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

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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 at a regional scale. Quantitative lichen indicator systems provide unique information about habitat conservation value that is not captured by traditional community metrics such as lichen species richness. More broadly, indicator systems based on expert experience can have strong biological relevance.

1. 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 (Spyreas, 2019; Veldman et al., 2015). Quantifying the conservation value of habitats for 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 (Bauer et al., 2018; Matthews et al., 2009).

Ecological and botanical community indices can be useful tools for evaluating the conservation value of ecological communities, and such indices may be particularly efficacious when they give insights into biodiversity data that are difficult for land managers to interpret 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 (e.g., 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,

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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 (Goward and Arsenault, 2018; Miller et al., 2017; Nascimbene et al., 2013; Petersen et al., 2017; Wolseley and Aguirre-Hudson, 1997); 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 (Campbell and Fredeen, 2004; Nascimbene et al., 2010; Rose, 1976; Tibell, 1992), independent, empirical tests of such indicators have usually been limited in scope because they are based on small sample sizes and narrow geographic regions. 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 interpret lichen survey results; forest managers in many parts of the world are tasked with management decisions that will affect lichens, such as the protection of rare lichen species, but rarely have specific training in lichenology (Allen et al., 2019; Miller et al., 2017; Rosso et al., 2000). 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 that is widely applied to 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. 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). To the best of our knowledge, this is the first continuous index for testing lichen affinities for forest stand age.

2. Materials and methods

2.1. 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 to 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 mostly 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). Although some groups of epiphytic lichens are more challenging to identify and require lab work (e.g., *Bryoria* and *Usnea*), these usually make up a relatively small proportion of community diversity. 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 ecology 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, 1976; 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 substantially correlated (average pairwise correlation coefficient = 0.56), and we developed a master index based on the three sets of individual rankings through consensus (Table S1).

2.2. 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 western slope of 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 surveyors search 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 (575 study plots) and a low elevation subset of the plots (240 study plots), since the relationship between the lichen conservation index and stand age appeared to be weaker at higher elevations. We included the quadratic term for stand age because we hypothesized that the lichen community response variables could have non-linear responses to stand age, such as saturating or hump-shaped responses.

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. AIC indicated that the refined model represented a substantial improvement over the original model (ΔAIC = ~3).

We chose to use the average plot-level lichen conservation index value as the focal 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 prior to all analyses to improve variable normality and better meet model assumptions. All analyses were performed in R (R Core Team, 2018).

3. Results

The species-level lichen conservation index was positively related to the average stand age where species occurred (P < 0.001 for all species and for species that occurred in five or more plots; Fig. 1). For species that occurred in at least five plots, species with a conservation index ranking of two occurred in plots with an average stand age of 62 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 114 years.

The average lichen conservation index values at the plot level were positively related to stand age across the entire dataset (R^2 = 0.169, P < 0.001), and this relationship became stronger when we analyzed low elevation (< 1000 m) sites only (R^2 = 0.24, 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 = 0.022, P = 0.002) and low-elevation sites only (R^2 = 0.049, P = 0.003), 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 = 0.04, P < 0.001 for all plots; R^2 = 0.116, P < 0.001 for low elevation plots only), as was the proportion of old-growth indicator species in a plot (R^2 = 0.057, P < 0.001 for all plots; R^2 = 0.158, 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 (P < 0.001), indicating that significant relationships between average plot-level lichen conservation index values and stand age in simple linear models were not caused by type I error inflation (Table S2; Miller et al. 2019).

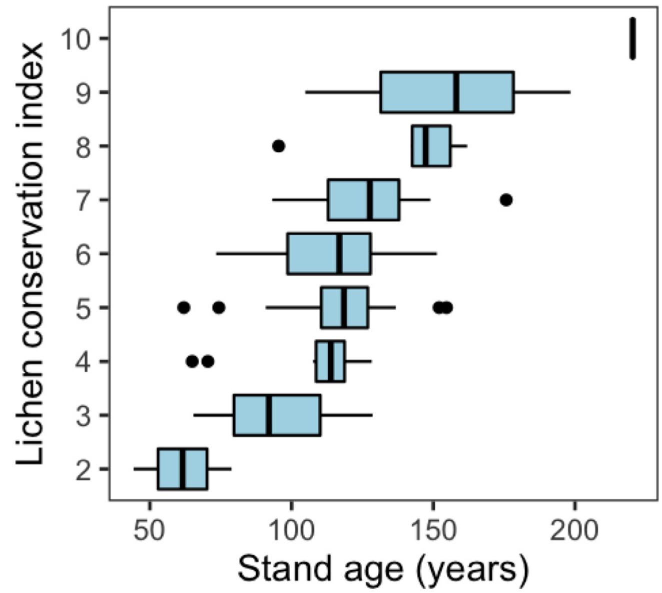

Fig. 1. The average stand age where lichen species occurred in the field plots increased with increasing lichen conservation index rankings. This analysis included species that occurred at five or more plots.

