Using lichen communities as indicators of forest stand age and conservation value

Jesse E. D. Miller[1,2]
John Villella[3]
Daphne Stone[4]
Amanda Hardman[5]

[1]Corresponding author: jedmiller@ucdavis.edu
[2]Department of Biology, Stanford University, Palo Alto, California, USA, 94305
[3]Siskiyou Biosurvey, LLC. Eagle Point, Oregon, USA, 97524
[4]Stone Ecosurveys LLC, Eugene, Oregon, USA, 97405
[5]US Forest Service, John Day, Oregon, USA, 97845

Running head: Testing lichens as old forest indicators

Abstract

Evaluating the conservation value of ecological communities is critical for forest management but can be challenging because it is difficult to survey all taxonomic groups of conservation concern. Lichens have long been used as indicators of late successional habitats with particularly high conservation value because lichens are ubiquitous, sensitive to fine-scale environmental variation, and some species require old substrates. However, the efficacy of such lichen indicator systems has rarely been tested beyond narrow geographic areas, and their reliability has not been established with well-replicated quantitative research. Here, we develop a continuous lichen conservation index representing epiphytic macrolichen species affinities for late successional forests in the Pacific Northwest, USA. This index classifies species based on expert field experience and is similar to the "coefficient of conservatism" that is widely used for evaluating vascular plant communities in the central and eastern USA. We then use a large forest survey dataset to test whether the community-level lichen conservation index is related to forest stand age. We find that the lichen conservation index has a positive, linear relationship with forest stand age. In contrast, lichen species richness has only a weak, unimodal relationship with forest stand age, and a binary indicator approach (where species are assigned as either old growth forest indicators or not) has a substantially weaker relationship with forest stand age than the continuous lichen conservation index. Our findings highlight that lichen communities can be useful indicators of late successional habitats of conservation concern, and that indicator systems based on expert experience can have strong biological relevance.

Keywords

Bioindicators, conservation, epiphytes, floristic quality analysis, indicator species, Forest Inventory and Analysis, lichens, Oregon, Washington

Introduction

Land managers around the globe are tasked with conserving biodiversity, and must evaluate the conservation value of ecological communities to develop conservation plans. Managers frequently seek to identify the extent to which communities contain species with affinities for undisturbed, late-successional habitats, since these are often the most imperiled species in contemporary landscapes that have largely been altered by anthropogenic activities (Veldman et al. 2015, Spyreas 2019). Identifying communities that contain late successional species can allow managers to evaluate the results of management practices and may facilitate the comparison of different areas or land parcels. However, simple ecological metrics such as species richness or environmental variables may not reliably indicate variation in biodiversity and conservation value, and additional tools are needed to help managers efficiently evaluate communities (Matthews et al. 2009, Bauer et al. 2018).

Ecological and botanical community indices can be useful tools for evaluating the conservation value of ecological communities, and such indices may be especially efficacious when they give insights into biodiversity patterns that are difficult for land managers to study directly, such as those of cryptic taxa. Generally, ecological community indices assign each species a rank corresponding to its affinity with regard to an ecological continuum, and use the distributions of species across sites to evaluate where sites fall along the continuum (Kindscher et al. 2006, Sivicek and Taft 2011). For example, the plant "wetness index" is used to delineate protected wetland areas, since plant species tend to have consistent hydrologic affinities (Lichvar 2012). Other indices seek to represent the extent to which communities have been altered by anthropogenic activities, or the degree to which they are associated with late-successional habitats. The "coefficient of conservatism" has been widely used to represent the conservation value of vascular plant communities in recent decades, particularly in central and eastern North America (Spyreas 2019). Coefficient of conservatism values are assigned by experts rather than based on quantitative field data, and much empirical evidence suggests that plant coefficient of conservatism rankings capture real ecological differences among species (Matthews et al. 2015, Bauer et al. 2018, Bried et al. 2018; reviewed by Spyreas 2019). For example, average plant community coefficients of conservatism have been shown to increase with time since anthropogenic disturbance (Matthews et al. 2009, Spyreas et al. 2012), and the species-level rankings correlate with plant life history tradeoffs between "slow" species (e.g., long-lived, slow-growing, stress tolerant species) and "fast" species (e.g., adventive species with short lifespans that disperse widely; Bauer et al., 2018).

Lichens—symbiotic organisms containing fungal and algal or cyanobacterial partners—may have particular value for indicating habitat successional status and conservation value. As ubiquitous groups of organisms that are sensitive to environmental conditions, lichen communities often vary predictably in relation to disturbance history and forest stand or tree age (Wolseley and Aguirre-Hudson 1997, Nascimbene et al. 2013, Miller et al. 2017, Petersen et al. 2017); lichens have also been widely used for monitoring air quality and forest health (Jovan, 2008; McCune, 2000). Although several systems for using lichens as indicators of old growth forests have been developed (Rose 1976, Campbell and Fredeen 2004, Nascimbene et al. 2010), empirical tests of such indicators have usually been based on small sample sizes and have thus been limited in scope. Recently, ecologists have called for more attention to lichens as indicators of forest age and forest continuity (McMullin and Wiersma, 2019). Lichen indicator systems may help land managers to interpret lichen survey results; managers in many parts of the world are tasked with management decisions that will affect lichens, such as the protection of rare lichen species (Rosso et al. 2000, Miller et al. 2017, Allen et al. 2019). Further, lichen indicator systems may help managers identify late successional ecosystems that provide habitat for other organisms of conservation concern (Arsenault and Goward 2016, McMullin and Wiersma 2019).

Here, we explore whether lichens may be effective indicators of forest conservation value and successional status. First, we introduce a lichen conservation index, in which lichen species are ranked by experts based on their estimated affinity for different habitat successional states (e.g., young or old forest). We then use a large forest survey data set to explore how the lichen conservation index corresponds to forest stand age and other environmental variables. The lichen conservation index that we present represents a lichen analog to the coefficient of conservatism index that is widely used for plant communities in central and eastern North America (Spyreas 2019). Using lichens for this purpose is appropriate because lichens exhibit a spectrum of ecological affinities, ranging from species that thrive under certain types of anthropogenic disturbance (e.g., nitrophiles that become especially abundant in nutrient enriched agricultural landscapes) to species that are very sensitive to most anthropogenic disturbance (e.g., species that are restricted to old-growth forests; McMullin and Wiersma, 2019).

While previous efforts to use lichens as old-growth indicators have usually taken a binary approach, where species are assigned as either old forest indicators or not, we use a continuous index of lichen habitat affinities, since many lichen species may have some degree of affinity for old forests even if they are not old growth obligates. To the best of our knowledge, this is the first continuous index for testing lichen affinities to forest stand age, and we explore how it performs relative to a binary approach. We focus here on lichen communities of forested areas in western Oregon and Washington, USA, a region with a long history of lichen monitoring and management (Derr et al. 2003). Lichen communities are relatively well studied in this region because lichen surveys have been required prior to most management activities on federal lands since the Northwest Forest Plan took effect following the spotted owl controversy in the mid-1990s (Molina et al. 2006).

Methods

Development of the lichen conservation index

We modeled the lichen conservation index on the plant coefficient of conservatism, which is widely used in central and eastern North America. The plant coefficient of conservatism is assigned to each vascular plant in a given region as a number from 0-10, representing a species' affinity for undisturbed, late-successional or remnant habitats (Swink and Willhelm 1994). Plants that tend to occur in disturbed or anthropogenically modified habitats receive lower values, while plants associated with late successional habitats receive higher values. Plant coefficients of conservatism are assigned by panels of regional floristic experts, often at the state level in the USA (i.e., for regions of approximately 10,000-500,000 km^2; Spyreas 2019).

We focused on epiphytic (tree-dwelling) macrolichens for the lichen conservation index because they are the most commonly studied group of lichens in most regions, and they are commonly surveyed in context of forest management (e.g., Jovan, 2008). Epiphytic macrolichens are relatively easy to identify in comparison to other groups of lichen taxa, such as crustose lichens and other saxicolous (rock-dwelling) or terricolous (soil-dwelling) lichens, and non-experts can be trained to identify them relatively rapidly (McMullin and Wiersma 2019). Standard lichen monitoring protocols, such as the Forest Inventory and Analysis lichen plot network in the USA, often examine only epiphytic macrolichens, and as a consequence the distributions and ecologies of these lichens are much better understood than those of more cryptic lichen groups (Jovan 2008). Epiphytic macrolichens have also been used for old forest lichen indices in Europe (Rose, 1974; Coppins and Coppins, 2002).

