIC 2016) and having enough locations to allow modeling. Species chosen to be modeled were *Pectenia plumbea* (n = 425), *Erioderma pedicellatum* (n = 692), *E. mollissimum* (n = 226) and *Pannaria lurida* (n = 88). To obtain absences of rare lichens, 1000 records out of the database of approximately 2500 locations of cyanolichen survey sites, where the modeled species did not occur, were chosen at random. The absence sites are where cyanolichen surveys had been undertaken in the last two decades. It is likely that these absence sites are true absences as they were conducted by experienced lichenologists, spending extensive time at each site. These efforts (experience and time searching) at the search sites correspond with those identified by Lauriault & Wiersma (2019) as needed to ensure the acceptable risk of false absences for cryptic species. Ten percent of sites were randomly selected and removed to reserve as testing data sets.

Independent variables were chosen from available Geographical Information System (GIS) databases (**Table 1**). The Nova Scotia Department of Lands and Forestry (L&F) Forest Inventory Database, derived from interpretation of 1:10,000 color aerial photography, was used to identify attributes of forest stands for locations. Forest attributes included covertype (softwood, hardwood, mixedwood), whether wetland or upland, percent crown closure, mean stand tree height and maturity based on scale of 1 to 6. The maturity scale used by L&F for each stand was as follows: 1 – regeneration (equal to or less than 1 meter in height and less than 20 years of age); 2 – young (less than 40 years of age and 6 meters or less in height); 3 – immature (less than 40 years of age and a volume less than or equal to 60 cubic meters per hectare and greater than 6 meters in height); 4 – pole (40 to 60 years of age or less than 40 years of age with a volume greater than 60 cubic meters per hectare for shade intolerant species and 40 to 79 years for shade tolerant species); 5 – mature (60 to 70 years of age for shade intolerant species and 80 to 150 years of age for shade tolerant species); and 6 – overmature (greater than 70 years

**Table 1.** Environmental variables used in the development of species distribution models for *Erioderma pedicellatum*, *E. mollissimum*, *Pectenaria plumbea* and *Pannaria lurida* in Nova Scotia, Canada.

Group	Variable name	Variable description	Source of data
Forest	Tree height	Mean height of trees in primary story of stand	Nova Scotia Department of Lands and Forestry <a href="https://novascotia.ca/natr/forestry/gis/forest-inventory.asp">https://novascotia.ca/natr/forestry/gis/forest-inventory.asp</a>
	Maturity	Forest stand maturity based on 6 classes	
	Cover type	Type of forest stand hardwood, softwood or mixedwood	
	Crown closure	Percentage of stand covered by tree crowns with 100% equalling complete cover of the ground by tree crowns	
	Wetland presence	Stand classified as wetland or not wetland as defined by L&F	
Climate	Mean annual precipitation	Mean in mm based on 30 years of data	Environment and Climate Change Canada <a href="https://climate.weather.gc.ca/climate_normals/index_e.html">https://climate.weather.gc.ca/climate_normals/index_e.html</a>
	Mean annual July temperature	Mean in degrees Celsius based on 30 years of data	
Geography	Distance from the coast	Proximity of study sites to coastline in metres using Proximity Analysis in ArcGIS with coastline data from Nova Scotia Atlas from GeoNova.	GeoNova <a href="https://geonova.novascotia.ca/geodata">https://geonova.novascotia.ca/geodata</a>
	Elevation	Elevation above sea level in meters using 5 m contour data	

of age for shade intolerant species and greater than 150 years of age for shade tolerant species). GIS climate data from Pearson et al. (2018) was used to calculate average annuals for the period 1981 to 2010 for total precipitation (mm) and July temperature (°C) for each location. Distance to the coast was calculated for each location using ArcMap software Near tool with Nova Scotia coastline from Nova Scotia Atlas data. Presence or absence of the other three species was used as a predictor variable for each modeled species. For each location of each species, it was recorded whether one or more of the other species was present and given a binary attribute (1=present, 0=absent) for the analyses.

