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Defining a Successional Metric for Lichen Communities in the Arctic Tundra

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Abstract

We provide an index of successional status for arctic macrolichen communities based on a synthesis of literature reports. We amassed research from the past 50 years that studied lichen communities following disturbance, such as fire or grazing. Species scores were derived from these reports depending on when a particular macrolichen species appeared following disturbance. Weighted averaging of these data with a community matrix can create a successional score for each sample unit of interest. These scores can be used as a surrogate for community age estimates that are otherwise difficult to obtain from tundra environments above treeline. We test this approach using an example data set of macrolichen communities collected from the Bering Land Bridge National Preserve, Alaska. We found that our successional scores represented roughly 17 and 19% of the community variation, depending on whether the community data set was binary or quantitative. Abundance data tended to yield successional scores that were slightly higher (older) than those derived from a presence-absence data set. We recommend use of our successional metric for lichen communities throughout the arctic tundra to infer successional status of an area.

Introduction

Succession has remained a central concept in plant ecology for over a century, and has aided ecologists in understanding the dynamics and relationships among plant communities. Progress in recent decades has encouraged a shift from conceptual to quantitative approaches. In temperate regions, time since disturbance is easily assessed by using counts of tree annual growth rings or fire scars to estimate stand age. This simple measure of successional status often represents a large component of variation in community composition.

These dating methods, however, are dependent upon the presence of trees, which may be absent or sparse in northern ecosystems beyond timberline. Research in the arctic tundra lacks the benefit of easily obtaining relatively quick and accurate field measures of stand age or time since disturbance from large conifer or deciduous tree records. Destructive age determination is possible with willow and birch shrubs (Kullman, 2002), but accurate ring counts on slow-growing shrubs are often difficult to determine. Additionally, shrubs may not establish for years or decades following disturbance; thus, a single shrub's age may considerably underestimate the actual time since disturbance. Furthermore, dateable stems present in these tundra ecosystems may be shorter lived than time since disturbance. Finally, some areas of arctic tundra lack willow and birch shrubs altogether.

A lack of methodology for measuring time since major disturbance for ecosystems above tree line greatly impedes our understanding of tundra dynamics. Just under a quarter of the North American landmass is covered by arctic tundra (Barbour et al., 1999). Within this ecosystem, lichens contribute nearly half the floral diversity and a large portion of the biomass (Neitlich and Hasselbach, 2001). Lichens are often cast as classic examples of facilitation in novel environments, owing to their mechanical and chemical weathering of rocks combined with their ability to acquire atmospheric nutrients (Cooper and Rudolph, 1953; Topham, 1977; Vitousek, 1994). These and other statements of the successional status or role of individual lichen species are available in the literature, but have not been collected into a single, useful form.

Our goal is to assign species scores to macrolichens reported in the literature and use these to develop an index of successional status for arctic macrolichen communities. We also compare successional scores derived from quantitative versus binary data. We demonstrate this successional metric with an example data set of macrolichen communities of the Bering Land Bridge National Preserve, Alaska.

Methods

WEIGHTED AVERAGING PROCEDURE

Weighted averaging is a direct gradient analysis technique that summarizes complex relationships according to their position along a single gradient (McCune and Grace, 2002). It is an ordination technique that uses previously assigned weights to calculate scores describing compositional gradients. Early examples include Curtis and McIntosh's (1951) vegetational continuum index, which arranged stands along a successional gradient. LeBlanc and De Sloover (1970) derived an index of atmospheric purity based on epiphyte species' substrate coverage weighted by their toxitolerance. The Federal Wetlands Manual also uses weighted averaging to help delimit wetlands (Federal Interagency Committee for Wetland Delineation, 1989). The predetermined weights were "wetland indicator status" ratings, representing a continuum from obligate wetland to obligate upland species. Final scores, or hydrophytic vegetation criteria, were derived from a combination of these weights and a community matrix of dominant vascular plant species for each proposed wetland site. Another successful management tool rooted in weighted averaging is the index of biotic integrity, which assesses water resource quality based on fish community attributes as they relate to regional reference sites (Karr, 1991).