To develop the lichen conservation index, three expert regional lichenologists (each with 19-24 years of lichen field experience in the Pacific Northwest) independently assigned values 1-10 to each epiphytic lichen species included in the authoritative regional lichen identification guide (McCune and Geiser 2009). Based on our field experience, we assigned low values to species with affinities for early successional and / or anthropogenically disturbed habitats, and we assigned high values to species that are largely or entirely restricted to late successional habitats. Generalist species and species that are most common in mid-seral habitats received intermediate values. Rankings between the three experts (AH, DS, and JV) were strongly correlated, and we developed a master index based on the three sets of individual rankings (Table S1).

Testing the index with empirical data

To explore relationships between the lichen conservation index and forest stand attributes such as stand age, we used the National Forest Lichen Air Quality Monitoring Program lichen data set for the Cascade Range of western Oregon and Washington (available at: www.gis.nacse.org). This database uses surveys that are conducted following Forest Inventory and Analysis (FIA) protocols: surveys are conducted in 0.39 ha plots that are widely distributed across Forest Service lands in the Pacific Northwest, mostly on 10 km grids. In each plot, the surveyor searches for all epiphytic macrolichens. Surveys are conducted by trained but non-expert surveyors; specimens are collected for all lichen species, and these are verified by experts. In our analyses, we dropped one outlying site that had (perhaps erroneously) much higher lichen species richness than any other, and one outlier that had a much lower average lichen conservation index ranking than any other. We conducted some analyses with a low-elevation subset of the sites (sites meeting the above criteria and occurring < 1000 m elevation). We checked the nomenclature of all species and made corrections as needed to ensure that species with recent taxonomic changes matched between our species list and the database. In our final species list (Table S1), we list species following nomenclature used by McCune and Geiser (2009) and include synonyms as used by Esslinger (2019), which in some cases represent more recent taxonomic changes.

To test whether the lichen conservation index was a significant predictor of forest stand age, we first calculated the average stand age where lichens of each conservation index integer value occurred. We then used a regression model with the average lichen conservation index value for each site as the response variable and stand age and its quadratic term (stand age squared) as predictor variables. To compare how the performance of the lichen conservation index compared to other potential lichen-based indicators of stand age, we also ran this model with three other response variables: total lichen species richness, the number of old-growth indicator species (species with lichen conservation index rankings >= 7), and the proportion of old-growth indicator species in the lichen community. These analyses were conducted for both the entire dataset (629 study plots) and a low elevation subset of the plots (261 study plots), since the relationship between the lichen conservation index and stand age appeared to be weaker at higher elevations.

To explore possible confounding effects of other environmental variables, we ran models for average lichen conservation index and lichen species richness where precipitation and elevation, as well as their quadratic terms, were included as additional predictors (along with stand age and its quadratic term). We initially included interaction terms for each pairwise combination of the three environmental variables (stand age, precipitation, and elevation), and then removed interaction terms that were not significant from the model. We chose to use the average plot-level lichen conservation index value as the response variable so that the model would be directly comparable to the lichen species richness model. Because averaging the lichen conservation index values at the plot level could lead to type I error inflation, we also ran a mixed effects logistic regression model to explore the influence of stand age and conservation index values on species occurrence following methods recommended by Miller et al. (2019). Stand age and precipitation were square-root transformed to improve variable normality and better meet model assumptions. All analyses were performed in R (R Core Team 2018).

Results

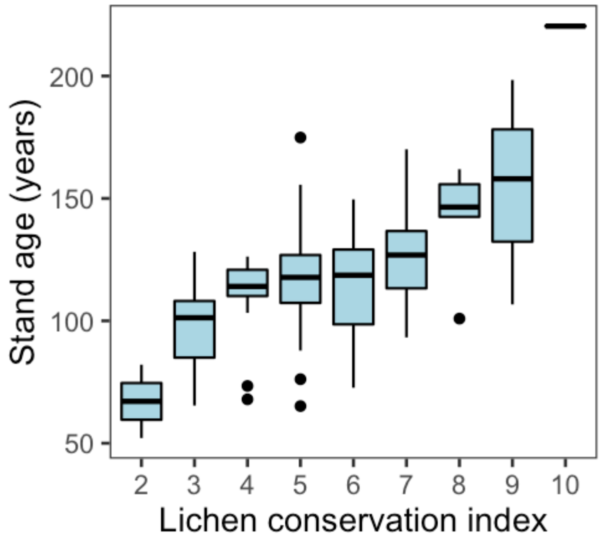

Fig. 1. The average stand age where lichen species occurred in the field plots increased with increasing lichen conservation index rankings. This analysis included species that occurred at five or more plots.

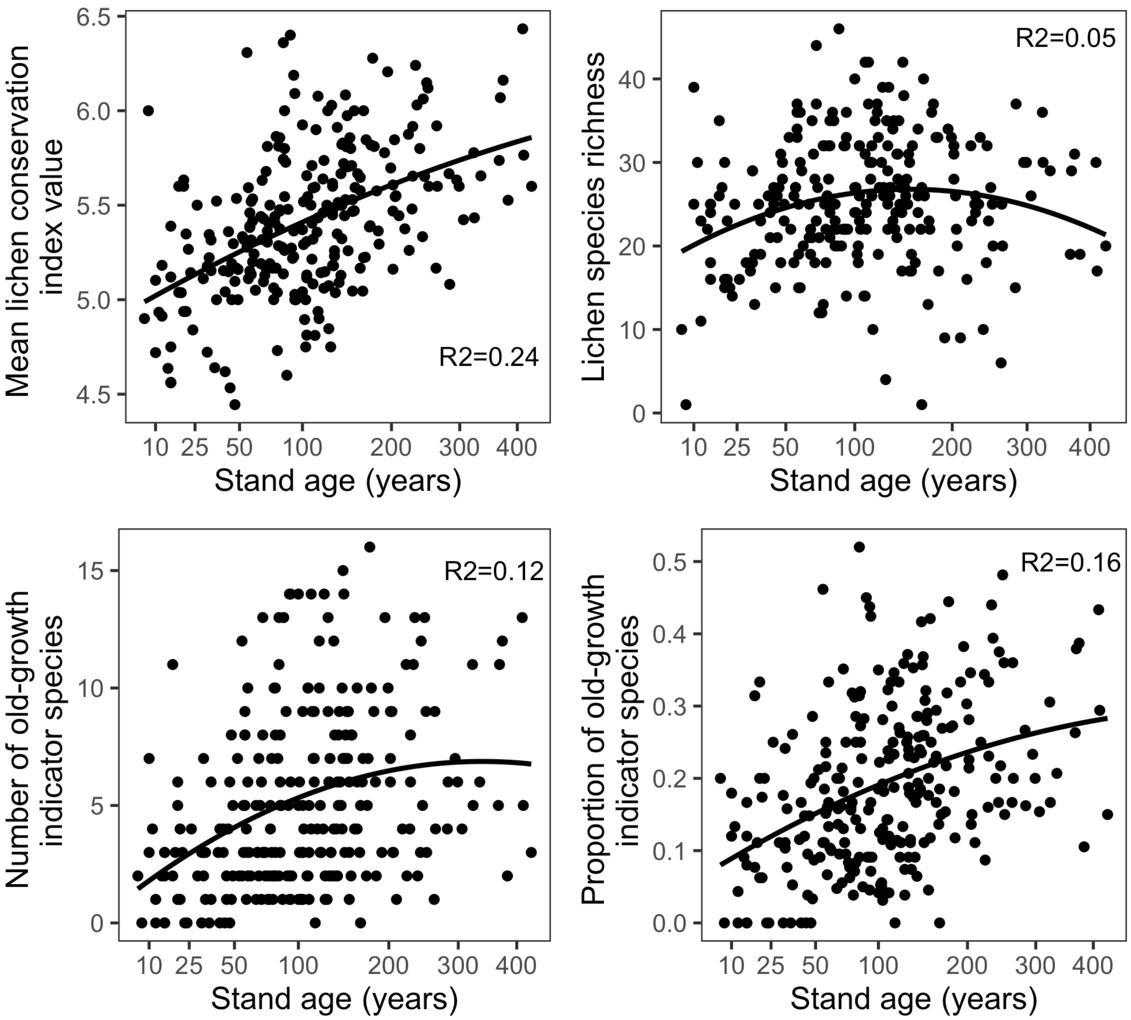

Figure 2. Relationship between estimated stand age and lichen community metrics in low elevation (< 1000 m) forests in the Cascade Range of Oregon and Washington, USA. These simple bivariate relationships do not account for environmental variables; note that these relationships all become stronger after accounting for elevation and precipitation. All relationships shown are significant (P < 0.01).

