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Lichen community change in response to succession in aspen forests of the southern Rocky Mountains

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ABSTRACT

In western North America, quaking aspen (*Populus tremuloides*) is the most common hardwood in montane landscapes. Fire suppression, grazing and wildlife management practices, and climate patterns of the past century are all potential threats to aspen coverage in this region. If aspen-dependent species are losing habitat, this raises concerns about their long-term viability. Though lichens have a rich history as air pollution indicators, we believe that they may also be useful as a metric of community diversity associated with habitat change. We established 47 plots in the Bear River Range of northern Utah and southern Idaho to evaluate the effects of forest succession on epiphytic macrolichen communities. Plots were located in a narrow elevational belt (2134–2438 m) to minimize the known covariant effects of elevation and moisture on lichen communities. Results show increasing total lichen diversity and a decrease in aspen-dependent species as aspen forests succeed to conifer cover types. The interactive roles of stand aspect, basal area and cover of dominant trees, stand age, aspen bark scars, and recent tree damage were examined as related to these trends. We developed an aspen index score based on lichens showing an affinity for aspen habitat (*Phaeophyscia nigricans, Physcia tenella, Xanthomendoza fulva, Xanthomendoza galericulata*) and found a significant negative relationship between the index and successional progression. Indicator species analysis showed the importance of all stages of aspen-conifer succession for lichen community diversity and highlighted the decline of aspen-dependent species with advancing succession. We present a landscape-level community analysis of lichens in the context of a conceptual model for aspen succession for the southern Rocky Mountains. We conclude that while total number of lichen species increases with succession, aspen-dependent species cover and richness will decline. In this way, epiphytic lichens communities may constitute an effective indicator of community-level diversity in for aspen-dependent species at-large.

1. Introduction

Quaking aspen (*Populus tremuloides*), the most widespread and abundant hardwood of the southern Rocky Mountains, USA, is purportedly in regional decline. Explanatory factors contributing to aspen change are fire suppression, climate change, impacts of European settlement, and effects of browsing by wildlife and livestock (Shepperd et al., 2006). Numerous studies have addressed the status of aspen forests in the region, with some showing declining coverage (Bartos and Campbell, 1998; Rogers, 2002; Gallant et al., 2003; Brown et al., 2006) and others describing aspen expansion (Manier and Laven, 2002; Kulakowski et al., 2004). Researchers agree that aspen succumb to conifer invasion where seral stands are devoid of recent disturbance. While some aspen display long-term stability, shade-tolerant conifers eventually invade most stands in the absence of disturbance (Mueggler, 1988). From this perspective succession in aspen communities plays a crucial role not only in the development and potential conversion of aspen to other types, but as a catalyst for change in associated species. There is strong support for the notion of aspen's unique contribution to biodiversity of western North American landscapes (DeByle, 1985; Mueggler, 1988; Ripple et al., 2001; Shepperd et al., 2006) and some have highlighted aspen as a "keystone" type, denoting their amplified role in supporting entire ecosystems (Campbell and Bartos, 2001; Manley et al., 2000).

Lichen community response to aspen-to-conifer succession is poorly understood in western North America. A review of landmark publications on aspen ecology in both the USA and Canada makes no mention of lichens (DeByle and Winokur, 1985;

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Peterson and Peterson, 1992) and overlooks the importance of the lichen communities' role in increasing aspen-related diversity in the region (Buckley, 2002; Case, 1977). In contrast, research and subsequent management actions in European forests have elevated the profile of aspen (*Populus tremula*) as a landscape element and found that aspen promotes species diversity including lichens (Hedenås and Ericson, 2000, 2004; Lipnicki, 1998).

In the United States, we know of two published works examining lichens specifically in quaking aspen. In the Colorado Front Range, lichen communities were inventoried on 10 riparian hardwood species, including aspen (Carmer, 1975). The author found 23 species on aspen, about half being macrolichens (i.e., foliose and fruticose forms) and the rest being microlichens (i.e., crustose) species. This study concluded that aspen was second only to narrowleaf cottonwood (*Populus angustifolia*) in terms of lichen species richness for riparian hardwoods (Carmer, 1975). Also, Martin and Novak (1999) compared the lichen flora of aspen stems in Idaho to those of adjacent Douglas-fir (*Pseudotsuga menziesii*) and noted a distinct lichen flora between tree substrates. Their work also highlighted the importance of tree age, trunk moisture gradients, bark pH, bark texture, and air pollutants on lichen species diversity in these forest communities. The importance of bark scarring in providing habitat for epiphytic lichens has been noted in a number of studies (Case, 1977; Martin and Novak, 1999; Rogers et al., 2007a). Since the bole of North American aspen is predominantly smooth white bark, a correlation may occur between scars on aspen boles originating as cankers, conks, physical wounds, and branch stubs and lichen diversity and abundance at the stand-level.

This paper focuses on change in epiphytic macrolichen communities associated with succession in aspen forests. Specifically, we have three objectives: (1) to determine the diversity of lichens associated with aspen forests in the Southern Rockies Ecoregion; (2) to assess trends in lichen communities as forests change from pure aspen to conifer-dominated stands; and (3) to evaluate the importance of specific successional stages on lichen community development. In conjunction with this final objective, we hope to gain specific understanding of how lichens exclusive to aspen substrates react to conifer encroachment.

An underlying theme of this work is to test the ability of epiphytic lichens to act as bioindicators of forest change. Since little research has been conducted on this subject in our region, there is significant potential for increased basic knowledge on lichen species presence, as well as interactions related to forest change. We are unaware of previous studies in western North America examining the interface between aspen dynamics and lichen communities. We anticipate that these findings will provide further insight to ecological change associated succession, as well as applications to forest management and monitoring.

2. Study area

The Bear River Range is a north-south trending block fault range straddling the Utah and Idaho border (Fig. 1). These mountains lie in the Southern Rocky Mountains Ecoregion Province between 1370 and 3040 m elevation, and receive between 51 and 102 cm of precipitation per year (Bailey, 1995). Most precipitation comes in the form of winter snowfall. The northern portion of the Southern Rocky Mountains experiences summer drought with occasional brief thunderstorms. Dry lightning storms provide the prime ignition source for fire-prone forests of the area (Bailey, 1995).