The model for the site-level lichen conservation index that included environmental variables had substantially higher explanatory power than the simple bivariate model (not surprisingly) and indicated that stand age interacted with elevation (P < 0.001; Fig. 3). Stand age had a strong, positive effect on the lichen conservation index at low elevations, but this relationship weakened with increasing elevation, and there was no relationship between stand age and the lichen conservation index at the highest elevations. Precipitation had a weak, marginally significant, hump-shaped relationship with the lichen conservation index (P = 0.07), and precipitation did not interact significantly with either elevation or stand age.

4. Discussion

Our analysis of several hundred study plots across ~500 km of the Cascade Range provides some of the strongest evidence yet that lichens can be used as reliable indicators of forest stand age, and potentially forest conservation value, even across relatively large geographic regions. The lichen conservation index that we developed based on expert field experience 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 (Gauslaa et al., 2007; Nascimbene et al.,

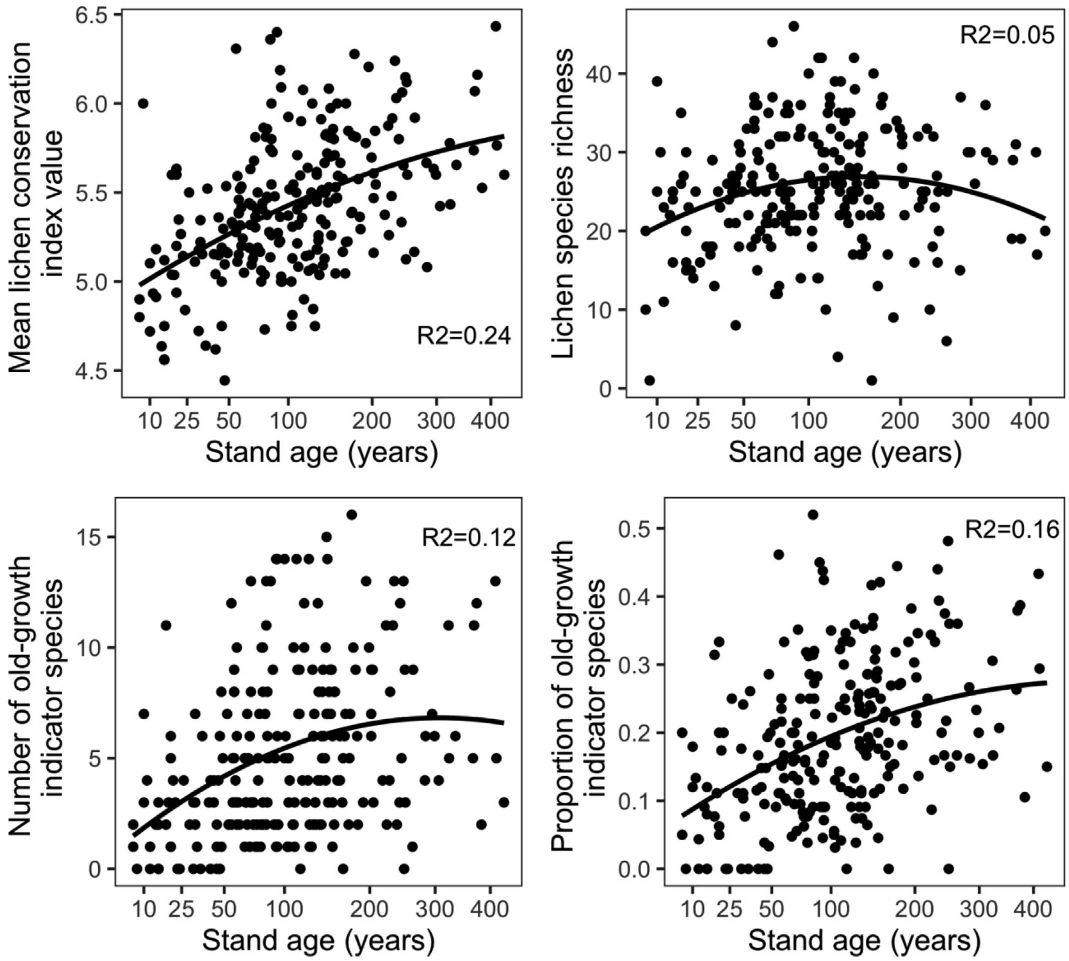

Fig. 2. Relationship between estimated stand age and lichen community metrics in low elevation (< 1000 m) forests in the Cascade Range of Oregon and Washington, USA. All relationships shown are significant (P < 0.01). These simple bivariate relationships do not account for environmental variables; note that the relationship between stand age and the mean lichen conservation index becomes stronger after accounting for elevation and precipitation (Fig. 3).