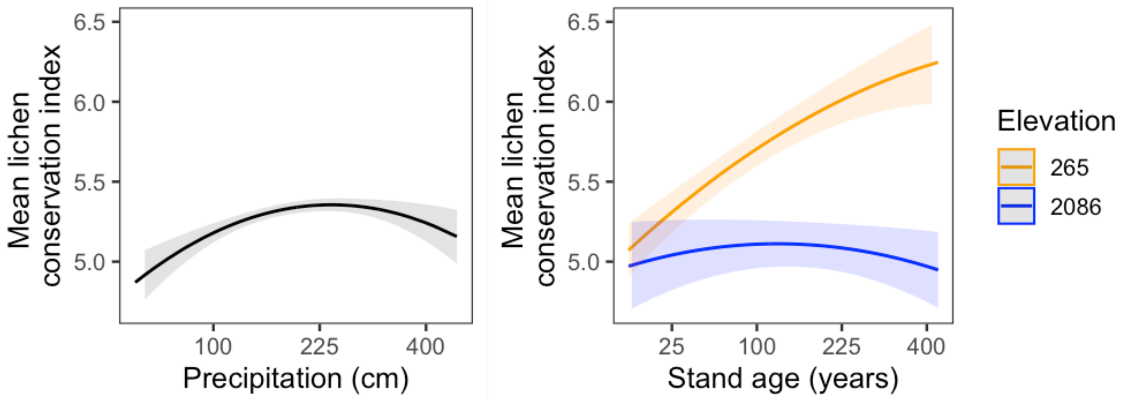

Figure 3. Model effects of predictors of the plot-level lichen conservation index across all study plots (including high elevation plots). Annual precipitation has a significant (P<0.001) but relatively weak, hump-shaped relationship with the lichen conservation index. Stand age has a strong, significant effect on the average lichen conservation index at low elevations, but this relationship weakens with increasing elevation, and disappears at the highest elevations (P<0.001 for interaction between stand age and elevation).

The lichen conservation index was significantly related to the average stand age where species occurred based on an analysis of species that occurred in five or more plots ($P < 0.001$; Fig. 1). Species with an index ranking of two occurred in plots with an average stand age of 67 years, while species with an index ranking of ten occurred in plots with an average stand age of 220 years. Intermediate species with a ranking of six occurred in stands with an average age of 115 years.

The average lichen conservation index values at the plot level were significantly correlated with stand age across the entire FIA dataset within the study region ($R^2=0.164$, $P<0.001$), and this relationship became stronger when we analyzed low elevation (< 1000 m) sites only ($R^2 = 0.235$, $P < 0.001$; Fig. 2). In contrast, species richness had a much weaker, though still significant, hump-shaped relationship with stand age for both the entire dataset ($R^2 = 0.023$, $P < 0.001$) and low-elevation sites only ($R^2 = 0.051$, $P = 0.001$), with species richness peaking in stands around 150-200 years old and then declining. The number of old-growth indicator species in a plot (defined as species with a conservation index value >= 7) was also positively related to stand age ($R^2 = 0.043$, $P < 0.001$ for all plots; $R^2 = 0.118$, $P < 0.001$ for low elevation plots only), as was the proportion of old-growth indicator species in a plot ($R^2 = 0.063$, $P < 0.001$ for all plots; $R^2 = 0.162$, $P < 0.001$ for low elevation plots only). The mixed effects logistic regression model for species occurrence showed a significant interaction between the lichen conservation index and stand age, indicating that significant relationships between average plot level index values and stand age in simple linear models were not caused by type I error inflation (Table S2; Miller et al. 2019).

The model that included environmental variables indicated that both precipitation and elevation had significant effects on the mean lichen conservation index, though their effects were weaker than stand age (Fig. 3, Table S3). The lichen conservation index peaked at sites with intermediate precipitation, and was lowest at sites with low precipitation ($P < 0.001$). There was a significant interaction between stand age and elevation ($P < 0.001$): stand age had a strong, positive effect on the lichen conservation index at low elevations, but the slope of this relationship decreased with increasing elevation, and there was no relationship between stand age and the index at the highest elevations.

Discussion

Lichen habitat affinity rankings assigned by experts appear to have a substantial relationship with the age of forest stands where the lichens occur; the lichen conservation index that we developed has a positive relationship with forest stand age that becomes stronger after we control for other environmental variables. The strong affinity of certain lichen species for late successional forests has long been recognized (Rose 1988, Gauslaa et al. 2007, Nascimbene et al. 2013), and several systems for using lichens as indicators of old growth forest have been developed (e.g., Rose 1976, Nascimbene et al. 2010). However, previous empirical tests of such indices have often been limited in scope, often using relatively small sample sizes and / or focusing on small geographic regions (e.g., Arsenault and Goward, 2016; Giordani et al., 2012). Another challenge to developing lichen indicator systems is that lichen indicator value may be context-dependent, varying with environmental conditions such as annual precipitation (Will-Wolf et al. 2006, Arsenault and Goward 2016), highlighting the need for tests of indicator species value across broad regional scales with large empirical data sets. Our analysis of several hundred study plots across a ~500 km region of the Cascade Range in the Northwest USA provides some of the strongest evidence yet that lichens can be sensitive indicators of forest stand age.

The relationship between the lichen conservation index and forest stand age becomes stronger when we include elevation and precipitation as additional predictor variables. The conservation index has a strong, positive relationship with stand age at low elevations, but this relationship weakens with increasing elevation. The influence of environmental covariates on the lichen conservation index suggests that the index is meaningful for comparing forest stands in the same general range of climatic conditions, but that it should be adjusted for environmental influences before being used as an absolute measure for comparing disparate communities growing under strongly varying climates (e.g., for comparing dry and wet forests). The lichen conservation index may have decreasing importance with increasing elevation because most archetypal old-growth forest lichens in our study region, such as cyano- and cephalo-lichens like *Lobaria oregana*, *Nephroma occultum* and *Pseudocyphellaria raineriensis*, occur only at low- to mid-elevations (Rosso et al. 2000, Berryman and McCune 2006). More intensive forest management generally occurs in the more productive forests at low and mid-elevations, and the lichen conservation index appears to be meaningful in these areas, where it is potentially most useful for management.

Our study suggests that a continuous lichen conservation index may have substantial advantages over binary approaches that assign lichens into a single class of old-growth indicators; most existing lichen habitat affinity indicator systems take the binary approach or use individual species as indicators (Rose 1976, Nascimbene et al. 2010). In this study, the number of old-growth indicator species (defined here as species with lichen conservation index rankings >= 7) and the proportion of old-growth indicator species in the community are both positively correlated with stand age in our study; the proportion of old-growth indicator species appears to predict stand age better than the number of old-growth indicator species, apparently because it is unaffected by variation in species richness. Nonetheless, both of these metrics based on binary species classifications have substantially less predictive power for stand age than the continuous lichen conservation index.