Aspen forests comprise the primary hardwood element of mid- and upper-elevations in the Southern Rockies Ecoregion (Rogers, 2002). In the Bear River Range, aspen's conifer cohorts are subalpine fir (*Abies lasiocarpa*), Douglas-fir (*P. menziesii*), lodgepole pine (*Pinus contorta*), and to a lesser degree Engelmann spruce

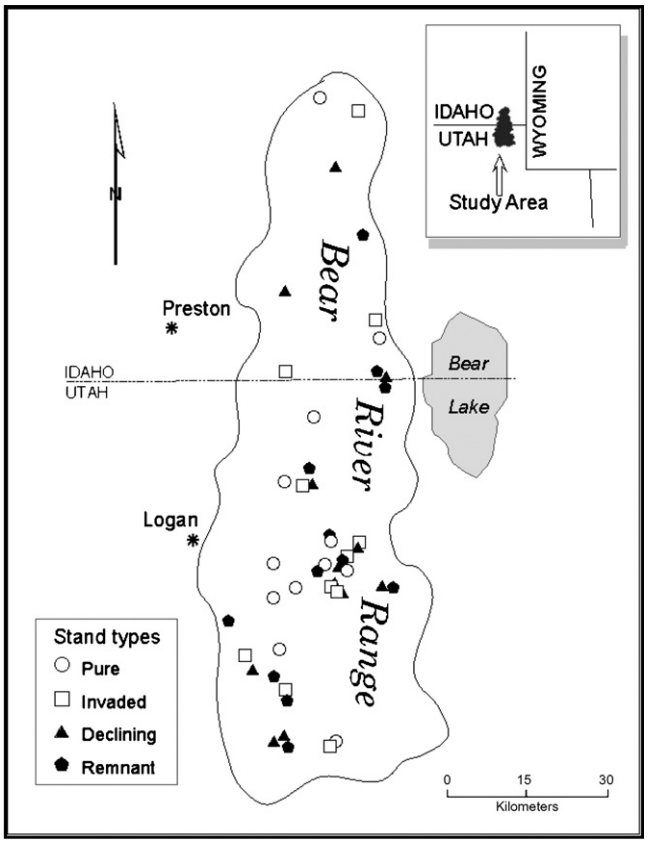

Fig. 1. Location of study area and plots in the Bear River Range of Idaho and Utah, USA.

(*Picea engelmannii*), Rocky Mountain juniper (*Juniperus scopulorum*), and limber pine (*Pinus flexilis*). Subalpine fir is the dominant conifer in this study area. Minor hardwoods of the area include bigtooth maple (*Acer grandidentatum*), Scouler willow (*Salix scouleriana*), western serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), and mountain mahogany (*Cercocarpus ledifolius*). The remaining vegetation cover of this range is made up of big sagebrush (*Artemisia tridentata* var. *vaseyana*) and subalpine meadow openings. Understory vegetation in aspen stands ranges from lush stands of diverse forb and grass groups, to shrubby cover dominated by snowberry (*Symphoricarpos* spp.), to sagebrush, and mixed assemblages of each of these groups (Mueggler, 1988).

A fire history in the Bear River Range concluded that during the settlement era (c. 1850–1900) fire frequencies increased due to amplified human fire ignitions related to extractive activities (i.e., logging, grazing, mining, hunting), while during the 20th century fire suppression and decreased grazing led to longer fire intervals (Wadleigh and Jenkins, 1996). This general pattern has favored shade-tolerant fir and spruce at the expense of fire-dependent aspen and lodgepole pine. Additionally, a relatively moist 20th century in this region, excepting the 1930s drought, probably served to augment fire suppression efforts in terms of favoring shade-tolerant conifer species (Gray et al., 2004).

3. Methods

3.1. Plot selection and field methods

The goal of plot selection was to attain at least 10 sample points in each of four qualitative succession groups evenly distributed across the study area. A "plot" is defined here as the primary

Table 1
Stand type codes, cover values, and plots sampled by stand type categories

	Stand types			
	Pure	Invaded	Declining	Remnant
Stand type code	1	2	3	4
Percent aspen cover[a]	>90	50–90	49–10	<10
Plots sampled	12	11	12	12

[a] Cover values are used for stratification of aspen stands for plot selection based on aerial photograph estimation.

sample unit consisting of a 0.378 ha fixed-area circle. An underlying assumption of this work is that all stands sampled could potentially succeed to conifer types. For this reason, dry south-facing aspects were avoided because they are the least likely to be invaded by conifers at mid elevations. Seral aspen stands (the subject of this study) are most commonly encountered on cooler, moist aspects where conifers thrive (Mueggler, 1988). The initial screening was made from a set of 422 potential aspen sample locations located between 2134 and 2438 m elevation and selected from a 500 m grid overlay of Utah and Idaho digital vegetation maps (USGS, 2004, 2005). Using ArcMap® geographic information system software (ESRI Corp.), we randomly selected 25% of potential aspen plots throughout the range for field sampling. The selected plots were randomly assigned stand type labels of 1–4 corresponding to "pure," "invaded," "declining," and "remnant" aspen populations. The 52 selected plots were adjusted before field sampling to move them into adjacent stands estimated from aerial photographs to meet the stand type qualifications (Table 1). Upon field sampling, plot centers were located using the same aerial photos, then either placed at the actual grid point intersections (unadjusted) or by chaining into stands (adjusted) a predetermined distance to allow for measuring the entire plot within the same type. Sixteen field plots were located on privately owned land. Five of these plots were dropped from the survey where owners denied access. A total of 47 field locations distributed in the four aspen cover categories (Table 1) are shown in Fig. 1.

Field measurements encompassed two broad categories: stand characterization composed of site descriptors and mensuration variables, and lichen sampling by species tally, voucher collection, and abundance estimation. Location descriptors include a plot identifier, GPS readings, slope, aspect, stand type, percent aspen cover, percent conifer cover, stand age, and aspen age. Five cover estimates for mature aspen, conifers, and no cover were taken at the plot center and 2 m inside the lichen plot perimeter (33 m radius) at the four cardinal directions. These ground-based estimates of cover were performed by looking upward and estimating the cover of an imaginary 4 m diameter cylinder extending from 2 m off the ground to the top of the forest canopy and averaging all five points for a stand-level cover (Mueggler, 1988). Stand ages were based on at least two cored aspen trees (stand types 1 and 2) and an additional two cores of dominant conifer species (stand types 3 and 4). We cored the nearest healthy co-dominant trees to the plot center for age determination. Stand ages were calculated by adding 5 years to the breast height average of aspen cored and 10 years to average conifer ages to account for the growth period between ground level and breast height (Campbell, 1981; USDA Forest Service, 2005). Where decayed heartwood was encountered in tree coring, we chose the nearest alternate tree of the same species and canopy position for aging. All tree cores were aged in the field by counting tree rings from the cambium to the pith. Though aspen cores are sometimes difficult to age due to indistinct annual rings, we modified laboratory methods for increasing aspen ring clarity (Campbell, 1981) for field use—wetting cores with water or saliva, backlighting cores with bright sunlight, and/or examining them with a hand lens (14× triplet)—to improve accuracy. Even with these techniques, and 20 years of field experience aging aspen by the lead author, we accept a certain level (<5%) of error in aspen stand ages, but do not feel this would markedly affect our results or conclusions.

Forest mensuration variables were collected on a single fixed-area subplot 7.3 m in radius and centered in the 0.378 ha lichen survey plot (Will-Wolf, 2002). Tree species, diameter at breast height (dbh = 1.3 m), size class, and status (live/dead) were collected on all trees 12.7 cm diameter and greater. Additionally, on aspen we tallied damage type and severity, plus percent of the main stem with bark scarring, lichen colonization of scars, and lichen colonization of smooth bark. Scarring and colonization variables consisted of percent area of stems from 1 to 2 m above the ground. Finally, we counted tree seedlings (>0.3 m and <1.3 m height) and saplings (≥1.3 m height <12.7 cm dbh) within the subplot by species to estimate per hectare regeneration levels. When referring to "seedlings" in our field protocol we mean all tree species meeting the size qualifications above; including aspen whose regeneration is vegetative and not from seed.