The resolution of the dependent variables was  $\pm 2$  to 5m; however, the explanatory data had a resolution of  $\pm 10$  to 20m. The difference in resolution between data was resolved by adjusting the resolution of the dependent variables to the resolution of the independent variables. The adjustment involved assigning each dependent variable location to a forest stand from the Forest Inventory Data. Stands in Forest Inventory Data were derived from interpretation of 1:10,000 color aerial photography and ranged in size from 0.5 ha to approximately 300 ha. If more than one dependent variable of the same species occurred in the same assigned stand, only one dependent location, chosen at

random, was retained. Assigning only one dependent variable per forest stand also helped reduce issues of spatial autocorrelation. Spatial autocorrelation occurs when there is lack of independence between neighboring observations. This correlation violates the assumption of independence of observations of many statistical tests (Legendre & Legendre 1998). By removing observations that occurred within the same forest stand in this study, the likelihood of dependence between observations is reduced.

Principal Component Analysis (PCA) was done initially to assess habitat variables and to characterize general trends along habitat gradients. The data were mean-centered, and correlations were calculated among the variables. Standardized data was then projected onto eigenvectors extracted from the correlation matrix. In this type of analysis, principal component 1 (PC1) explains the maximum character variance and each subsequent PC explains the maximum remaining variance. Bray-Curtis distance was used to create a proximity matrix. To determine number of dimensions for PCA analyses, five runs were done for each species using 1 to 5 dimensions. Scree plots were created by plotting dimensions against stress. The number of dimensions was determined at the point where stress levelled off. Shepard diagrams were also created for each run by

plotting reduced distances against the observations input data.

SDMs have been previously developed for all species (Cameron et al. 2011; Cameron & Neily 2008; COSEWIC 2008, 2016). However, different methods and environmental datasets had been used for these models. In order to standardize to one modeling method and data set, new models were created for all four species.

An information-theoretic approach (Anderson 2008; Anderson et al. 2000), was performed on a set of five *a priori* developed models for each studied species. The five *a priori* models included variables that were assumed to be important as predictors of species occurrence based on previous studies (Cameron et al. 2011; Cameron & Neily 2008; COSEWIC 2008, 2016; Wiersma & Skinner 2011). Environmental variables were grouped into four categories and the five *a priori* models were created with various combinations of the groupings. The groupings were climate, which included mean annual precipitation and mean July temperature; geography, which included distance from the coast and elevation; forest structure included covertype (softwood, hardwood, mixedwood), whether wetland or not, percent crown closure, mean stand tree height and maturity based on scale of 1 to 6; and presence of other species group included a binary response whether one or more of the other lichens was present.

Akaike's Information Criterion corrected for small samples ( $AIC_C$ ), differences between  $AIC_C$  values and Akaike's weights were calculated for each model in order to identify the 'best' model in the set. Model averaging was carried out on all the models to assess the relative importance of the habitat variables (Anderson et al. 2000).

Testing data sets were used to create receiver operating characteristics curve (ROC) for each species best model. Sensitivity (the proportion of observations that were correctly predicted to be positive out of all positive observations) was plotted against false positive rate (the proportion of observations that are incorrectly predicted to be positive out of all negative observations). The area of the graph below the ROC line is known as Area Under the Curve (AUC). The AUC was also calculated for species best model and models were judged fit when the AUC value was greater than 0.7 (Pearce & Ferrier 2000). The residuals of best

models were tested for spatial autocorrelation using Moran's I in ArcMap GIS.