Macrolichen species richness is not a useful indicator of stand age in this dataset, since it has a weak and hump-shaped relationship with stand age. Although numerous previous studies have found that total lichen richness increases linearly with forest stand or tree age (Lie et al. 2009, Moning et al. 2009, Petersen et al. 2017), our results highlight that non-monotonic (e.g., hump-shaped) relationships between lichen richness and stand age can also occur. Indeed, other studies have found mostly positive but non-monotonic relationships (Nascimbene et al. 2009), positive relationships only in younger stands (Johansson et al. 2007), and negative or non-significant relationships between lichen species richness and stand age (Bäcklund et al. 2016). Thus, we suggest that continuous indicator approaches are likely to have better predictive power for stand age than other commonly used lichen community metrics such as species richness or binary indicator systems.

In addition to their association with stand age, lichen communities may respond to forest continuity--the amount of time that a landscape has been continuously forested (Selva 2003, Villella et al. 2013, McMullin and Wiersma 2019). While stand age and forest continuity are sometimes treated as synonymous concepts (Moning et al. 2009), researchers have recently pointed out they should be recognized as potentially independent variables of interest (Janssen et al. 2019). This distinction is probably more important in Europe and eastern North America than in western North America, since the reversion of agricultural lands to forest has been rare in western North America but is more common in other regions. Since none of the sites we analyzed here has been converted to forest from other land uses to the best of our knowledge, our study probably provides an assessment of the influence of stand age on lichen communities independent from the influence of forest continuity. Additional quantitative studies in regions with more heterogeneous histories of forest continuity could provide more evidence about how forest continuity influences lichen communities relative to stand age.

The coefficient of conservation, an index for vascular plants that is similar to the lichen conservation index we present here, has a long history of use by botanists and land managers but has also been criticized at times (Spyreas 2019). Because values are assigned by experts, rather than based on field data, some researchers have suggested that they may be biased. Empirical studies, however, have shown that the coefficient of conservatism appears to be meaningful, since it is correlated with independent measures of habitat conservation value, and species with similar coefficients of conservatism are more likely to co-occur (Matthews et al. 2009, 2015). There is also evidence that the coefficient of conservatism provides unique information beyond that provided by simpler metrics such as species richness (Matthews et al. 2009). Applying this concept to lichens is likely to help land managers interpret lichen community data. For example, the lichen conservation index could help managers prioritize conservation or management decisions by providing a means to compare different forest stands. Old growth character—the degree to which forest stands have ecological characteristics associated with old growth forests—should be generally correlated with stand age, but the lichen conservation index may provide additional information related to stand conservation value beyond stand age alone. Ultimately, the development of similar indices in other parts of the world could make lichen biomonitoring approaches more accessible to land managers.

Acknowledgements

We thank Peter Nelson and Linda Geiser for helping us access and understand the National Forest Lichen Air Quality Monitoring Program lichen data set we used to test the lichen conservation index. We thank Tom Carlberg for assistance with this project, and the Fukami lab at Stanford for helpful comments at an early stage of the project.

Author contributions

JM conceived of the project, analyzed the data and wrote the manuscript. JV led the assignment of the lichen index values, curated the species list, and contributed to background research. All authors contributed to assigning lichen index values and editing the manuscript.

Literature cited

Allen, J. L., R. T. McMullin, E. A. Tripp, and J. C. Lendemer. 2019. Lichen conservation in North America: a review of current practices and research in Canada and the United States. Page Biodiversity and Conservation. Springer Netherlands.

Arsenault, A., and T. Goward. 2016. Macrolichen diversity as an indicator of stand age and ecosystem resilience along a precipitation gradient in humid forests of inland British Columbia , Canada. Ecological Indicators 69:730–738.

Bäcklund, S., M. Jönsson, J. Strengbom, A. Frisch, and G. Thor. 2016. A Pine Is a Pine and a Spruce Is a Spruce – The Effect of Tree Species and Stand Age on Epiphytic Lichen Communities. PLoS ONE 11:1–18.

Bauer, J. T., L. Koziol, and J. D. Bever. 2018. Ecology of Floristic Quality Assessment: Testing for correlations between coefficients of conservatism, species traits and mycorrhizal responsiveness. AoB PLANTS 10:1–13.

Berryman, S., and B. McCune. 2006. Estimating epiphytic macrolichen biomass from topography, stand structure and lichen community data. Journal of Vegetation Science 17:157–170.

Bried, J. T., B. E. Allen, E. T. Azeria, V. E. Crisfield, and M. J. Wilson. 2018. Experts and models can agree on species sensitivity values for conservation assessments.

Biological Conservation 225:222–228.

Campbell, J., and A. L. Fredeen. 2004. Lobaria pulmonaria abundance as an indicator of macrolichen diversity in Interior Cedar-Hemlock forests of east-central British Columbia. Canadian Journal of Botany 82:970–982.

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

Esslinger, T. L. 2019. A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada, Version 23. Opuscula Philolichenum 18:102–378.

Gauslaa, Y., K. Palmqvist, K. A. Solhaug, H. Holien, O. Hilmo, L. Nybakken, L. C. Myhre, and M. Ohlson. 2007. Growth of epiphytic old forest lichens across climatic and successional gradients 1845:1832–1845.

Giordani, P., G. Brunialti, G. Bacaro, and J. Nascimbene. 2012. Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. Ecological Indicators 18:413–420.

Janssen, P., L. Bergès, M. Fuhr, and Y. Paillet. 2019. Do not drop OLD for NEW: conservation needs both forest continuity and stand maturity. Frontiers in Ecology and the Environment 17:370–371.

Johansson, P., H. Rydin, and T. Goran. 2007. Tree age relationships with epiphytic lichen diversity and lichen life history traits on. Ecoscience 14:81–91.

Jovan, S. 2008. Lichen Bioindication of Biodiversity, Air Quality, and Climate: Baseline Results From Monitoring in Washington, Oregon, and California.

General Technical Report PNW-GTR-737:115.

Kindscher, K., E. Questad, B. Foster, and H. Loring. 2006. Floristic Quality as an Indicator of Native Species Diversity in Managed Grasslands 26:149–167.

Lichvar, R. W. 2012. The National Wetland Plant List. ERDC/CRREL TR-12-11. U.S. Army Engineer Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, New Hampshire. Hanover, New Hampshire.

Lie, M., U. Arup, J. A. Grytnes, and M. Ohlson. 2009. The importance of host tree age , size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. Biodiversity and Conservation 18:3579–3596.

Matthews, J. W., G. Spyreas, and A. G. Endress. 2009. Trajectories of vegetation-based indicators used to assess wetland restoration progress. Ecological applications 19:2093–107.

Matthews, J. W., G. Spyreas, and C. M. Long. 2015. A null model test of Floristic Quality Assessment: Are plant species' Coefficients of Conservatism valid ? Ecological Indicators 52:1–7.

Mccune, B. 2000. Lichen Communities as Indicators of Forest Health. The Bryologist 103:353–356.

McCune, B., and L. Geiser. 2009. Macrolichens of the Pacific Northwest. 2nd edition. Oregon State University Presse, Corvallis, Oregon.

McMullin, R. T., and Y. F. Wiersma. 2019. Out with OLD growth, in with ecological continNEWity: new perspectives on forest conservation. Frontiers in Ecology and the Environment 17:1–6.

Miller, J. E. D., E. I. Damschen, and A. R. Ives. 2019. Functional traits and community composition: A comparison among community-weighted means, weighted correlations, and multilevel models. Methods in Ecology and Evolution 10:415–425.

Miller, J. E. D., J. Villella, G. Carey, T. Carlberg, and H. T. Root. 2017. Canopy distribution and survey detectability of a rare old-growth forest lichen. Forest Ecology and Management 392:196–201.

Molina, R., B. G. Marcot, and R. Lesher. 2006. Protecting rare, old-growth, forest-associated species under the survey and manage program guidelines of the Northwest Forest Plan. Conservation Biology 20:306–318.

Moning, C., S. Werth, F. Dziock, C. Bassler, J. Bradtka, and T. Hothorn. 2009. Lichen diversity in temperate montane forests is influenced by forest structure more than climate. Forest Ecology an d Management 258:745–751.

Nascimbene, J., G. Brunialti, S. Ravera, L. Frati, and G. Caniglia. 2010. Testing Lobaria pulmonaria (L.) Hoffm. as an indicator of lichen conservation importance of Italian forests. Ecological Indicators 10:353–360.