Lichen sampling was modeled after the procedure used in the USDA Forest Service, Forest Health Monitoring program (McCune, 2000; Will-Wolf, 2002). In short, epiphytic macrolichens were systematically examined on a 0.378 ha plot for up to 2 h. We did not sample microlichens (crustose forms) as they are not easily distinguished for purposes of a national monitoring system (McCune, 2000; Will-Wolf, 2002) and they appear to comprise a minor component of the local epiphytic flora; in contrast to the greater diversity of crustose species found at some riparian sites (Carmer, 1975) or in moister environments on European aspen (Lipnicki, 1998; Ellis and Coppins, 2006). Only species occurring on woody substrates at least 0.5 m above the forest floor were sampled. Lichens were not sampled below 0.5 m to avoid overlap with terricolous and saxicolous species and their accompanying forest floor influences (i.e., soil type, moisture, leaf litter, vascular plant abundance). The method allowed workers to examine fresh litter fall as surrogate for upper canopy lichens. At least 40 min was spent traversing the area, the last 10 min without new species tally, before the survey was terminated. On average, 60–75 min were needed for the survey. Field workers performing this method quickly develop a search technique that accommodates local conditions and facilitates notation of greater species diversity: for example, look in moist microhabitats, on uphill side of trees, in aspen scars, at each tree species, or where abundant lichens are obvious. When a new species is suspected, close examination with a hand lens (14× triplet) was used to key species by unique physical characteristics.

After completion of lichen tally, each species was assigned an abundance class score for the entire area: 1 = 1–3 individuals (distinct thalli); 2 = 3–10 individuals; 3 = between 10 individuals and occurrence on half of all trees/shrubs on the plot; 4 = greater than half of all woody substrates on the plot exhibited the lichen. Previous research found that for sparsely populated vegetation in large sample areas, visual abundance classes were preferable to continuous cover measures because accuracy was comparable while efficiency was greatly increased (McCune and Lesica, 1992). Unknown species were collected as vouchers for later verification under a dissecting scope and with chemical tests, or if needed, by other lichen experts. One modification of the standard protocol was that we noted tree substrate groups (aspen, conifer, other) on which lichens were tallied.

3.2. Data analysis

After data compilation and error checking, several derived variables were calculated for tree and lichen data at the plot-level.

Aspen and subalpine fir seedlings and saplings were tabulated on a per hectare basis. Though seedlings of other species were tallied, there were not enough individuals for meaningful analysis. Likewise, we calculated per hectare basal area separately for aspen, conifer, and standing dead trees. For all plots with live aspen present we computed average percent bole scarring, lichen colonization of scars, and colonization of smooth bark. Stand level aspen damage was determined by the proportion of bole-damaged versus undamaged live aspen stems tallied. For lichens, the two primary plot-level variables were species richness (number of distinct species) and total abundance (cumulative abundance class scores for all species).

Analyses were conducted to quantify lichen diversity in each of the four stand types that corresponded to different stages of conifer encroachment. Prior to analyses, the following statistics were generated to assess community diversity: gamma diversity (γ), the total number of distinct species identified in the study; alpha diversity (α), the mean species richness per sample plot; and beta diversity (β), γ/α, which yields an estimate of "community turnover." We conducted simple Pearson correlations (SAS proc CORR) for all plot-level variables to identify initial relationships. Analysis of variance (ANOVA; SAS proc GLM) was the primary analytical tool (SAS Institute, 2005). Random selection of approximately equal number of plots for each "treatment" (stand type) justifies the use of one-way ANOVA to test multiple response variables (Zar, 1999). Response variables, at the plot-level, were lichen species richness and total abundance. These variables were further examined for normality of distribution (SAS proc UNIVARIATE) and equality of variance using Brown and Forsythe's test (SAS proc GLM, hovtest = bf welch) (Zar, 1999).

To pinpoint individual species reactions to succession from aspen to conifer forests we used indicator species analysis (ISA), a multivariate approach to testing for no difference between *a priori* groups (i.e., stand type) regarding individual species affinity, or faithfulness, based on species abundance scores in particular groups (Dufrêne and Legendre, 1997; McCune et al., 2002). Perfect "faithfulness" is defined as always being present in the identified group and being exclusive to that group (McCune et al., 2002). The ISA calculation is composed of PC-ORD© (McCune and Mefford, 1999) computations of relative abundance and a relative frequency of each lichen species by group, then multiplying those scores to give a final indicator value. The statistical significance of the maximum indicator value for each species is tested by 5000 runs of a Monte Carlo randomization procedure. The resulting p-value represents the probability that the calculated indicator value for any species is greater than that found by chance. Output includes the group for which the maximum indicator value is found, the indicator score for that group, and the associated p-value for each species. Results were considered significant for ISA where $p < 0.05$.

Finally, we combined lichen species showing preference for aspen substrates (*Xanthomendoza fulva, Xanthomendoza galericulata, Phaeophyscia nigricans*) using ISA (Dufrêne and Legendre, 1997) in previous work (Rogers et al., 2007a) with *Physcia tenella*, which was only found on aspen in the present study, into an "aspen index score" using the following formula:

$$\text{Aspen index score} = 100\left(\frac{S_{\text{asp}}}{S}\right)$$

where S_{asp} is the sum of plot abundances for the four indicator species and S equals the total of all abundance scores for each plot. The aspen score had a minimum of zero, indicating none of these species was present, and a maximum of 100, indicating that only these species were present and all in the highest abundance class. Index scores could be useful as a metric of aspen community health as we track aspen-dependent species through successional stages. If the index is successful, it should produce declining scores with advancing conifer succession. We tested this assumption using a one-way ANOVA test for differences in the effect of succession classes on aspen index scores.