Weighted averaging is an ideal method, using over 50 years of lichen studies from several countries, for inferring the successional status of arctic tundra communities. Weighted averaging can combine prior knowledge with current estimates of lichen abundance to assess the successional status of a particular area. In effect, our species scores are weighted by evaluations of presence or abundance to yield successional scores for a particular area. Future applications of our method require no additional measurements apart from community estimates of lichen presence or abundance.

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TABLE 1

Literature used to create successional species scores, including the type of disturbance that initiated lichen succession. Reference number is used in Table 2 for each lichen species.

Reference no.	Citation	Disturbance
1	Ahti (1959)	Grazing
2	Ahti and Hepburn (1967)	Grazing
3	Arseneault et al. (1997)	Fire
4	Black and Bliss (1978)	Fire
5	Caroll and Bliss (1982)	Fire
6	Churchill and Hansen (1958)	Grazing
7	Coxson and Marsh (2001)	Fire
8	Fortin et al. (1999)	Fire
9	Foster (1985)	Fire
10	Gorshkov (1995)	Fire
11	Helle and Aspi (1983)	Grazing
12	Johnson (1981)	Fire
13	Kershaw (1978)	Fire
14	Lutz (1956)	Fire
15	Magnusson (1982)	Dunes
16	Maikawa and Kershaw (1976)	Fire
17	Manseau et al. (1996)	Grazing
18	Morneau and Payette (1989)	Fire
19	Moser et al. (1979)	Grazing
20	Pegau (1970)	Grazing
21	Scotter (1964)	Fire
22	Steen (1965)	Grazing
23	van der Wal et al. (2001)	Grazing
24	Yarranton (1975)	Fire

We surveyed the disturbance ecology literature for lichen community studies in the arctic tundra. The scarcity of detailed tundra research led us to also include several studies from northern boreal forests, which overlap considerably in community composition. Moreover, due to circumpolar distributions of many tundra lichens, we compiled reports from Canada, Alaska, Scandinavia, and Russia.

Our investigation focused primarily on grazing and fire research (Table 1). Although many other types of disturbance occur in the Arctic (e.g., cryoturbation, solifluction movement, volcanic or mining activity), grazing and fire studies are well represented because their disturbances can span large areas and are often easily quantifiable. We recognize that small-scale disturbances undeniably occur within these larger disturbances, yet those responses are reflected in the local variability. We selected studies that described lichen communities before and after disturbances as well as those that outlined a successional change in lichen species composition following disturbance. We excluded all studies that did not identify lichen taxa to species, as genera can include both early and late successional species.

For every study, each species was categorized as early, mid-, or late successional. These categories were assigned scores of one, two, or three, respectively. Most authors independently segregated the lichens they reported into groupings similar to our early, mid-, and late successional stages. Macrolichens cited as increasing or decreasing with grazing were assigned scores of one and three, respectively. In addition, an approximate time scale was assigned based on lichen growth rates (Ahti, 1959; Vasander, 1981) and descriptions of succession in the literature. Dominant species in the first few decades following disturbance (roughly 30 yr) were labeled as early successional. Mid- and late successional classifications varied among studies, dependent upon the time considered or longevity of the study. Considering the range of years among all studies, the mid-successional stage encompassed the time span between 20 and 80 yr, while late successional species dominated from about 40 to 300 yr post-disturbance. In some instances, different authors or even the same author listed a single species in more than one category. For example, *Cladina mitis* was often listed in both mid- and late successional stages. In such cases, instead of subjectively assigning it a species score of 2 or 3 for a particular study, we would assign it 2.5. For each species, species scores were averaged across all studies to create a vector of average species scores (Table 2).

The final successional plot score for a particular sample unit is calculated as an average of abundances from p species, weighted by p

TABLE 2

List of lichen species present following disturbance, as cited in literature from Table 1. Species scores range from 1 (early successional) to 3 (late successional).