Nascimbene, J., L. Marini, R. Motta, and P. L. Nimis. 2009. Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. Biodiversity and Conservation 18:1509–1522.

Nascimbene, J., G. Thor, and P. Luigi. 2013. Effects of forest management on epiphytic lichens in temperate deciduous forests of Europe – A review. Forest Ecology an d Management 298:27–38.

Petersen, K., L. M. Calabria, J. E. D. Miller, J. Brown-Clay, L. Hynson, T. Steen, K. Johnston, A. Ulbrich, E. Chandler, M. Miller, and J. Villella. 2017. Substrate age influences species richness and community composition of calicioid lichens and fungi on wooden buildings. Bryologist 120:19–24.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rose, F. 1976. Lichenological indicators of age and environmental continuity in woodlands. Pages 279–307 *in* D. H. Braun, D. L. Hawksworth, and R. H. Bailey, editors. Lichenology: progress and problems. Academic Press, London.

Rose, F. 1988. Phytogeographical and ecological aspects of Lobarion communities in Europe. Botanical Journal of the Linnean Society 96:69–79.

Rosso, A. L., B. McCune, and T. R. Rambo. 2000. Ecology and conservation of a rare, old-growth-associated canopy lichen in a silvicultural landscape. The Bryologist 103:117–127.

Selva, S. B. 2003. Using calicioid lichens and fungi to assess ecological continuity in the Acadian Forest Ecoregion of the Canadian Maritimes. Forestry Chronicle 79:550–558.

Sivicek, V. a., and J. B. Taft. 2011. Functional Group Density as an index for assessing habitat quality in tallgrass prairie. Ecological Indicators 11:1251–1258.

Spyreas, G. 2019. Floristic quality assessment: a critique, a defense, and a primer. Ecosphere 10:e02825.

Spyreas, G., S. J. Meiners, J. W. Matthews, and B. Molano-Flores. 2012. Successional trends in Floristic Quality. Journal of Applied Ecology 49:339–348.

Swink, F., and G. Willhelm. 1994. Plants of the Chicago Region. 4th Ed. Indiana Academy of Science, Indianapolis.

Veldman, J. W., E. Buisson, G. Durigan, G. W. Fernandes, S. Le Stradic, G. Mahy, D. Negreiros, G. E. Overbeck, R. G. Veldman, N. P. Zaloumis, F. E. Putz, and W. J. Bond. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. Frontiers in Ecology and the Environment 13:154–162.

Villella, J., D. Stone, L. M. Calabria, and G. D. Eide. 2013. Macrolichen communities of Quercus garryana in the Puget Trough and Columbia River Gorge areas of Washington State. North American Fungi 8:1–22.

Will-Wolf, S., L. H. Geiser, P. Neitlich, and A. H. Reis. 2006. Forest lichen communities and environment – How consistent are relationships across scales ? Journal of Vegetation Science 17:171–184.

Wolseley, P. A., and B. Aguirre-Hudson. 1997. Fire in tropical dry forests: Corticolous lichens as indicators of recent ecological changes in Thailand. Source Journal of Biogeography journal of Biogeography 24:345–362.

Supplemental materials for online publication

Table S1. List of lichen conservation index values for macrolichens in the Pacific Northwest of North America. Higher conservation index values indicate species with stronger affinities for old growth forests, and lower conservation index values indicate species with greater tolerance for anthropogenic disturbance. Rankings are assigned based on the occurrences of these species as epiphytes only; some of these species may also grow on other substrates. Species are listed by nomenclature following McCune and Geiser (2009), since this is the most widely used field guide for lichens in our region, as well as nomenclature following Esslinger (2019), which includes more recent taxonomic updates.

Species (McCune)	Authority (McCune)	Species (Esslinger)	Authority (Esslinger)	Conservation index value
Ahtiana sphaerosporella	(Müll. Arg.) Goward	Ahtiana sphaerosporoella	(Müll. Arg.) Goward	7
Alectoria imshaugii	Brodo & D. Hawksw.	Alectoria imshaugii	Brodo & D. Hawksw.	6
Alectoria lata	(Taylor) Lindsay	Alectoria lata	(Taylor) Lindsay	7
Alectoria sarmentosa	(Ach.) Ach.	Alectoria sarmentosa	(Ach.) Ach.	5
Alectoria vancouverensis	(Gyelnik) Gyelnik	Alectoria vancouverensis	(Gyelnik) Gyelnik ex Brodo & D. Hawksw.	6
Anaptychia crinalis	(Schaerer) Vězda in Poelt and Vězda	Anaptychia crinalis	(Schaerer) Vězda	10
Bryoria bicolor	(Ehrh.) Brodo & D. Hawksw.	Bryoria bicolor	(Ehrh.) Brodo & D. Hawksw.	9
Bryoria capillaris	(Ach.) Brodo & D. Hawksw.	Bryoria fuscescens	(Gyelnik) Brodo & D. Hawksw.	5
Bryoria fremontii	(Tuck.) Brodo & D. Hawksw.	Bryoria fremontii	(Tuck.) Brodo & D. Hawksw.	5
Bryoria friabilis	Brodo & D. Hawksw.	Bryoria friabilis	Brodo & D. Hawksw.	6
Bryoria furcellata	(Fr.) Brodo & D. Hawksw.	Bryoria furcellata	(Fr.) Brodo & D. Hawksw.	8
Bryoria fuscescens	(Gyelnik) Brodo & D. Hawksw.	Bryoria fuscescens	(Gyelnik) Brodo & D. Hawksw.	5
Bryoria glabra	(Mot.) Brodo & D. Hawksw.	Bryoria glabra	(Motyka) Brodo & D. Hawksw.	5

Bryoria lanestris	(Ach.) Brodo & D. Hawksw.	Bryoria lanestris	(Ach.) Brodo & D. Hawksw.	6
Bryoria pseudofuscescens	(Gyelnik) Brodo & D. Hawksw.	Bryoria pseudofuscescens	(Gyelnik) Brodo & D. Hawksw.	4
Bryoria subcana	(Nyl. ex Stizenb.) Brodo & D. Hawksw.	Bryoria fuscescens	(Gyelnik) Brodo & D. Hawksw.	6
Bryoria trichodes	(Michaux) Brodo & D. Hawksw.	Bryoria trichodes	(Michaux) Brodo & D. Hawksw.	7
Bunodophoron melanocarpum	(Sw.) Wedin	Bunodophoron melanocarpum	(Sw.) Wedin	10
Candelaria concolor	(Dickson) B. Stein	Candelaria concolor	(Dickson) Stein	3
Candelaria "pacifica"	M. Westb. ined.	Candelaria pacifica	M. Westb. & Arup	2
Cetraria californica	Tuck.	Kaernefeltia californica	(Tuck.) A. Thell & Goward	8
Cetraria chlorophylla	(Willd.) Vainio	Tuckermannopsis chlorophylla	(Willd.) Hale	5
Cetraria merrillii	Du Rietz	Kaernefeltia merrillii	(Du Rietz) A. Thell & Goward	6
Cetraria orbata	(Nyl.) Fink	Tuckermannopsis orbata	(Nyl.) M. J. Lai	5
Cetraria pallidula	Tuck. ex Riddle	Ahtiana pallidula	(Tuck. ex Riddle) Goward & A. Thell	7
Cetraria platyphylla	Tuck.	Tuckermannopsis platyphylla	(Tuck.) Hale	4
Cetraria subalpina	Imshaug	Tuckermannopsis subalpina	(Imshaug) Kärnefelt	7
Cetrelia cetrarioides	(Duby) Culb. & C. Culb.	Cetrelia cetrarioides	(Duby) W. L. Culb. & C. F. Culb.	7
Cladonia albonigra	Brodo & Ahti	Cladonia albonigra	Brodo & Ahti	8
Cladonia bacillaris	Nyl.	Cladonia macilenta var. bacillaris	(Ach.) Schaerer	5
Cladonia bellidiflora	(Ach.) Schaerer	Cladonia bellidiflora	(Ach.) Schaerer	7
Cladonia carneola	(Fr.) Fr.	Cladonia carneola	(Fr.) Fr.	5
Cladonia cenotea	(Ach.) Schaerer	Cladonia cenotea	(Ach.) Schaerer	4
Cladonia chlorophaea	(Flörke) Sprengel	Cladonia chlorophaea	(Flörke ex Sommerf.) Sprengel	5
Cladonia coniocraea	(Flörke) Sprengel	Cladonia coniocraea	(Flörke) Sprengel	4
Cladonia fimbriata	(L.) Fr.	Cladonia fimbriata	(L.) Fr.	3
Cladonia furcata	(Hudson) Schrader	Cladonia furcata	(Hudson) Schrader	3
Cladonia macilenta	Hoffm.	Cladonia macilenta	Hoffm.	4
Cladonia norvegica	Tønsberg & Holien	Cladonia norvegica	Tønsberg & Holien	8
Cladonia ochrochlora	Flörke	Cladonia ochrochlora	Flörke	3
Cladonia squamosa	Hoffm.	Cladonia squamosa	(Scop.) Hoffm.	6
Cladonia squamosa var. subsquamosa	(Nyl. Ex Leighton) Vainio	Cladonia subsquamosa	Kremp.	6
Cladonia transcendens	(Vainio) Vainio	Cladonia transcendens	(Vainio) Vainio	5
Cladonia umbricola	Tønsberg & Ahti	Cladonia umbricola	Tønsberg & Ahti	6
Collema curtisporum	Degel.	Collema curtisporum	Degel.	9