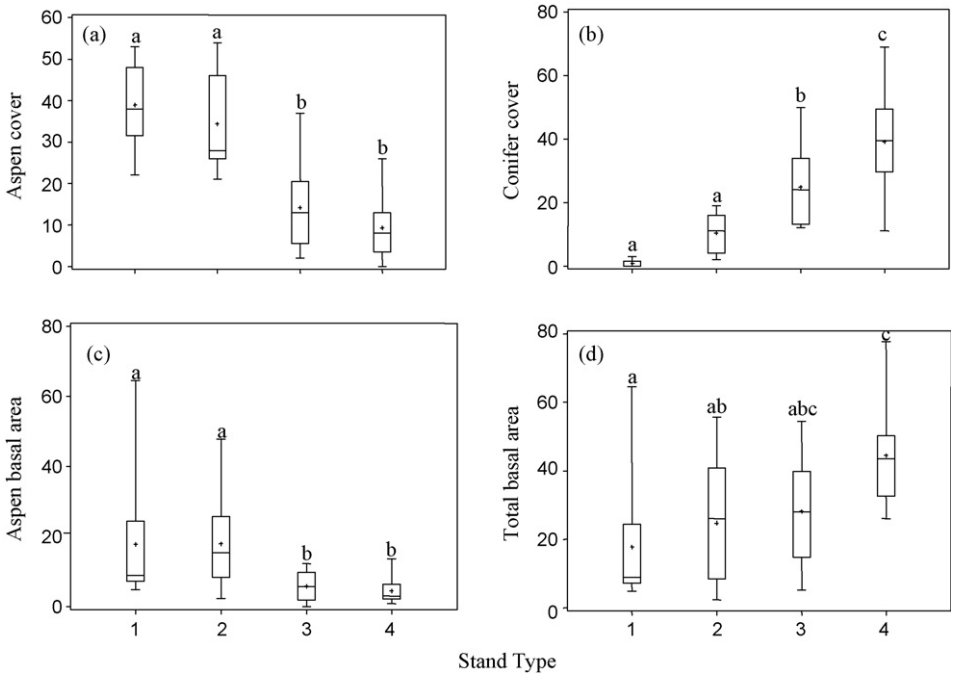

Fig. 2. Stand structure trends over four successional classes (stand types) for: (a) aspen cover, (b) conifer cover, (c) aspen basal area (m^2), and (d) total basal area (m^2). The "+" inside the box symbolizes the mean by stand type, while bottom and top of the box represents the 25th and 75th percentiles, respectively. The horizontal line inside each box is the median value. Whiskers represent extreme observations (variance). Bars with the same letter represent quantities that are not significantly different (Tukey–Kramer, $p < 0.05$).

4. Results

4.1. Stand characteristics

We stratified our sample into broad succession groups based on estimation of aerial coverage of aspen prior to field visits. Field measures fell within the group cover parameters (Table 1) 70% of the time. However, where cover estimates appeared to be inaccurate for the stand type, basal area measurements did comply with our stand types. This offsetting of objective measures (cover and BA) led us to maintain the original groupings based on the assumption that cover measures near heterogeneous stand edges had produced erroneous results (when compared to aerial photo estimates and plot-center BA) in about 30% of the plots.

Overall, we believe our groupings adequately capture successional trends in basal area, tree cover, and regeneration. Aspen cover (ANOVA, $F = 26.77$, $p < 0.0001$) and aspen basal area declined (ANOVA, $F = 5.13$, $p = 0.004$), while conifer cover (ANOVA, $F = 28.81$, $p < 0.0001$) increased with stand type progression (Fig. 2a–c). Total basal area (Fig. 2d) also increased from pure through remnant aspen stands (ANOVA, $F = 5.80$, $p = 0.002$). These figures illustrate the largest differences between invaded and declining stands (stand types 2 and 3) are more evident in cover estimates than basal area measures. Both seedlings and saplings reflect the same basic trend, although most relationships are statistically weaker. The number of aspen seedlings tallied was not correlated with conifer cover ($r = -0.16$, $p = 0.28$), but was positively correlated with subalpine fir seedling counts ($r = 0.55$, $p < 0.0001$). The strongest correlation among regeneration measures was between conifer cover and aspen saplings ($r = -0.52$, $p = 0.0002$), indicating a marked decrease in aspen sapling survival as conifers invade and eventually dominate stands.

Sample plots were located on slopes from 3% to 55%, with the average slope being 24% (13°). Mean plot slopes increased with stand type, meaning remnant aspen stands were more likely to be on steeper slopes than pure aspen. The average slope was 30% for remnant stands and 20% for pure aspen; invaded and declining stands averaged 24% and 25%, respectively. As stated earlier, we chose sample locations from all aspects except the south (135–225°). Of the 47 sample plots, most stands were on north aspects (22), followed by west (15), and east (10). Pure aspen were predominantly found on east and west aspects (5 each), while declining and remnant stands were found mostly on north aspects (9 and 7, respectively) and fewer on west slopes (2 and 5, respectively). Invaded stands were evenly distributed among north (4), east (4), and west aspects (3).

Stand age was not significantly different among stand types (ANOVA, $F = 0.24$, $p = 0.87$), even though there was a slight overall advance in mean stand ages from pure (87) to remnant (89) aspen. When we removed three locations where pure or invaded stands were long lived (ages 156, 132, 127) for this area—i.e., those perhaps not meeting our overarching goal of a seral aspen sample—the stand age–stand type relationship clearly improved, but still was not statistically valid (ANOVA, $F = 3.59$, $p = 0.06$). Stand age was not related to lichen species richness (ANOVA, $F = 1.16$, $p = 0.29$) or total lichen abundance (ANOVA, $F = 0.43$, $p = 0.52$).

4.2. Lichen species diversity and abundance

Twenty-four lichen species (γ diversity) and a single specimen identifiable to genus only were tallied on the 47 plots in our study. Additional diversity statistics are $\alpha = 10.66$ (S.D. = 2.38) and $\beta = 2.5$. Most species were either cosmopolitan (multiple substrates) or found only on associated conifer species (Table 2). Fifty-four percent ($N = 13$) of lichen species found were on aspen substrates, though most of these were also found on adjacent conifers. Two species were confined to aspen substrates and a single occurrence of *Physconia isidiigera* was found on the upland Scouler willow. Three species (*Physcia adscendens, Xanthomendoza montana, X. galericulata*) were sampled on every plot ($N = 47$) in our study area, and two others, *Melanelia elegantula* ($N = 45$) and *X. fulva* ($N = 45$), were located on most plots. The minimum number of lichen species sampled on a plot was six and the maximum was 16. Lichen abundance class score averaged 27.45 (S.D. = 5.25) for all plots, with a minimum score of 16 and a maximum of 38.

Lichen species richness (ANOVA, $F = 17.31$, $p < 0.0001$) and abundance (ANOVA, $F = 16.18$, $p < 0.0001$) increased from pure aspen through remnant stands (Fig. 3a and b). The aspen index declined (ANOVA, $F = 14.32$, $p < 0.0001$) from pure to remnant aspen stands (Fig. 3c). Correlations between conifer cover and species richness ($r = 0.70$, $p < 0.0001$), total abundance ($r = 0.73$, $p < 0.0001$), and aspen index score ($r = -0.61$, $p < 0.0001$) were all strong. Relations between stand type and conifer cover so closely parallel each other (Table 3, $r = 0.81$, $p < 0.0001$) that further analysis focuses on stand type groups, though conifer cover (and aspen cover conversely) describe the same trends. Because of concern that the aspen index score was overly influenced by fewer species in pure aspen stands and washed out by greater diversity in conifer forest types, we ran an additional ANOVA test on absolute abundances for the four index species against stand types. Again we found significant declines in combined abundances of these species with increasing succession classes ($F = 4.12$, $p = 0.0118$).