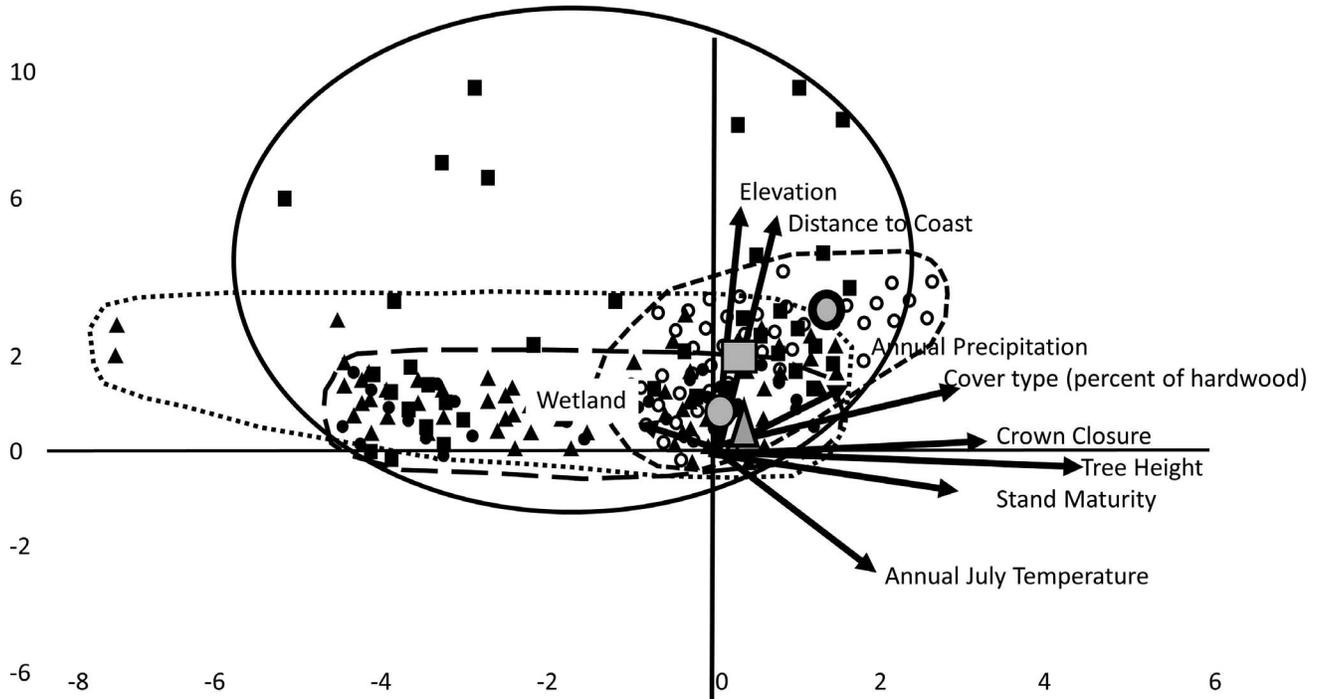
Residuals are tested to assess the assumption of independent errors which can lead to misleading model fitness measures (Lichstein et al. 2002; Zhang et al. 2009). Presence of spatial autocorrelation in model residuals can also suggest whether an autoregressive model is more appropriate (Cliff & Ord 1971). Moran's I test was judged significant at the  $p = 0.05$  level. Predicted habitat was spatially mapped for each species using the best model (lowest  $AIC_C$ ) in a GIS. Best model SDMs for each species were overlaid on each other using GIS to identify areas of geographical overlap.

To better assess how variables separated between species, each environmental variable was divided into categories and the proportion of the number of times each species occurred in a category was calculated (**Supplementary File S1**).

All statistical analysis was done using Xlstat statistical software (Addinsoft 2020).

## RESULTS

The eigenvalue for the first dimension for the PCA was 33.41 and 21.33 for the second dimension. The PCA plot (**Fig. 1**) showed significant overlap between all species within two dimensional space. However, each species occupied its own unique area within this space. The best model (lowest  $AIC_C$ ) for *Erioderma pedicellatum* included all four groups of environmental variables (**Table 2**). The best model accounted for more than 99% of the total  $AIC_C$  weight of all models considered. The influence of some variables is questioned because of low  $\beta$  and standard error with upper and lower bounds overlapping zero (**Table 3**). These variables contribute little to the model. The explanatory variables coefficients overlapping zero include tree height, wetland presence, distance from the coast and presence of other cyanolichen species. Akaike's weights for each group suggest that each environmental variable group is equally important in describing habitat for *E. pedicellatum* (**Table 4**). The best model for *E. mollissimum* also included all four groups of environmental variables and this model accounted for over 98% of the total  $AIC_C$  weight of all models considered. Explanatory variables with low  $\beta$  and large standard errors overlapping zero do not contribute to the model and include crown closure, wetland presence,



**Figure 1.** Biplot result from Principle Component Analysis of four lichen species in Nova Scotia, Canada with ten environmental variables. Triangles represent *Erioderma pedicellatum*, dots represent *Erioderma mollissimum*, squares represent *Pectenia plumbea* and open circles represent *Pannaria lurida*. Eigenvalue for the first dimension for the PCA was 33.41 and 21.33 for the second dimension. Centroids are indicated by enlarged symbols (triangles, dots, squares, open circles)

**Table 2.** Species distribution models for *Erioderma pedicellatum*, *E. mollissimum*, *Pectenia plumbea* and *Pannaria lurida* and results from logistic regression used to predict occurrence ranked by Akaike’s Information Criteria corrected for small samples values ( $AIC_c$ ). For = forest structure (five features), Climate = mean annual precipitation and mean July temperature, Geog = geography (2 features), OS = presence of other studied lichens.