Lichen species	Cited in reference no.	Average successional score
Alectoria ochroleuca	3, 17	2.5
Asahinea chrysantha	19	1.0
Bryocaulon divergens	3	3.0
Cetraria andrejevii	24	3.0
Cetraria cucullata	3, 4, 20	2.3
Cetraria delisei	24	3.0
Cetraria ericetorum	20	2.5
Cetraria islandica	1, 4, 20, 24	2.0
Cetraria nigricans	3	3.0
Cetraria nivalis	3, 4, 5, 17, 21	2.2
Cladina arbuscula	10, 20, 24	2.3
Cladina mitis	1, 2, 3, 4, 5, 7, 8, 9, 11, 12, 15, 16, 18, 21	2.1
Cladina rangiferina	1, 4, 5, 7, 8, 9, 10, 11, 12, 14, 17, 18, 20, 21, 24	2.3
Cladina stellaris	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 14, 16, 17, 18, 20, 21, 24	2.7
Cladonia amaurocraea	12, 21	2.3
Cladonia bacillaris	21	2.0
Cladonia bellidiflora	14	2.0
Cladonia botrytes	21	2.0
Cladonia carneola	7, 21	1.5
Cladonia cenotea	7	1.0
Cladonia cervicornis	7	1.0
Cladonia coccifera	5, 9, 13, 14, 18, 21	1.5
Cladonia cornuta	2, 3, 7, 9, 10, 12, 13, 18, 21	1.2
Cladonia crispata	1, 7, 10, 18	1.8
Cladonia cristatella	1, 13, 21	1.7
Cladonia deformis	1, 3, 7, 10, 13, 14, 18, 21	1.6
Cladonia ecmocyna	7	2.0
Cladonia glauca	7	2.0
Cladonia gracilis	2, 5, 7, 9, 10, 12, 13, 14, 21	1.2
Cladonia macrophylla	9, 18, 21	1.7
Cladonia phyllophora	7	1.0
Cladonia pleurota	9	1.0
Cladonia pyxidata	13, 21	2.0
Cladonia sulphurina	3, 9, 18	1.3
Cladonia uncialis	1, 2, 5, 7, 10, 15, 16, 18, 21	2.1
Cladonia verticillata	21	2.0
Coelocaulon muricatum	15	1.0
Nephroma arcticum	7	3.0
Peltigera aphthosa	4, 7, 21, 23	2.5
Peltigera canina	4, 21	1.8
Peltigera malacea	4	1.0
Peltigera rufescens	23	2.0
Sphaerophorus globosus	23	3.0
Stereocaulon alpinum	7	1.0
Stereocaulon paschale	6, 12, 13, 14, 16, 17, 22	1.6
Stereocaulon tomentosum	21	3.0

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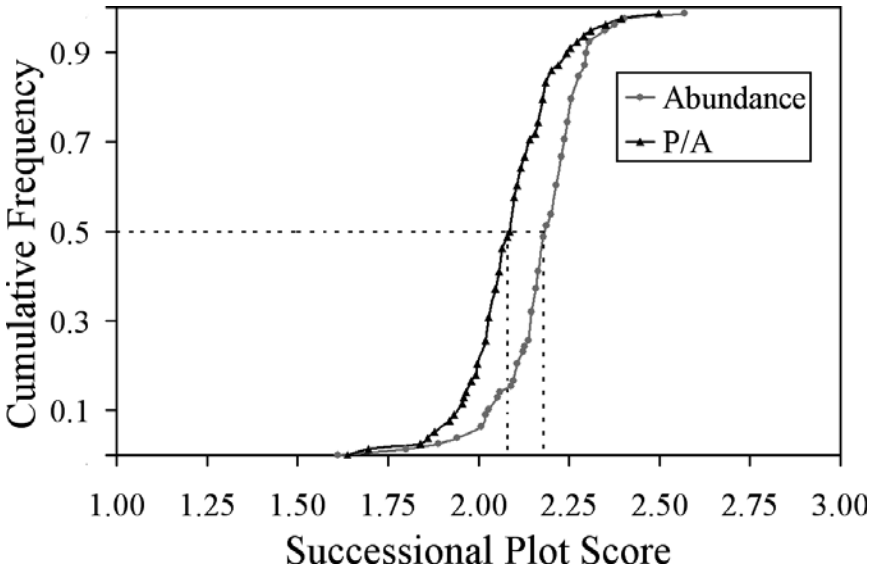


FIGURE 1. Cumulative frequency distribution (proportion of values below indicated score) of successional plot scores for 78 sample units in the Bering Land Bridge National Preserve example data set. Dashed lines indicate the median score for each data set.

species scores (Equation 1). For an observed abundance a_{ij} (abundance or presence-absence element of the community matrix) of species j in a sample unit i, let

v_i = successional plot score for sample unit i,
w_j = average species score for species j, and
p = number of species for which there are species scores.

$$v_i = \frac{\sum_{j=1}^{p} a_{ij} w_j}{\sum_{j=1}^{p} a_{ij}} \quad (1)$$

Ideally, the resulting successional plot scores would be validated against time-since disturbances of known ages. Such data were not available, so for now, the validity of our method rests on the collective wisdom of the 24 sources cited in Table 1.