2013; Rose, 1988), 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). Our conclusions are particularly important in light of previous work suggesting that the efficacy of lichen indicator systems may be context-dependent—and therefore of limited utility across broad regions (Arsenault and Goward, 2016; Will-Wolf et al., 2006). Our findings suggest that the lichen conservation index could help forest managers who have little training in lichenology interpret lichen survey data to inform management decisions.

The relationship between the lichen conservation index and forest stand age becomes stronger when we include elevation and precipitation as additional predictor variables, though precipitation has only a weak and marginally significant effect on the conservation index. The

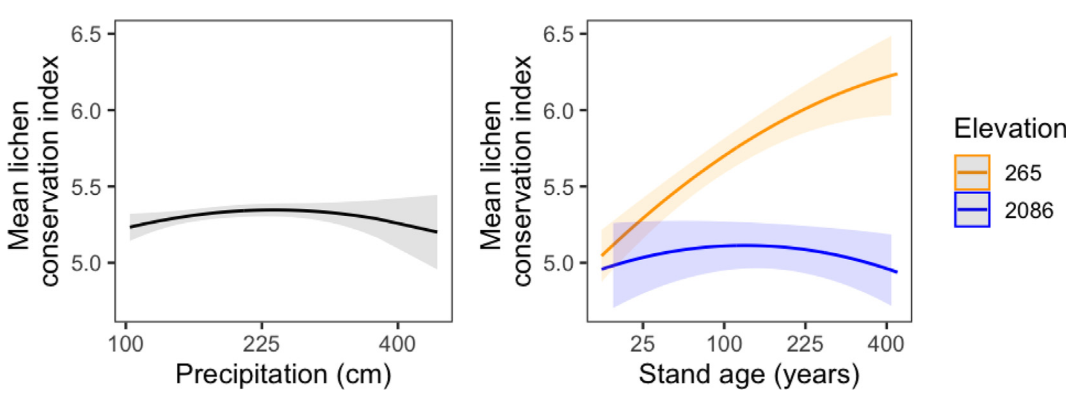

Fig. 3. Model effects of predictors of the plot-level lichen conservation index across all study plots (including high elevation plots). Annual precipitation has a significant (P < 0.001) but relatively weak, hump-shaped relationship with the lichen conservation index. Stand age has a strong, significant 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).

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 (e.g., low elevation forests), 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., low and high elevation forests, or wet and dry forests), since lichens may vary in their degree of affinity for old growth forests depending on environmental conditions. 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 cephalolichens like *Lobaria oregana*, *Nephroma occultum* and *Pseudocyphellaria raineriensis*, occur only at low- to mid-elevations (Berryman and McCune, 2006; Rosso et al., 2000). 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 (Nascimbene et al., 2010; Rose, 1976). 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, but the proportion of old-growth indicator species has a stronger relationship with stand age, perhaps 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, single-species indicators, or other binary indicator systems.

In addition to their association with stand age, lichen communities may be strongly affected by forest continuity–the amount of time that a landscape has been continuously forested (McMullin & Wiersma, 2019; Selva, 2003; Villella et al., 2013). 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; Wiersma and McMullin, 2019). This distinction may be more important in Europe and eastern North America than in western North America. Although forests in western North America have been highly modified by human activities, the reversion of agricultural lands to forest has been rare in this region, while it is more common in some 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.

Although our findings suggest that the lichen conservation index has substantial biological relevance, there are of course limitations to our study. We tested the index using forest survey data from the west slope of the Cascade Range in Oregon and Washington, but the index may be ecologically relevant somewhat more broadly (e.g., in the Coast Ranges of Oregon and Washington), and this remains to be further explored. The index would probably be less likely to perform well in extremely wet regions of the Pacific Northwest, such as coastal forests on northern Vancouver Island, where lichen communities are relatively depauperate even in old growth forests and bryophytes become more dominant (personal communication, Trevor Goward). Although our index was developed by four experienced lichenologists, input from additional experts could improve the ranking system. We envision that the lichen conservation index will be refined in the future after it has been further explored and tested by field biologists and forest managers, and we hope to receive feedback from those who use it.

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; Spyreas, 2019). The coefficient of conservatism appears to provides unique information that is not represented by species richness (Matthews et al., 2009). This previous research examining a plant indicator system, in combination with our findings here, suggests that the lichen conservation index may have useful biological relevance for management. 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.

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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118436.

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