Species	Model	K	$AIC_c$	$\Delta_i$	$W_i$
<i>Erioderma pedicellatum</i>	For+Climate+Geog+OS	12	846.19	0	0.999
	Climate+Geog+OS	7	878.37	32.37	<0.001
	Climate+geog	4	1116.02	270.02	<0.001
	For+Climate+Geog	9	1135.91	289.91	<0.001
	For+Climate	7	2105.07	1259.07	<0.001
<i>Erioderma mollissimum</i>	For+Climate+Geog+OS	12	304.12	0	0.984
	Climate+Geog+OS	7	312.20	8.20	0.016
	For+Climate+Geog	9	662.00	357.98	<0.001
	Climate+geog	4	704.29	400.29	<0.001
	For+Climate	7	1047.02	743.02	<0.001
<i>Pectenia plumbea</i>	Climate+Geog+OS	7	833.28	0	0.788
	For+Climate+Geog+OS	12	835.63	2.63	0.212
	For+Climate+Geog	9	1337.23	504.23	<0.001
	Climate+geog	4	1345.33	512.33	<0.001
	For+Climate	7	1639.98	806.98	<0.001
<i>Pannaria lurida</i>	For+Climate+Geog+OS	12	259.80	0	0.448
	Climate+Geog+OS	7	260.91	0.91	0.285
	Climate+geog	4	261.04	1.04	0.267
	For+Climate+Geog	9	347.17	87.17	<0.001
	For+Climate	7	409.61	149.61	<0.001

**Table 3.** Estimates of environmental variables  $\beta$  for *Erioderma pedicellatum*, *E. mollissimum*, *Pectenaria plumbea* and *Pannaria lurida* as well as standard error for the best species distribution models using logistic regression.

Environmental Variables		<i>Erioderma pedicellatum</i>		<i>Erioderma mollissimum</i>		<i>Pectenaria plumbea</i>		<i>Pannaria lurida</i>	
Group	Measure	Estimate $\beta$	Standard Error	Estimate $\beta$	Standard Error	Estimate $\beta$	Standard Error	Estimate $\beta$	Standard Error
Forest	Tree height	-0.06	0.051	-0.358	0.109	—	—	0.054	0.074
	Maturity	0.164	0.069	0.500	0.149	—	—	0.275	0.132
	Cover Type	-0.440	0.105	0.145	0.128	—	—	-0.050	0.117
	Crown closure	0.021	0.007	0.010	0.020	—	—	0.001	0.017
	Wetland presence	0.002	0.011	-9.116	104.120	—	—	-12.958	1985.337
Climate	Mean Annual Precipitation	-1.869	0.311	-1.505	0.743	-0.440	0.228	1.546	0.257
	Mean Annual July Temperature	0.482	0.057	-0.637	0.118	-0.109	0.037	-0.019	0.080
Geography	Distance from the coast	<-0.001	<0.001	<-0.001	<0.001	<-0.001	<0.001	<0.001	<0.001
	Elevation	0.052	0.005	0.076	0.009	0.033	0.003	0.029	0.004
Presence of other species	E.p.	—	—	27.409	32281.560	18.923	771.561	0.653	2971.022
	E.m.	19.238	1043.136	—	—	20.234	643.576	18.810	1552.012
	P.p.	18.241	631.364	45683.779	521587.002	—	—	20.316	1631.533
	P.l.	3.647	2506.617	22.569	33288.903	16.554	911.402	—	—