Table 2
Frequency[a] of epiphytic lichen species[b], by primary tree substrate groups, in the Bear River Range, Idaho and Utah

Multiple substrates[c]	Conifer	Aspen	Minor substrates
Melanelia elegantula (45)	*Bryoria fuscescens* (13)	*Phaeophyscia nigricans* (38)	*Physconia isidiigera* (1)
Melanelia exasperatula (33)	*Candelaria concolor* (12)	*Physcia tenella* (24)	
Melanelia subolivacea (39)	*Imshaugia aleurites* (1)		
Physcia adscendens (47)	*Letharia columbiana* (4)		
Physcia biziana (10)	*Letharia vulpina* (14)		
Physcia dimidiata (8)	*Parmelia sulcata* (1)		
Physciella chloantha (13)	*Parmeliopsis ambigua* (3)		
Xanthomendoza fallax (32)	*Phaeophyscia orbicularis* (1)		
Xanthomendoza fulva (42)	*Usnea hirta* (1)		
Xanthomendoza montana (47)	*Usnea lapponica* (24)		
Xanthomendoza galericulata (47)	*Usnea* spp. (1)		

[a] Numbers in parentheses represent total frequencies of species on all plots ($N = 47$).
[b] Nomenclature follows Brodo et al. (2001), except for recent revisions of *Xanthomendoza* (formerly *Xanthoria*) Lindblom (2004, 2006).
[c] Multiple substrates include lichen species found on two or more of the substrate groups shown. Minor substrate species include (in order of prominence): *Acer grandidentatum, Salix scouleriana, Amelanchier alnifolia, Prunus virginiana, Cercocarpus ledifolius,* and *Juniperus scopulorum.* Infrequent occurrence (<10% of total frequency) on minor substrates did not remove species from their major group affiliations (i.e., conifer or aspen).

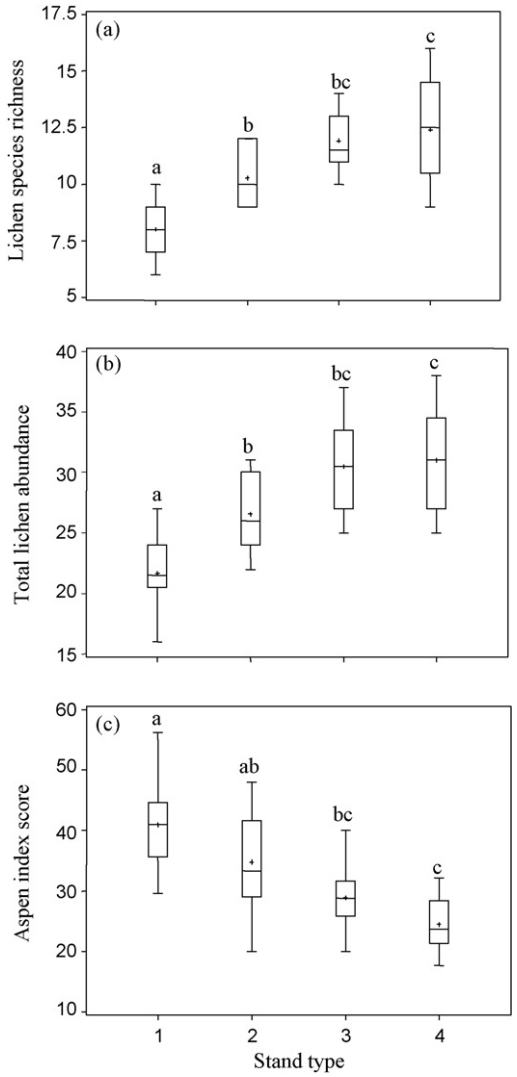

Fig. 3. Lichen community trends over four successional classes (stand types) for: (a) lichen species richness, (b) total lichen abundance, and (c) aspen index score. The "+" inside the box symbolizes the mean by stand type, while bottom and top of the box represents the 25th and 75th percentiles, respectively. The horizontal line inside each box is the median value. Whiskers represent extreme observations (variance). Bars with the same letter represent quantities that are not significantly different (Tukey–Kramer, $p < 0.05$).

Table 4 presents the results of ISA for those species tallied on more than a single plot in our study area. Only five species were significant as "indicator species" for particular succession groups based on corresponding maximum indicator groups and *p*-values. Of these, *X. galericulata* is the only lichen that displayed faithfulness to aspen forest types (either group, pure or invaded). The other four species showed preference for declining (*Melanelia exasperatula* and *Usnea lapponica*) or remnant (*Bryoria fuscescens* and *Letharia vulpina*) stands (Table 4, Fig. 4). Three of four of these species preferring advanced succession forest types were fruticose. No fruticose species were tallied throughout the study on aspen stems; thus it follows that none exhibited faithfulness for aspen forest types. Of the remaining three species used in calculation of aspen index scores, *P. nigricans*, *X. fulva*, and *P. tenella*, none displayed significant preference for a particular aspen type (Table 4). Trends across stands types for each species that occurred more than once in the study area are given in Fig. 4. Though these bar charts do not carry the statistical rigor of ISA (Table 4), they do provide an overview of species high and low points as succession advances. For example, we see that *P. nigricans* and *X. fulva* appear to drop in remnant aspen forests and several species begin with relatively low presence in pure stands, then level off as conifers appear (Fig. 4).

4.3. Lichen colonization of aspen

Both casual observation and measurement results suggest that most lichen colonization of aspen takes place on scars found on primary stems and branches. Only 0.24% of lichens on aspen were located on smooth bark based on cover estimates across our study area. Our prediction was that increasing damage may lead to further bole scarring, resulting in greater lichen habitat on aspen at the stand-level. We tested whether there was a relationship between amount of aspen stem damage and stand age (see Hinds, 1985) and succession classes. While we found no relationship between stand age and stand type (see above), or between percent of aspen damage and stand type ($F = 0.38$, $p = 0.76$), we found moderately strong correlations between percent of the aspen bole scarred and stand age ($r = 0.31$, $p = .04$) and percent of scars colonized and stand type ($F = 3.37$, $p = 0.03$). Lichen species richness was not correlated with percent damage ($r = -0.13$, $p = 0.42$) and percent of aspen bole scarring ($r = 0.11$, $p = 0.47$). Moderately strong correlations were found between total lichen abundance and level of lichen colonization of scars ($r = 0.32$, $p = 0.04$) and smooth bark ($r = 0.33$, $p = 0.03$). However, smooth bark colonization, at 0.24%, was very low overall compared to bark scar colonization levels (15%).

5. Discussion

5.1. Successional trends from aspen to conifer cover

Due to a dry climate, epiphytic lichen diversity is relatively low in the Southern Rockies Ecoregion as compared to other US regions (Ambrose et al., 2005). Even within Idaho, the Southern Rockies Ecoregion averages only 7.3 epiphytic lichens in forest stands, while monitoring sites in the moister Central and Northern Rockies average 8.1 and 12.2 species, respectively (Neitlich et al., 2003). Similar results were found for the Utah portion of the Southern Rockies (Keyes et al., 2001), though data in that study were not averaged at the plot-level as was done in Idaho. However, summaries at regional scales may be incomplete. Lichen diversity

Table 3
Pearson correlation coefficients (*r*) for key variables describing relationships between lichen communities and succession in aspen forests[a]

	Aspen cover	Conifer cover	Stand type	Species richness	Total lichen abundance	Aspen index score
Aspen cover	–	−0.7168	−0.7773	−0.6757	−0.6609	0.6203
Conifer cover		–	0.8140	0.7031	0.7277	−0.6142
Stand type			–	0.7147	0.6945	−0.7051
Species richness				–	0.9565	−0.6731
Total abundance					–	−0.6345

[a] $N = 47$ plots. All correlations were significant with $p < 0.0001$.