We measured the proportion of variance that successional plot scores represented in the community data matrix by correlating differences in successional scores with a matrix of Relative Euclidean distances among plots (McCune and Mefford, 1999). We also calculated score variability for species with three or more citations using pooled standard deviations. An example spreadsheet of successional plot score calculations is available at http://oregonstate.edu/~holtem/.

EXAMPLE DATA SET

We sampled lichen communities from the Bering Land Bridge National Preserve located on the Seward Peninsula in northwestern Alaska in 2003 (65°14′–66°36′N, 162°44′–167°32′W). We used a stratified random sample design. Geographic blocks and GIS land cover data (Markon and Wesser, 1997) were used as the basis for our stratification. Within each of 21 geographic blocks, roughly four plots from each cover type were randomly located, for a total of 78 plots.

Sample units were 34.7-m-radius circular plots. Lichen community composition was evaluated using a variant of long-term lichen monitoring protocol established by the USDA/Forest Service Health Monitoring Program (McCune, 2000; USDA/Forest Service, 2002). Designed for forests, these protocols focus on epiphytic macrolichens. We adapted these methods for tundra ecosystems by including terricolous macrolichens and epiphytic macrolichens on shrubs. Ocular estimates of cover were based on measurements of species abundance categories adapted from the abundance scale of Forest Health Monitoring Program (USDA/Forest Service, 2002). Each species encountered was assigned an abundance value: 1 = rare (<3 thalli), 2 = uncommon (4–10 thalli), 3 = common (<1% cover), 4 = abundant (1–5% cover), 5 = prolific (6–25% cover) and 6 = dominant (>26% cover). In addition to analyzing abundance data, we transformed each value into presence-absence to compare effects of data type on our weighted averaging.

For our purposes, we amended the community matrix through species additions and deletions to match the number of species in our vector of species scores. Extraneous species, for which successional values are not known and which do not appear in Table 2, are excluded from the community matrix. Similarly, species that do not occur in the original matrix but are present in the species scores vector can be added as empty columns into the community matrix or simply deleted.

Results and Discussion

We provide species scores for 46 arctic macrolichens, which served as the basis for our successional plot scores. Successional plot scores for 78 Bering Land Bridge plots were approximately normally distributed. Scores ranged roughly between 1.5 and 2.5 within the possible range of 1.0 to 3.0. The mean plot score from the abundance data set was 2.17 (±0.13 SD) and 2.08 (±0.14 SD) for the presence-absence data set (Fig. 1). Scores based on the abundance data were more negatively skewed (–1.15) than those based on binary data (–0.14). In general, the abundance data set had higher (older) successional plot scores than did the presence-absence data set (Fig. 2). The disparities between data sets may be a consequence of species with higher successional species scores generally having higher average abundances (Fig. 3). Successional plot scores represented 19% of the variance in the quantitative community matrix, and 17% based on binary data.

The weighted averaging method described here can produce successional plot scores for data sets that include any number of the species listed in Table 1. The more species for which there are species scores will produce better estimates of successional plot scores. This metric serves as a surrogate for stand age estimates, which are difficult to obtain in arctic tundra environments. These estimates can be used for both management and scientific studies of arctic lichens. We are currently applying these successional scores to data from the Bering Land Bridge National Preserve to understand lichen community

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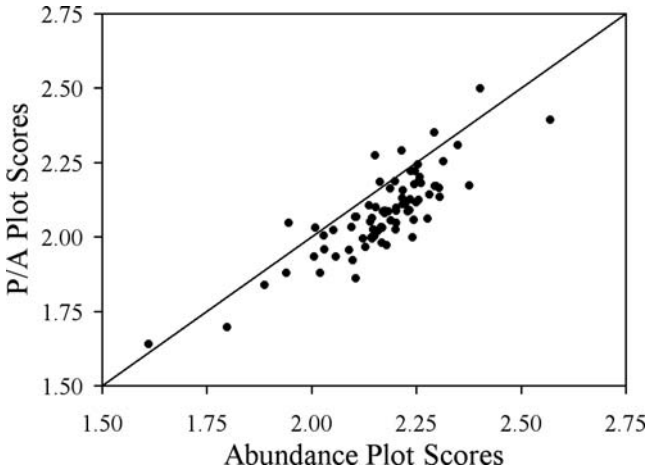