distance from the coast and presence of other cyanolichen species (Table 3). Climate, geography and presence of other species had equal Akaike's weight while forest structure had slightly less weight (Table 4). *Pectenaria plumbea* best model included climate, geography and presence of other species and this model accounted for 79% of the total  $AIC_C$  weight of all models considered. This is reflected in the equal  $AIC_C$  weights for each group of climate, geography and presence of other species but with forest structure having the least  $AIC_C$  weight. Explanatory variables with low  $\beta$  and large standard errors overlapping zero do not contribute to the model and include distance from the coast and presence of other cyanolichen species (Table 3). *Pannaria lurida* best model included forest structure, climate, geography and presence of other species. However, this best model accounted only 45% of the total  $AIC_C$  weight of all models considered. Explanatory variables with low  $\beta$  and error bounds overlapping zero do not contribute to the model and include tree height, cover type, crown

closure, wetland presence, mean July temperature, distance from the coast and presence of other cyanolichen species. Climate and geography had the greatest Akaike's weight followed by presence of other species and forest structure.

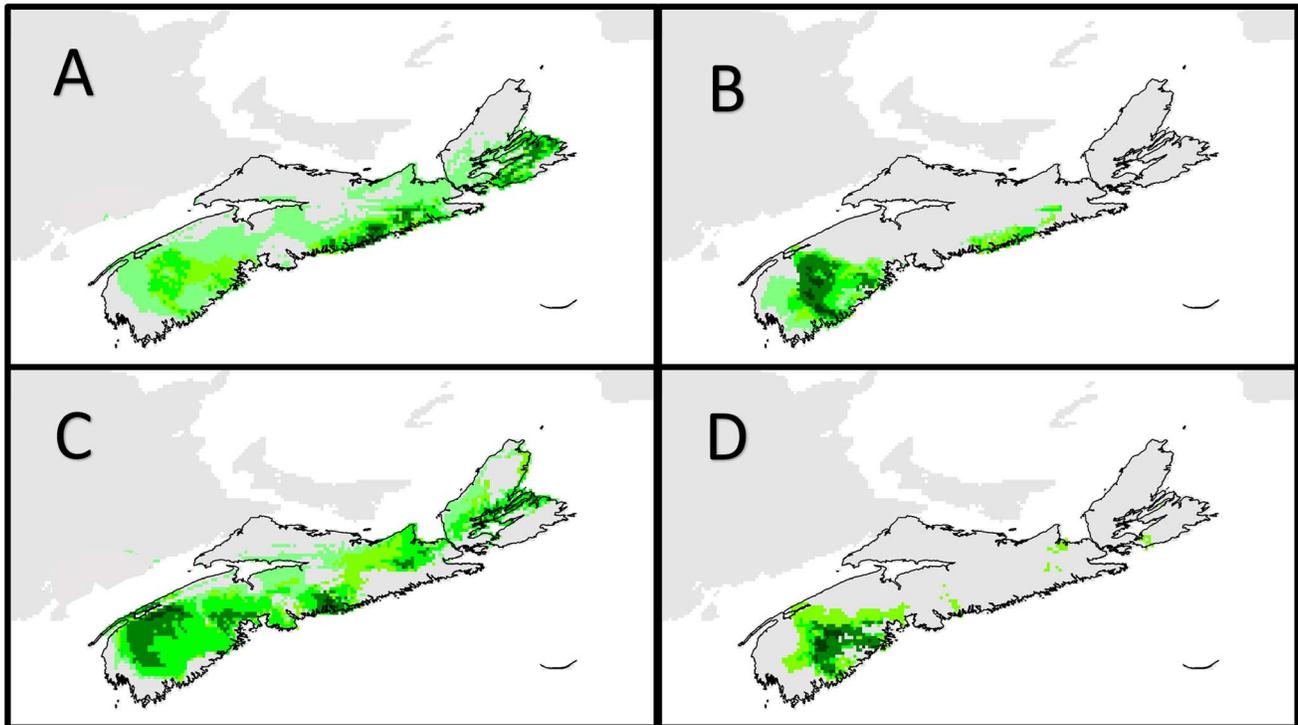
The AUC was high for all species best models. The *Erioderma pedicellatum* best model had an AUC of 0.959. *Erioderma mollissimum* AUC was slightly better at 0.975 while *P. plumbea* and *P. lurida* had slightly less AUC with 0.904 and 0.956, respectively.

Spatially mapped predicted habitat for each species, using the best model, indicates overlapping geographical areas of potential occupation between species as well as areas unique to some species (Figs. 2 & 3).