Table 4
Indicator species analysis values for species[a] tallied by maximum score group[b]

Species	Maximum score group	Indicator value	Indicator values from randomization		
			Mean	Standard deviation	p^*
Bryoria fuscescens	4	46.3	16.5	5.83	**0.0010**
Candelaria concolor	3	17.5	15.8	5.70	0.3340
Letharia columbiana	4	9.8	10.1	5.35	0.5574
Letharia vulpina	4	30.6	16.9	5.64	**0.0246**
Melanelia elegantula	4	27.4	27.0	0.92	0.3020
Melanelia exasperatula	3	33.9	25.5	3.82	**0.0276**
Melanelia subolivacea	2	30.3	26.8	2.63	0.1722
Parmeliopsis ambigua	4	11.1	8.7	5.57	0.4598
Phaeophyscia nigricans	3	22.7	27.1	3.24	0.9536
Physcia adscendens	3	26.4	26.0	0.64	0.2414
Physcia biziana	4	12.6	14.5	5.80	0.6158
Physcia dimidiata	4	11.1	13.2	5.83	0.6394
Physcia tenella	2	19.2	22.1	5.13	0.6952
Physciella chloantha	2	11.6	16.4	5.76	0.7870
Usnea lapponica	3	38.7	21.9	4.96	**0.0042**
Xanthomendoza fallax	4	24.6	25.1	4.04	0.5104
Xanthomendoza fulva	1	28.5	27.2	1.98	0.3050
Xanthomendoza montana	3	26.0	26.2	0.65	0.8210
Xanthomendoza galericulata	1	27.8	26.2	0.68	**0.0150**

[a] Single-occurrence species have no value as indicators; therefore, they are not shown here.
[b] Maximum score group = stand types: 1 = pure aspen, 2 = invaded, 3 = declining, 4 = remnant.
[*] Significant *p*-values are shown in **bold type**, denoting lichen species preference for particular stand type groups.

is highly influenced by both macro- and micro-scale moisture gradients. Locally, elevation presents the most obvious moisture gradient, so we would expect lichen diversity to parallel increased precipitation and decreased evapotranspiration patterns associated with increasing elevation. The current study limited elevational variability in order to focus specifically on aspen stand dynamics.

Without disturbance, aspen stands in this area are generally susceptible to increased encroachment by fir, spruce, Douglas-fir, and lodgepole pine (Mueggler, 1988). The mid-elevation belt sampled here was believed to comprise a locally optimum zone of aspen growth and, as southern aspects were excluded, a landscape prone to invasion by competing conifers. Areas at moisture, elevation, or geographic limits of aspen would be expected to display atypical successional patterns and perhaps support uncharacteristic lichen communities.

Pure, invaded, declining, and remnant aspen groups in this study were designed to mimic classic forest succession patterns. Recorded basal area and cover of either aspen or conifer, for any particular site, were better predictors of successional class that stand ages. This seems logical given the fact that where different site conditions prevail stands will reach these successional stages on a varied time scale. Having said that, we found a generalized pattern of correspondence between age and stand type when more persistent aspen stands were removed from the dataset. The largest differences in aspen cover were between invaded and declining stand types, which also constitute the difference between changes in forest types (i.e., plurality of tree cover). The theme of a "tipping point" between aspen and conifer forest types was explored in previous work conducted at a regional scale by Rogers (2002). He concluded that condition and presence of regenerating conifers in aspen stands were the strongest factors in predicting change to conifer plurality. Though not measured specifically, it was apparent that tree species diversity in the current study also increased along the successional gradient. A telling pattern here was the decline in aspen sapling survival with increasing conifer invasion. While aspen suckers may continue to emerge within small canopy openings, their proliferation becomes increasingly limited without larger disturbance. Survival of aspen regeneration in conifer-dominated stands is often low due to increasing resource limitations and the well documented impacts of ungulate browsing (Baker et al., 1997; Hessl and Graumlich, 2002; Kay and Bartos, 2000; Ripple et al., 2001). Moreover, reduced aspen cover has resulted in limitations on further asexual reproduction: the fewer healthy trees above ground, the less likely new suckers will emerge either on a continuous basis or in a flush following disturbance (Shepperd et al., 2006).

5.2. The lichen community in aspen forests

Twenty-four epiphytic macrolichens (γ diversity) were tallied. Four of these species occurred only once. Lichens that occurred rarely were of little value in terms of analysis, though it is useful to note their presence for future comparison. A mean species richness per plot (α diversity) of 10.66 was greater than found in a statewide inventory of Idaho (9.2) (Neitlich et al., 2003), but community turnover (β diversity) was much higher in their work (8.2) than in this study (2.2). Our work, covering a much smaller geographic area, was expected to have lower β diversity due to relative limitations in distance, elevation, and substrates. For comparison, the Idaho-wide study yielded a γ diversity of 75 epiphytic macrolichens (Neitlich et al., 2003).

One species that was not collected in our previous tree-level survey (Rogers et al., 2007a), but was common here, is *P. tenella*. It is possible we missed this species due to potential confusion with the ubiquitous *P. adscendens* (McCune and Geiser, 1997). Because this species was only located on aspen substrates it was added to the list of species shown to be consistent indicators of aspen communities (Rogers et al., 2007a) and used as a component of the aspen index score.

Total lichens tallied here contrasts with species diversity documented by a study of aspen and Douglas-fir in southwestern Idaho (Martin and Novak, 1999). They found a total of six macrolichens in their study, and only one species (*Xanthoria ulophyllodes*) exclusive to aspen. Work on European aspen (*P. tremula*) in Sweden describes a much broader lichen community, consisting of a wide variety of foliose, fruticose, crustose, and cyanolichens species (Hedenås and Ericson, 2000). While broad differences might be expected in aspen types between continents, even within the same region there apparently is enough contrast in