Collema furfuraceum	(Arnold) Du Rietz	Collema furfuraceum	(Arnold) Du Rietz	8
Collema nigrescens	(Hudson) DC.	Collema nigrescens	(Hudson) DC.	8
		Rostania quadrifida	(D. F. Stone & McCune) McCune	9
Dendriscocaulon intriculatum	see Lobaria amplissima and Sticta oroborealis	Dendriscocaulon intriculatum	(Nyl.) Henssen	9
Erioderma sorediatum	D. J. Galloway & P. M. Jørg.	Erioderma sorediatum	D. J. Galloway & P. M. Jørg.	9
Esslingeriana idahoensis	(Essl.) Hale & M. J. Lai	Esslingeriana idahoensis	(Essl.) Hale & M. J. Lai	7
Evernia prunastri	(L.) Ach.	Evernia prunastri	(L.) Ach.	2
Flavoparmelia caperata	(L.) Hale	Flavoparmelia caperata	(L.) Hale	4
Flavopunctelia flaventior	(Stirton) Hale	Flavopunctelia flaventior	(Stirton) Hale	4
Fuscopannaria laceratula	(Hue) P. M. Jørg.	Fuscopannaria laceratula	(Hue) P. M. Jørg.	10
Fuscopannaria leucostictoides	(Ohlsson) P. M. Jørg.	Fuscopannaria leucostictoides	(Ohlsson) P. M. Jørg.	8
Fuscopannaria mediterranea	(Tav.) P. M. Jørg.	Fuscopannaria mediterranea	(Tav.) P. M. Jørg.	8
Fuscopannaria pacifica	P. M. Jørg.	Fuscopannaria pacifica	P. M. Jørg.	6
Fuscopannaria pulveracea	(P. M. Jørg. & Henssen)	Fuscopannaria pulveracea	(P. M. Jørg. & Henssen)	8
Fuscopannaria ramulina	P. M. Jørg. & Tønsberg	Fuscopannaria ramulina	P. M. Jørg. & Tønsberg	10
Heterodermia japonica	(Sato) Swinsc. & Krog	Heterodermia japonica	(M. Satô) Swinscow & Krog	10
Heterodermia leucomela	(L.) Poelt	Heterodermia leucomela	(L.) Poelt	10
Heterodermia sitchensis	Goward & W. Noble	Heterodermia sitchensis	Goward & W. Noble	10
Heterodermia speciosa	(Wulfen) Trevisan	Heterodermia speciosa	(Wulfen) Trevisan	10
Hypogymnia apinnata	Goward & McCune	Hypogymnia apinnata	Goward & McCune	6
Hypogymnia austerodes	(Nyl.) Räsänen	Hypogymnia austerodes	(Nyl.) Räsänen	7
Hypogymnia canadensis	Goward & McCune	Hypogymnia canadensis	Goward & McCune	7
Hypogymnia duplicata	(Ach.) Rass.	Hypogymnia duplicata	(Ach.) Rass.	10
Hypogymnia enteromorpha	(Ach.) Nyl.	Hypogymnia enteromorpha	(Ach.) Nyl.	6
Hypogymnia heterophylla	L. Pike	Hypogymnia heterophylla	L. Pike	5
Cavernularia hultenii	Degel.	Hypogymnia hultenii	(Degel.) Krog	7
Hypogymnia imshaugii	Krog	Hypogymnia imshaugii	Krog	6
Hypogymnia inactiva	(Krog) Ohlsson	Hypogymnia inactiva	(Krog) Ohlsson	6
Hypogymnia lophyrea	(Ach.) Degel.	Hypogymnia lophyrea	(Ach.) Krog	7
Hypogymnia metaphysodes	(Asah.) Rass.	Misidentified for North America	(Asahina) Rass.	4
Hypogymnia occidentalis	L. Pike	Hypogymnia occidentalis	L. Pike	6
Hypogymnia oceanica	Goward	Hypogymnia oceanica	Goward	6

Hypogymnia physodes	(L.) Nyl.	Hypogymnia physodes	(L.) Nyl.	4
Hypogymnia rugosa	(G. Merr.) L. Pike	Hypogymnia rugosa	(G. Merr.) L. Pike	7
Hypogymnia tubulosa	(Schaerer) Hav.	Hypogymnia tubulosa	(Schaerer) Hav.	4
Hypotrachyna afrorevoluta	(Krog & Swinsc.) Krog & Swinsc.	Hypotrachyna afrorevoluta	(Krog & Swinscow) Krog & Swinscow	8
Hypotrachyna revoluta	(Flörke) Hale	Hypotrachyna revoluta	(Flörke) Hale	9
Hypotrachyna riparia	McCune	Hypotrachyna riparia	McCune	9
Hypotrachyna sinuosa	(Sm.) Hale	Hypotrachyna sinuosa	(Sm.) Hale	5
Imshaugia aleurites	(Ach.) S. F. Meyer	Imshaugia aleurites	(Ach.) S. F. Meyer	7
Leioderma sorediatum	D. J. Galloway & P. M. Jørg.	Leioderma sorediatum	D. J. Galloway & P. M. Jørg.	9
Leptogium brebissonii	Mont.	Leptogium brebissonii	Mont.	9
Leptogium cyanescens	(Rabenh.) Körb.	Leptogium cyanescens	(Rabenh.) Körber	10
Leptogium gelatinosum	(Wirth.) J. R. Laudon	Scytinium gelatinosum	(With.) Otálora, P. M. Jørg. & Wedin	8
Leptogium pseudofurfuraceum	P. M. Jørg. & Wallace	Leptogium pseudofurfuraceum	P. M. Jørg. & Wallace	8
Leptogium saturninum	(Dickson) Nyl.	Leptogium saturninum	(Dickson) Nyl.	7
Letharia columbiana	(Nutt.) J.W. Thomson	Letharia columbiana	(Nutt.) J.W. Thomson	5
Letharia gracilis	Kroken in McCune & Altermann	Letharia gracilis	Kroken ex McCune & Altermann	10
Letharia vulpina	(L.) Hue	Letharia vulpina	(L.) Hue	5
Pseudocyphellaria anomala	Brodo & Ahti	Lobaria anomala	(Brodo & Ahti) T. Sprib. & McCune	7
Pseudocyphellaria anthraspis	(Ach.) H. Magn.	Lobaria anthraspis	(Ach.) T. Sprib. & McCune	7
Lobaria hallii	(Tuck.) Zahlbr.	Lobaria hallii	(Tuck.) Zahlbr.	7
Lobaria linita	(Ach.) Rabenh.	Lobaria linita	(Ach.) Rabenh.	10
Lobaria oregana	(Tuck.) Müll. Arg.	Lobaria oregana	(Tuck.) Müll. Arg.	9
Lobaria pulmonaria	(L.) Hoffm.	Lobaria pulmonaria	(L.) Hoffm.	6
Lobaria scrobiculata	(Scop.) DC.	Lobaria scrobiculata	(Scop.) DC.	7
Massalongia carnosa	(Dickson) Körber	Massalongia carnosa	(Dickson) Körber	10
Melanelixia subargentifera	(Nyl.) O. Blanco et al.	Melanelixia subargentifera	(Nyl.) O. Blanco et al.	4
Melanelixia fuliginosa	(Fr. ex Duby) O. Blanco et al.	Melanelixia glabratula	(Lamy) Sandler & Arup	4
Melanelixia subargentifera	(Nyl.) O. Blanco et al.	Melanelixia subargentifera	(Nyl.) O. Blanco et al.	3
Melanelixia subaurifera	(Nyl.) Blanco et al.	Melanelixia subaurifera	(Nyl.) Blanco et al.	3
Melanohalea elegantula	(Zahlbr.) Blanco et al.	Melanohalea elegantula	(Zahlbr.) Blanco et al.	4
Melanohalea exasperatula	(Zahlbr.) O. Blanco et al.	Melanohalea exasperatula	(Nyl.) O. Blanco et al.	4
Melanohalea multispora	(A. Schneider) Blanco et al.	Melanohalea multispora	(A. Schneider) Blanco et al.	4
Melanohalea subelegantula	(Essl.) O. Blanco et al.	Melanohalea subelegantula	(Essl.) O. Blanco et al.	4