Frequency plots reveal some trends less obvious than in the biplot or models (Supplementary File S1). All species had highest frequency of occurrence in mid to high precipitation categories with *Pectenaria plumbea* occurring more frequently in the highest class of annual precipitation. All species had the highest frequency of occurrence in forest stand

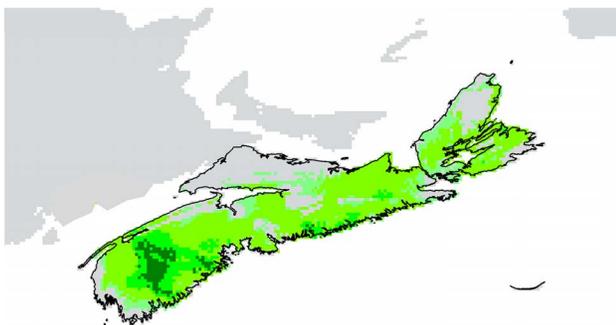
**Table 4.** Akaike's weights for each group of environmental variables used in five logistic regression models for *Erioderma pedicellatum*, *E. mollissimum*, *Pectenaria plumbea* and *Pannaria lurida*.

Environmental variable group	<i>Erioderma pedicellatum</i>	<i>Erioderma mollissimum</i>	<i>Pectenaria plumbea</i>	<i>Pannaria lurida</i>
Forest	1.00	0.99	0.22	0.45
Climate	1.00	1.00	1.00	1.00
Geography	1.00	1.00	1.00	1.00
Presence of other species	1.00	1.00	1.00	0.73



**Figure 2.** Species distribution models for lichens in Nova Scotia, Canada. A. *Erioderma pedicellatum*. B. *E. mollissimum*. C. *Pectenia plumbea*. D. *Pannaria lurida*. Darker color represents higher probability of occurrence.

maturity class 4, “Pole” (40 to 60 years of age or less than 40 years of age with a volume greater than 60 cubic metres per hectare for shade intolerant species and 40 to 79 years for shade tolerant species). Frequency of occurrence in tree height categories showed a tendency toward heights of 8 to 17 m, with the exception of *P. lurida* occurring more frequently in stands with tree heights of 14 m or more. Crown



**Figure 3.** Area of overlapping geographic space for species distribution models (SDM) for *Erioderma pedicellatum*, *E. mollissimum*, *Pectenia plumbea* and *Pannaria lurida* in Nova Scotia, Canada. Darkest color indicates areas where all four SDMs overlap and decreasing darkness (lighter color) indicates areas where there is decreasing number of lichen SDMs overlap.

closure showed a peak in frequency of occurrence for all species between 45 and 70%. For distance from the coast, all species with the exception of *Pannaria lurida*, peaked at the category nearest the coast. Most species peaked in frequency of occurrence between 25 and 75 m (a.s.l.) in elevation with the exception of *P. lurida* which also showed high occurrence at 150 to 175 m in elevation. *Erioderma pedicellatum* had highest frequency of occurrence in the areas with coolest mean July temperatures. *Erioderma mollissimum* occurred more frequently in areas of warmer July temperature classes than the other species.

#### DISCUSSION

SDMs from this study indicate all species inhabit slightly different niches. Although there are many similarities among the species, in each comparison between two species there was at least one environmental variable in which there was very little overlap. For example, *Erioderma pedicellatum*, *E. mollissimum* and *Pectenia plumbea* all occurred most frequently at mid-elevations. However, *Erioderma mollissimum* tended to be found more often in warmer regions than either *E. pedicellatum* or

*Pectenien plumbea*. *Pectenien plumbea* occurred more often in areas where July temperature was slightly warmer than areas where *E. pedicellatum* was found but cooler than where *E. mollissimum* was found. *Pannaria lurida* tended to inhabit areas of higher elevations than the other species. *Pectenien plumbea* had little preference with respect to forest type with the exception of occurring more often in deciduous dominated forests although forest type was not a variable in the SDM. *Erioderma pedicellatum*, *E. mollissimum* and *Pannaria lurida* had more specific forest structural features for which they were associated.