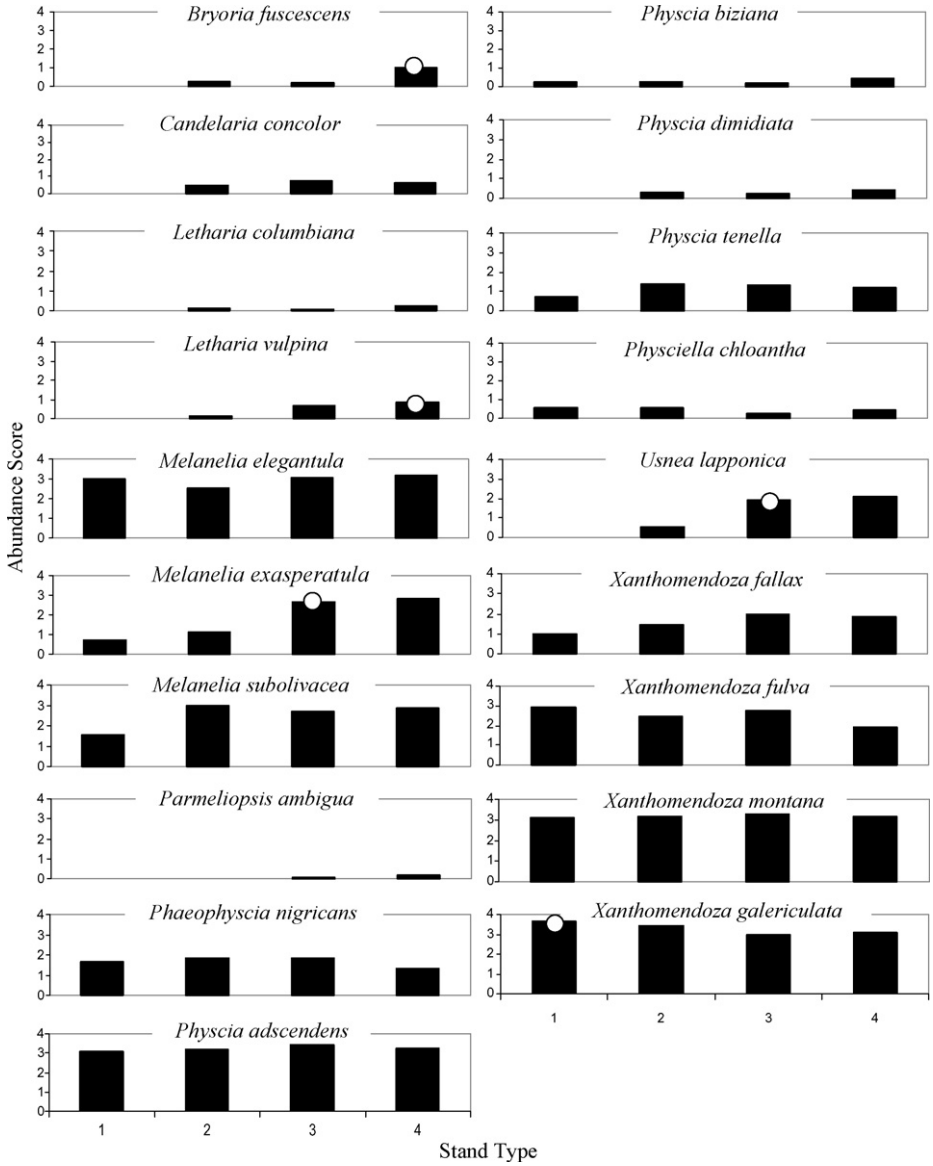

Fig. 4. Bar charts of lichen species occurring multiple times in the study area. Bars are average abundance scores for species by stand type. White circles on some bars denote significant ($p < 0.05$) preference by species for stand types in indicator species analysis (see Table 4).

moisture conditions to facilitate disparity in lichen communities. Martin and Novak's (1999) study sites were in the same elevation range as those found here, but although they do not give precipitation data they do refer to both of their study locations as being "dry, rocky soil supporting *A. tridentata*"—a nominal moisture distinction from our predominantly moister mollisol, forb, and non-*A. tridentata* stands. In our work, two pure aspen stands with the fewest lichen species ($N = 6$) equaled Martin and Novak's (1999) total diversity of macrolichens in drier mixed Douglas-fir aspen stands.

Another trend found in the composition of lichen species in this study was the clear preference for conifers by fruticose species (*Bryoria, Letharia, Usnea*). No fruticose species were tallied on aspen substrates here, nor by Martin and Novak (1999). In addition to their use by wildlife for food and nesting (Rosentreter, 1995), fruticose lichens are among the most sensitive to air pollution regionally (Neitlich et al., 2003). In contrast, genera common on aspen substrates, like *Physcia* and *Xanthomendoza*, appear to react favorably to nitrogen-based pollutants and air-borne dust particles (Rosentreter, 1990; Jovan and McCune, 2006). The presence of both pollution intolerant and tolerant species in aspen forests suggests linkages to local air quality patterns. Qualitatively, we noted a paucity of pollution sensitive lichens and an abundance of several tolerant "cosmopolitan" species.

5.3. The effects of aging stands and damage on lichen habitat

One of our objectives was to better understand the relationship between aging stands, stem scarring, and lichen richness and abundance. First we examined the cause, amount, and percent lichen colonization of aspen stem scars in relation to stand age. There was a nearly exclusive lichen preference for scarred portions of aspen stems versus the dominant smooth bark. Percent of aspen damage was not only lower in our study (31%) than statewide levels (45%) (Keyes et al., 2001), but could not be directly related to the age of stands. We found that stand age was positively correlated to percent of bole scarring, and that there was a moderate positive relationship between conifer encroachment and the percent area of scars on aspen that have been colonized by lichens. Even so, overall (grand mean) levels of aspen scar

colonization are only 15%. Additionally, results indicate no relationship between species richness and scarring, but a moderately strong correlation to total abundance. While these results are informative, they were confounded by the significant presence of lichen species that occurred only on conifers.

Ample scarring (habitat) occurred on aspen, regardless of amounts and types of damage, to allow for the level of lichen colonization recorded. Several sources of scars were not recorded as "damage" under our methods. For example, many stem scars originate at former branch junctions and aspen branches in the lower crown commonly die from upper crown shading. Other sources of stem scarring are healed over cankers and animal browsing and rubbing (Hinds and Krebill, 1975) that were not recorded as active damages here. Hinds and Krebill (1975) attributed most of this scarring to foraging by elk (*Cervus elaphus*) and moose (*Alces alces*), plus wounds initiated under the winter snow pack, which may reach three meters, by chewing of voles (*Microtus longicaudus*). Aspen are also frequently scarred by humans near recreation sites (Shepperd et al., 2006). Finally, very old aspen may have fissured or roughed bark that accumulates under normal conditions in the largest diameter ramets. Though aspen accumulation of lichens seems to be associated with aging trees and their accumulated scars, we were unsuccessful in linking this trend to specific damage agents.

5.4. Lichen community change over time

Forest succession groups may be viewed as a surrogate for temporal change in aspen-associated landscapes. Succession from one overstory tree species to a more diverse cover apparently leads to increase epiphytic lichen diversity. When the presence of a particular substrate decreases then dependent species are expected to decline, as was demonstrated by the aspen index score along the gradient from pure to remnant stands. Likewise, we saw a strong relationship between aspen basal area per hectare and presence of aspen lichen specialists. However, as discussed earlier, confounding factors like scarring levels and colonization densities suggest further complexity.

Overall, quaking aspen provides a limited substrate for macrolichens compared to conifer cohorts. We suspect this difference is primarily related to the abundance of smooth bark—in contrast to conifer stems and twigs—which is less hospitable to lichen colonization. We are aware, however, that other physiological factors not explored here, such as bark pH, bark peeling, texture, or aspect, may also play a role in colonization and persistence (Martin and Novak, 1999). For example, European aspen generally possesses a rougher bark and a more diverse lichen flora (Hedenås and Ericson, 2000). In earlier work, we used ISA to assess differences in lichen faithfulness to aspen and conifer substrates (Rogers et al., 2007a). Three species, *P. nigricans*, *X. fulva*, and *X. galericulata*, demonstrated a preference for aspen. In the present study we found that only *X. galericulata* displayed exclusive preference for aspen *forest types*. The difference in the two studies is that Rogers et al. (2007a) examined individual tree faithfulness to lichens, while this study focused on whole communities in succession classes. While Rogers et al. (2007a) were confined by individual stems along transects, here we sampled a greater diversity of tree species, tree forms, and microhabitats within a larger plot area. In sum, ISA results at the community-level reflected a larger number of factors and samples so we were not surprised to see fewer indicator species at the stand-level versus the tree species-level.