Melanohalea subolivacea	(Nyl.) Blanco et al.	Melanohalea subolivacea	(Nyl.) Blanco et al.	4
Menegazzia subsimilis	(H. Magn.) R. Sant.	Menegazzia subsimilis	(H. Magn.) R. Sant.	6
Menegazzia terebrata	(Hoffm.) A. Massal.	Menegazzia terebrata	(Hoffm.) A. Massal.	5
Nephroma bellum	(Sprengel) Tuck.	Nephroma bellum	(Sprengel) Tuck.	8
Nephroma helveticum	Ach.	Nephroma helveticum	Ach.	7
Nephroma laevigatum	Ach.	Nephroma laevigatum	Ach.	7
Nephroma occultum	Wetmore	Nephroma occultum	Wetmore	10
Nephroma parile	(Ach.) Ach.	Nephroma parile	(Ach.) Ach.	7
Nephroma resupinatum	(L.) Ach.	Nephroma resupinatum	(L.) Ach.	7
Niebla cephalota	(Tuck.) Rundel & Bowler	Niebla cephalota	(Tuck.) Rundel & Bowler	8
Nodobryoria abbreviata	(Müll. Arg.)	Nodobryoria abbreviata	(Müll. Arg.)	6
Nodobryoria oregana	(Tuck.) Common & Brodo	Nodobryoria oregana	(Tuck.) Common & Brodo	6
		Normandina pulchella	(Borrer) Nyl.	7
Pannaria rubiginella	P. M. Jørg. & Sipman	Pannaria rubiginella	P. M. Jørg. & Sipman	10
Pannaria rubiginosa	(Ach.) Bory	Pannaria rubiginosa	(Thunb.) Delise	10
		Parmelia barrenoae	Divakar, M. C. Molina & A. Crespo	5
Parmelia hygrophila	Goward & Ahti	Parmelia hygrophila	Goward & Ahti	4
Parmelia pseudosulcata	*Gyelnik*	Parmelia pseudosulcata	Gyelnik	5
Parmelia saxatilis	(L.) Ach.	Parmelia saxatilis	(L.) Ach.	5
Parmelia squarrosa	Hale	Parmelia squarrosa	Hale	8
Parmelia sulcata	Taylor	Parmelia sulcata	Taylor	3
Parmeliella parvula	P. M. Jørg.	Parmeliella parvula	P. M. Jørg.	9
Parmeliella triptophylla	(Ach.) Müll. Arg.	Parmeliella triptophylla	(Ach.) Müll. Arg.	9
Parmelina coleae	Argüello & A. Crespo	Parmelina coleae	Argüello & A. Crespo	8
Parmeliopsis ambigua	(Wulfen) Nyl.	Parmeliopsis ambigua	(Wulfen) Nyl.	5
Parmeliopsis hyperopta	(Ach.) Arnold	Parmeliopsis hyperopta	(Ach.) Arnold	6
Parmotrema arnoldii	(Du Rietz) Hale	Parmotrema arnoldii	(Du Rietz) Hale	5
Parmotrema crinitum	(Ach.) Choisy	Parmotrema crinitum	(Ach.) Choisy	6
Peltigera britannica	(Gyelnik) Holtan-Hartw. & Tønsberg	Peltigera britannica	(Gyelnik) Holt.-Hartw. & Tønsberg	7
Peltigera collina	(Ach.) Schrader	Peltigera collina	(Ach.) Schrader	5
Peltigera pacifica	Vitik.	Peltigera pacifica	Vitik.	8
Phaeophyscia orbicularis	(Necker) Moberg	Phaeophyscia orbicularis	(Necker) Moberg	2
Phaeophyscia rubropulchra	(Degel.) Essl.	Phaeophyscia rubropulchra	(Degel.) Essl.	1
Physcia adscendens	(Fr.) H. Olivier	Physcia adscendens	(Fr.) H. Olivier	2
Physcia aipolia	(Ehrh. ex Humb.) Fürnr.	Physcia aipolia	(Ehrh. ex Humb.) Fürnr.	3

		Physcia alnophila	(Vainio) Loht., Moberg, Myllys & Tehler	3
Physcia biziana	(A. Massal.) Zahlbr.	Physcia biziana	(A. Massal.) Zahlbr.	4
Physcia tenella	(Scop.) DC. In Lam. & DC.	Physcia tenella	(Scop.) DC.	3
Physconia americana	Essl.	Physconia americana	Essl.	4
		Physconia californica	Essl.	4
Physconia enteroxantha	(Nyl.) Poelt	Physconia enteroxantha	(Nyl.) Poelt	3
Physconia isidiigera	(Zahlbr.) Essl.	Physconia isidiigera	(Zahlbr.) Essl.	4
Physconia perisidiosa	(Erichsen) Moberg	Physconia perisidiosa	(Erichsen) Moberg	4
Platismatia glauca	(L.) Culb. & C. Culb.	Platismatia glauca	(L.) W. L. Culb. & C. F. Culb.	4
Platismatia herrei	(Imshaug) Culb. & C. Culb.	Platismatia herrei	(Imshaug) W. L. Culb. & C. F. Culb.	5
Platismatia lacunosa	(Ach.) Culb. & C. Culb.	Platismatia lacunosa	(Ach.) W. L. Culb. & C. F. Culb.	7
Platismatia norvegica	(Lynge) Culb. & C. Culb.	Platismatia norvegica	(Lynge) W. L. Culb. & C. F. Culb.	7
Platismatia stenophylla	(Tuck.) Culb. & C. Culb.	Platismatia stenophylla	(Tuck.) W. L. Culb. & C. F. Culb.	5
		Platismatia wheeleri	Goward, Altermann & Björk	5
Xanthoria candelaria	(L.) Th. Fr.	Polycauliona candelaria	(L.) Frödén, Arup, & Søchting	3
Caloplaca coralloides	(Tuck.) Hulting	Polycauliona coralloides	(Tuck.) Hue	3
Xanthoria polycarpa	(Hoffm.) Rieber	Polycauliona polycarpa	(Hoffm.) Frödén, Arup, & Søchting	3
Polychidium contortum	Henssen	Leptogidium contortum	(Henssen) T. Sprib. & Muggia	8
Pseudocyphellaria crocata	(L.) Vainio	Pseudocyphellaria citrina	(Gyeln.) Lücking, Moncada & S. Stenroos	8
Pseudocyphellaria perpetua	Maidl. & McCune	Pseudocyphellaria hawaiiensis	H. Magn.	8
Pseudocyphellaria mallota	(Tuck.) H. Magn.	Pseudocyphellaria mallota	(Tuck.) H. Magn.	10
Pseudocyphellaria rainierensis	Imshaug	Pseudocyphellaria rainierensis	Imshaug	10
Psoroma hypnorum	(Vahl) Gray	Psoroma hypnorum	(Vahl) Gray	8
Punctelia perreticulata	(Räs.) G. Wilh. & Ladd	Punctelia perreticulata	(Räsänen) G. Wilh. & Ladd	2
		Punctelia subrudecta	(Nyl.) Krog	2
Ramalina dilacerata	(Hoffm.) Hoffm.	Ramalina dilacerata	(Hoffm.) Hoffm.	5
Ramalina farinacea	(L.) Ach.	Ramalina farinacea	(L.) Ach.	3
Ramalina menziesii	Taylor	Ramalina menziesii	Taylor	5
Ramalina pollinaria	(Westr.) Ach.	Ramalina labiosoridiata	Gasparyan, Sipman & Lücking	9