Results of the PCA indicate *Erioderma mollissimum* and *Pannaria lurida* had a very narrow breadth of environmental envelope suggesting these species have very specific environmental requirements. *Erioderma mollissimum* appears to occupy a small subset of *Erioderma pedicellatum* habitat, specifically those habitats with more deciduous dominated forests in a warmer climate. *Pannaria lurida* tended to occur in older forests at mid and higher elevations and farther from the coast. *Pectenien plumbea*, on the other hand, had the largest breadth of environmental envelope, suggesting this species can occur in more areas and varied habitats on the landscape than the other species in this study. This may in part be due to the lack of preference for any specific forest type. Larger breadth of environmental envelope of *Pectenien plumbea* is also reflected in the larger geographical area of predicted habitat.

*Erioderma pedicellatum* results from this study suggest this species occurs in cooler wet climate at mid-elevations in older closed canopy coniferous forest. The Cameron & Neily (2008) habitat model likewise indicated this species occurs in older coniferous forest. Their model also suggested proximity to Sphagnum wetlands and proximity to the coast, as significant predictor variables. Wiersma & Skinner (2011) also found that distance to the coast was a significant environmental variable for their habitat model for *Erioderma pedicellatum* in Newfoundland. However, their model performed poorly with low kappa and low sensitivity. It was suggested by Cameron & Neily (2008) and Wiersma & Skinner (2011) that proximity to the coast may be because of a need for higher humidity, which may be satisfied with humid coastal air and frequent fog. Both previous studies of *E. pedicellatum* found that aspect was an important predictor variable in their

models, likely because preferred North or Northeast aspect would be more humid than other aspects. Aspect was not tested in the present study.

The results from this study indicate *Erioderma mollissimum* occurs in old to mature deciduous dominated forests at low to mid-elevation in warm, moderately wet climates. Cameron et al. (2011) also found annual precipitation and temperature both to be important predictor variables for *E. mollissimum* in eastern Canada. *Erioderma mollissimum* occurs most often in the warmer but wetter southeastern area of Nova Scotia. *Erioderma mollissimum* habitat was most similar to *Erioderma pedicellatum* but these species appear to separate out mostly along a temperature gradient with *E. pedicellatum* in cooler northeastern parts of the coast and *E. mollissimum* in warmer southeastern parts of the coast.

*Pectenien plumbea* tended to occur more often at mid to low-elevations in areas with moderately cool temperature and high to mid-range mean annual precipitation. Richardson et al. (2010) suggested *P. plumbea* inhabits humid old deciduous forests close to the coast in Nova Scotia. Forest stand maturity was not found to be a predictor variable, but this species did occur more frequently in more mature forest stands. The affinity for deciduous forest may be because of the requirement for deciduous substrate; and proximity to the coast, like the other species of cyanolichens, may reflect a requirement for humidity.

*Pannaria lurida* tended to occupy mature to old forests in areas with mid-range annual precipitation and at higher elevation. COSEWIC (2016) describe *P. lurida* habitat as mature deciduous trees in open canopied deciduous dominated forests close to wetlands or floodplains at mid-elevations. The proximity to wetlands suggested by COSEWIC (2016) may be due to a need for humid habitat as reflected in the high annual precipitation found in this study as a significant habitat predictor.

Although *Erioderma pedicellatum*, *E. mollissimum* and *Pectenien plumbea* are noted as occurring in or near wetlands (Cameron & Neily 2008; COSEWIC 2016), wetlands were not found to contribute to models for any of these species in this study. The lack of association with wetlands found in this study could be due to errors in the wetlands data. Westwood (2016) and Magnussen & Russo (2012) documented errors (misidentified attributes) in Nova Scotia Forest Inventory Data. The amount of

error varied by attribute and neither study specifically measured error levels for wetland identification. However, Cameron & Neily (2008) noted that wetland identification was a particular problem in their habitat model for *Erioderma pedicellatum* using Forest Inventory Data, although they did not measure the amount of error.

One noteworthy observation from these data is the high frequency of occurrence and significance in the models of mature or older forests. There was very low frequency of occurrence in young forests by comparison. This can be of conservation concern if forestry operations are harvesting mature forests with lichens (Cameron et al. 2013).