We developed an aspen index score comprised of species favoring aspen substrates to test for differences in succession classes (i.e., change over time). A clear trend depicting declining aspen index score with advancing succession contrasted with overall species diversity and abundance increases. We cannot attribute this pattern solely to concurrent declines of total aspen ramets with advancing succession, as scarring on individual stems increased with encroachment. While abundant lichen habitat is available in conifer-invaded forests and the density of colonization appeared to increase, fewer aspen specialists proliferated. Perhaps there is a mechanism at work here that exercises a 'carrying capacity' for sparsely colonized aspen. Regardless of process, it is clear that the surrounding forest community is simultaneously attracting greater overall lichen diversity while limiting conditions for aspen specialists. Thus, a broader theme emerges: a caution against using total species richness as a sole metric in changing landscapes where particular habitat specialists may provide a better index of target communities.

5.5. Lichens as indicators of community change

Ecologists have long debated the notion of keystone species. Recently this term has been applied to aspen in the western US (Campbell and Bartos, 2001; Manley et al., 2000). Ripple et al. (2001) traced the trophic interactions of wolves, elk, and aspen survival in Yellowstone National Park emphasizing the critical nature of carnivores in regulating large ungulates that browse on aspen regeneration. Without successful regeneration following large-scale disturbance, future aspen forests, dependent on vegetative suckering to persist, will dwindle on the landscape. Here we discussed the dependence of species, namely epiphytic lichens, on aspen forests: effectively an added trophic level. Aspen likely provide habitat for many floral and faunal species. Widespread human activities, such as fire suppression, game and livestock regulation, and climate warming, have and will continue to alter these communities (Logan et al., 2007; Rogers et al., 2007b). We feel that lichen communities, including derived metrics such as an aspen index score, may be used to monitor forest conditions at large.

In the successional gradient from pure aspen to conifer, vascular plant diversity and abundance decreases as conifer encroachment advances (Mueggler, 1985). Yet it is relatively difficult to monitor the large number of understory plants (versus lichens) dependent on aspen cover. Epiphytic lichens appear to increase with succession, unless we focus on the aspen-dependent species comprising the index score. When we look at all species in terms of succession classes, some lichens favored succession endpoints, while others (e.g., *Candelaria concolor, M. exasperatula, M. subolivacea, P. tenella, U. lapponica*) showed preference for aspen-conifer transition stages (Fig. 4, stand types 2 and 3).

A generalized model depicting aspen forest change over time is shown in Fig. 5. Numerous biotic factors influence stand development and are prominent during different successional periods (Shepperd et al., 2006). We have shown here that along a successional trajectory, aspen-dependent lichen species will decline with aspen overstory. Likewise, we expect old growth-, conifer-, or shade-dependent species to follow a similar trajectory as the conifer canopy. If we wish to manage for particular aspen conditions we can expect to influence lichen species populations favoring those stages. Of course, natural biotic factors, or management surrogates, may influence successional stages (Fig. 5) to achieve varied overstory and epiphyte goals.

This successional model provides a way to forecast the trajectory of aspen-dependent species in stands at various stages and across mosaics of aspen and conifer forests. Key elements that correspond to succession stages outlined above are preservation of natural disturbance cycles (declining and remnant stands), reduction of livestock and wildlife browsing on aspen suckers

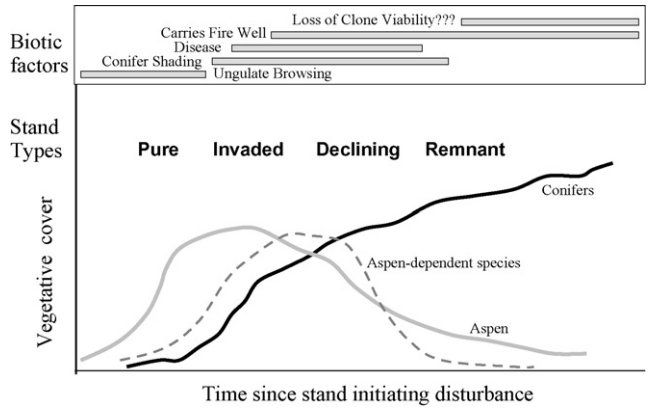

Fig. 5. A generalized model of aspen succession in forests prone to conifer encroachment in the Rocky Mountains, USA. Several biotic factors affect stand development at various stages in the life cycle of aspen (top). Stand types addressed in this study are superimposed onto the time sequence presented (middle). The dashed line, representing the hypothesized trajectory of aspen-dependent species such as epiphytic lichens, peaks after pure aspen stands are established and plunges prior to mortality of remnant aspen. The transition period from aspen to conifer overstory dominance—between invaded and declining stands—depicts a "tipping point" for predominant disturbances (biotic factors) and aspen-dependent species.

(pure and invaded stands), and maintenance of an adequate growing environment (all stand types). This final point argues for balance in successional stages, while avoiding exclusive management toward the extremes of pure and remnant stands. Preservation of ecosystem functions, such as historical disturbance regimes and native browsing levels, is important to maintaining balance across forest mosaics (Rogers et al., 2007b). Management implications of these ideas are addressed further by Shepperd et al. (2006). Our purpose here was to point out changes in epiphytic lichens associated with conifer encroachment in the southern Rocky Mountains. The pattern described here for aspen index species may apply equally to other aspen-dependent plants and animals. For example, aspen dependence by particular birds (Turchi et al., 1995), mammals (DeByle, 1985), and vascular communities (Mueggler, 1988) have already been demonstrated and deleterious effects from advancing succession on these species are commonly implied.

In a broader context, we have seen that many factors affect the aspen community on which lichens depend. Historic management and climatic factors have often conspired against aspen proliferation in the form of reduced wildfire, herbivory, human interventions, and moist climates (Rogers et al., 2007b). Furthermore, future climate warming scenarios predict dire consequences for quaking aspen if exotic species such as gypsy moth (*Lymantria dispar*) are able to penetrate montane environments (Logan et al., 2007). Though these factors are not universal, when they combine we may expect parallel declines in aspen-dependent species. Questions of species loss are difficult to assess at single locations or by stand-level studies. The condition of the wider forest mosaic, occurring at many successional stages in the case of aspen, gives us the clearest picture of individual species or functional group (e.g., aspen indicator species) conditions. We feel a focus on preserving forest structure (i.e., succession stages) and ecosystem function (i.e., disturbance regimes) will improve the prospects for the future of aspen and its community of dependent species.

6. Conclusions

Landscape-level studies are needed to capture the breadth of species variations relating to environmental conditions and cover changes. In this paper we have described how epiphytic lichen communities change with advancing succession of aspen forests in the relatively dry southern Rocky Mountains. We found 24 epiphytic macrolichens in mid-elevation aspen-associated forests of the Bear River Range. General trends showed increased lichen diversity and abundance, while simultaneously tracking a decrease in those species dependent on aspen. Indicator species analysis determined *X. galericulata* as being the most aspen-dependent species at the stand-level. We presented an aspen index score based on dependent lichen species and suggest its further utility for monitoring and post-treatment recovery efforts as a surrogate for greater community diversity and health. Simple species richness measures may not provide the most useful method for assessing landscape health, most notably where systems are dependent on seral cover types such as in aspen communities.

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