FIGURE 2. Scatterplot of successional plot scores based on a single community data set using abundance codes and presence-absence (P/A) values. Most points fall below the one-to-one line (shown), demonstrating that abundances tend to yield higher successional scores than presence-absence values of the same data.

dynamics and successional patterns in the Preserve. In addition, resource management agencies could use these scores to track changes in lichen communities experiencing active reindeer grazing, mining, or other disturbances.

Our method, however, has the following limitations. (1) These successional scores reflect community change induced primarily by grazing and fire disturbances. Other disturbance factors, however, with their own response patterns may not be captured in our metric. (2) Some of the studies in Table 1 are based on years of experience and observation, but their assessments of species successional status are nevertheless subjective. (3) The species scores we derived are averaged over 24 studies, which occasionally disagreed on the successional status of a particular species. For example, *Cetraria islandica* was listed by two authors as early-successional (score of one), while two others labeled it late-successional (score of three). By averaging these values, our final score compromises both views. The overall variability across assessments, from species with three or more values, was minimal (pooled standard deviation = 0.63). The only two species with standard deviations greater than one were *Cetraria cucullata* and *C. islandica*. (4) The amount of information available differed among species. Even within a single species, geographic differences may potentially change the successional meaning of these indicators, dependant upon locality. Moreover, we have species scores for 46 macrolichens, which may omit many species of the actual arctic tundra lichen flora. Redundancy inherent in community data, however, probably enables this number of species to provide good estimates for most arctic tundra lichen communities.

(5) Finally, species concepts may differ among investigators. This could conceivably alter particular species' successional indicator values. For example, *Cladina stellaris* was cited as a late-successional indicator in about 80% of the studies we encountered (Table 2). Many of the studies treated *C. stellaris* in the broad sense (i.e., including the psoromic acid chemotype, *C. stellaris* var. *aberrans*; Ahti, 1961, 1984), but we do not know if the varieties differ in indicator value. We recommend refining species scores presented here as taxonomic concepts evolve and as application of the method to disturbances of known ages affords more precise calibration.

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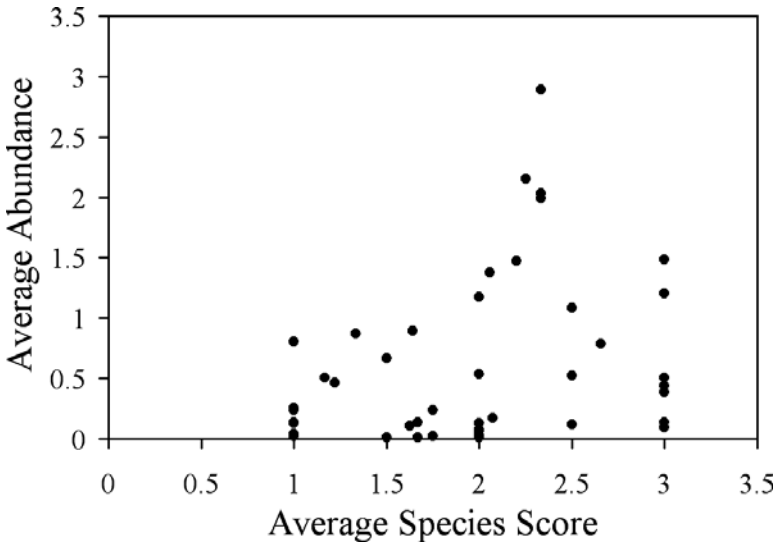


FIGURE 3. Scatterplot of average abundance of each species versus average species score for all 46 lichen species. A weak positive correlation ($R^2 = 0.11$) exists between average species score and average abundance, especially in plots with higher species scores, explaining the weak disparity between successional plot scores derived from binary versus abundance data.

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