Presence of other species was a predictor of modeled species presence for all of the species in the best models. However, there was large standard error in coefficients for all species. It might be hypothesized that if a modeled species presence increased in likelihood as the likelihood of another species presence decreased, then competitive exclusion may be occurring. Similarly, one could hypothesize that if the likelihood of presence of one species increased with the likelihood of presence of another species, they may inhabit the same or very similar habitat. The suggestion of inhabiting slightly different habitats is supported by the PCA. But it is unclear with the present data how species may be interacting.

Changing climate could affect all these species. Nova Scotia is expected to have an increase in annual average temperature of 1.2°C by the year 2050 and 2.4°C by 2080 (Nova Scotia Environment 2020). All four species in this study indicated an association with climate which could suggest an affect with climate change. *Erioderma pedicellatum* is at the southern extent of its range in Nova Scotia and occurred more often in areas of low average annual July temperature in this study. Both *Pannaria lurida* and *Pectania plumbea* occurred in mid to cooler areas of average annual July temperature in this study and therefore could be negatively affected by increasing temperature. All the studied species showed an association with mean annual precipitation. *Pannaria lurida* occurred more often in areas of high annual precipitation while the two *Erioderma* species were found more often in mid-range annual precipitation. Total annual precipitation and number of days with rain are projected to increase over the next 60 years (Nova

Scotia Environment 2020) and this could have a positive affect on *Pannaria lurida*. The affect of higher annual precipitation on the two *Erioderma* species is uncertain.

These SDMs only address habitat niche and thus can only explain how these species separate habitat on the landscape. Grubb (1977) describes four component niches for plants: 1. Habitat niche; 2. Life-form niche; 3. Phenological niche; and 4. Regeneration niche. An example of how this might play a part in niche separation with these four lichen species is in the reproductive niche. *Erioderma mollissimum* reproduces mainly from soredia, which are relatively large structures containing genetic replicates of both the fungi and cyanobacteria (Jørgensen & Arvidsson 2001). The other species reproduce from apothecia, which produce relatively small spores containing genetic material from two different individual fungal donors (Jørgensen 2000). Spores tend to disperse farther than soredia because they are lighter but also need to find a suitable cyanobacteria symbiont (Richardson & Cameron 2004). Another way in which these species may separate is through life-form niche. *Erioderma mollissimum*, *E. pedicellatum* and *Pannaria lurida* all have well developed tomentum on the under surface which likely increases water retention during dryer periods. However, *Pannaria lurida* has a much thicker and well developed undersurface tomentum than either *Erioderma* species. *Pectenia plumbea* has a thick hypothallus which creates a thick complex under surface and likely retains more moisture than the other three species (Jørgensen 2000; Richardson et al. 2010). Scale must also be considered when considering niche, and the present study likely only captures a small portion of the habitat niche at the landscape scale.

The models in this study only include average annual climate data. Other climatic factors may play a role in describing lichen distribution including episodic stress events such as drought or winter freeze-thaw events, or hydration events in the form of dew, rain or duration of fog. Maximal and minimal temperatures have been shown to affect net photosynthetic rate (Insarov & Schroeter 2012) and freeze thaw events can cause mortality in lichens (Bjerke 2011). Rain, fog, dew and vapor pressure events can affect thallus water content which are linked to a number of metabolic processes (Gauslaa 2014). Changes to metabolic processes can lead to

changes in species range and distribution in the landscape (Gauslaa 2014; Insarov & Schroeter 2012). These types of data are often not available for many climate stations, but some variables can be approximated using existing data (Fick & Hijmans 2017).

Overfitting can be a concern with IT methods of model selection and other methods of model development (Hegyí & Garamszegi 2011). Overly complex models that use more explanatory variables than are necessary are overfit (Hawkins 2004). This results in variables included in models that may have very little effect and predicted occurrences may be overly optimistic. The most useful approach to reduce overfitting is to have a large sample size (Babyak 2004). However, this can be challenging for rare species and in this case particularly for *Pannaria lurida*. Model development for rare species becomes a balance between having enough explanatory variables to reasonably explain the data while not overfitting the model.

Despite this, differences can be observed between these four sympatric species with seemingly similar habitat.

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### Supplementary documents online:

**Supplementary File S1.** Proportion of occurrences out of total number of occurrences for *Erioderma pedicellatum*, *E. mollissimum*, *Pectenia plumbea* and *Pannaria lurida* in classes of six environmental variables in Nova Scotia, Canada.