Ramalina roesleri	(Hochst. *ex* Schaerer) Hue	Ramalina roesleri	(Hochst. ex Schaerer) Hue	5
Ramalina subleptocarpha	Rundel & Bowler	Ramalina subleptocarpha	Rundel & Bowler	2
Ramalina thrausta	(Ach.) Nyl.	Ramalina thrausta	(Ach.) Nyl.	7
Leptogium cellulosum	P. M. Jørg. & Tønsb.	Scytinium cellulosum	(P. M. Jørg. & Tønsberg) Otálora, P. M. Jørg. & Wedin	8
Leptogium lichenoides	(L.) Zahlbr.	Scytinium lichenoides	(L.) Otálora, P. M. Jørg. & Wedin	7
Leptogium palmatum	(Hudson) Mont.	Scytinium palmatum	(Hudson) Gray	7
Leptogium polycarpum	(P. M. Jørg. & Goward)	Scytinium polycarpum	(P. M. Jørg. & Goward) Otálora, P. M. Jørg. & Wedin	6
Leptogium siskiyouensis	D. F. Stone & Ruchty	Scytinium siskiyouensis	(D. F. Stone & Ruchty) Otálora, P. M. Jørg. & Wedin	9
Leptogium tacomae	P. M. Jørg. & Tønsb.	Scytinium tacomae	(P. M. Jørg. & Tønsberg) McCune	7
Leptogium teretiusculum	(Wallr.) Arnold	Scytinium teretiusculum	(Wallr.) Otálora, P. M. Jørg. & Wedin	6
Sphaerophorus tuckermanii	Räsänen	Sphaerophorus tuckermanii	Räsänen	7
Sphaerophorus venerabilis	Wedin, Högnabba & Goward	Sphaerophorus venerabilis	Wedin, Högnabba & Goward	7
Sticta fuliginosa	(Hoffm.) Ach.	Sticta fuliginosa	(Hoffm.) Ach.	8
Sticta limbata	(Sm.) Ach.	Sticta limbata	(Sm.) Ach.	9
Sticta weigelii	(Ach.) Vainio	Sticta weigelii	(Ach.) Vainio	9
Sulcaria badia	Brodo & D. Hawksw.	Sulcaria badia	Brodo & D. Hawksw.	9
Teloschistes flavicans	(Sw.) Norman	Teloschistes flavicans	(Sw.) Norman	10
Tholurna dissimilis	(Norman) Norman	Tholurna dissimilis	(Norman) Norman	10
Usnea cavernosa	Tuck.	Usnea cavernosa	Tuck.	8
Usnea ceratina	Ach.	Usnea ceratina	Ach.	8
Usnea chaetophora	Stirton	Usnea chaetophora	Stirton	7
Usnea cornuta	Körber	Usnea cornuta	Körber	6
Usnea diplotypus	Vainio	Usnea diplotypus	Vainio	8
Usnea filipendula	Stirton	Usnea dasopoga	(Ach.) Nyl.	6
Usnea flavocardia	Räs.	Usnea flavocardia	Räsänen	6
Usnea fragilescens var. mollis	(Vainio) Clerc	Usnea fragilescens var. mollis	(Vainio) Clerc	7
Usnea fulvoreagens	(Räs.) Räs.	Usnea fulvoreagens	(Räsänen) Räsänen	6
Usnea glabrata	(Ach.) Vainio	Usnea glabrata	(Ach.) Vainio	6
Usnea lapponica	Vainio	Usnea perplexans	Stirton	6
Usnea longissima	Ach.	Dolichousnea longissima	(Ach.) Articus	7
		Usnea occidentalis	Motyka	10
Usnea pacificana	P. Halonen	Usnea pacificana	P. Halonen	6

Usnea rubicunda	Stirton	Usnea rubicunda	Stirton	8
Usnea scabrata	Nyl.	Usnea scabrata	Nyl.	5
Usnea schadenbergiana	Göpp. & Stein	Usnea subgracilis	Vainio	9
Usnea silesiaca	Motyka	Usnea silesiaca	Motyka	7
Usnea subfloridana	Stirton	Usnea subfloridana	Stirton	6
Usnea subgracilis	Vainio	Usnea subgracilis	Vainio	7
Usnea substerilis	Mot.	Usnea perplexans	Stirton	6
Usnea wasmuthii	Räs.	Usnea wasmuthii	Räsänen	7
Vulpicida canadensis	(Räsänen) J.-E. Mattsson	Vulpicida canadensis	(Räsänen) J.-E. Mattsson & M. J. Lai	6
Vulpicida pinastri	(Scop.) J.-E. Mattsson & M. J. Lai	Vulpicida pinastri	(Scop.) J.-E. Mattsson & M. J. Lai	6
Xanthomendoza fallax	(Hepp.) Søchting et al.	Xanthomendoza fallax	(Hepp ex Arnold) Søchting, Kärnefelt & S. Y. Kondr.	2
Xanthomendoza fulva	(Hoffm.) Søchting et al.	Xanthomendoza fulva	(Hoffm.) Søchting, Kärnefelt & S. Y. Kondr.	2
Xanthomendoza hasseana	(Räs.) Søchting et al.	Xanthomendoza hasseana	(Räsänen) Søchting, Kärnefelt & S. Y. Kondr.	2
Xanthomendoza montana	(L. Lindblom) Søchting et al.	Xanthomendoza montana	(L. Lindblom) Søchting, Kärnefelt & S. Y. Kondr.	2
Xanthomendoza oregana	(Gyelnik) Søchtinget al.	Xanthomendoza oregana	(Gyelnik) Søchting, Kärnefelt & S. Y. Kondr.	2
Xanthoria parietina	(L.) Th. Fr.	Xanthoria parietina	(L.) Th. Fr.	1

Table S2. Model summary for a mixed effects logistic regression model testing whether stand age and lichen conservation index value interact to predict species occurrences. A total of 145 species across 629 sites were analyzed using the function glmer (Bates et al. 2015) in the R computing language (R Core Team 2018).

Fixed effects

	Estimate	Std. Error	P-value
(Intercept)	-0.820	0.494	0.097
Stand age	-0.397	0.103	<0.001
Cons. Index value	-0.356	0.079	<0.001
Stand age ^ 2	-0.098	0.010	<0.001
Stand age : Index	0.068	0.017	<0.001

Random effects

Group	Name	Variance	Std.Dev.
Species	(Intercept)	4.511	2.124
	Plot age	0.125	0.353

Table S3. Model summary for linear model testing environmental drivers of the average plot-level lichen conservation index value.

	Estimate	Std. Error	t-value	P-value
Intercept	3.532	0.318	11.120	< 0.001
Stand age	0.116	0.016	7.191	< 0.001
Elevation	0.000	0.000	-1.782	0.07
Precipitation	-0.002	0.001	-2.988	< 0.001
Stand age ^ 2	0.177	0.041	4.374	0.003
Precipitation ^ 2	-0.006	0.001	-3.963	< 0.001
Elevation ^ 2	0.000	0.000	1.909	0.057
Stand age : Elevation	0.000	0.000	-3.626	< 0.001

Literature cited

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. lme4: Linear mixed-effects models using Eigen and S4. Journal of Statistical Software 67:1–48.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.