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Quantifying the consequences of conifer succession in aspen stands: decline in a biodiversity-supporting community

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Abstract Quaking aspen (*Populus tremuloides* Michaux) stands are important for biodiversity in conifer-dominated forest landscapes. Our goal was to quantify the consequences of conifer succession on understory diversity and litter quality, as well as associated changes in aspen stand condition. We studied aspen stands on national park land in the transition zone between the northern Sierra Nevada and southern Cascade mountain ranges. We field-measured ten metrics of aspen stand condition in 29 aspen stands. Along a gradient of increasing current conifer cover, we observed decreases in herbaceous species diversity and richness and an increase in forest floor O horizon depth. We interpreted aerial photos from 1952 and 1998 to determine whether directional changes in conifer cover had occurred in the stands over the past half century, and used regression modeling to associate succession with the observed range of aspen stand condition. From the period 1952 to 1998, we found that conifer encroachment occurred in half the sampled stands, with an average increase in conifer cover of 1 % a year. Aspen were persistent in the remaining stands. Stand cover dynamics and percent total canopy cover interacted to influence species richness, diversity, aspen sprouting, and litter quality. In stands with conifer encroachment, both understory species richness and diversity declined. Although aspen sprouting increased, aspen establishment declined and the relative mass of woody to fine soil litter increased.

Keywords California · Sierra Nevada · Cascade · Populus tremuloides

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Introduction

Quaking aspen (*Populus tremuloides* Michaux) contribute disproportionately to ecosystem functions and services such as increasing habitat heterogeneity, supporting biodiversity, and accelerating nutrient cycling rates (Legare et al. 2005; Stump and Binkley 1993). In the Sierra, surveys of intact aspen stands and adjacent meadow and conifer communities found that aspen and meadows supported significantly higher levels of plant species richness, diversity, and evenness than conifer communities, and that many species were unique to the aspen understory (Kuhn et al. 2011).

Potter (1998) observed that diversity in aspen stands in California is not just due to high numbers of species but also to high cover values for a relatively large number of species. High levels of species richness and unique species have also been recorded in aspen in montane stands in Colorado (Stohlgren et al. 1997).

Studies of forest processes under conifer and aspen canopies provide evidence for the processes driving high diversity in aspen stands. In stands dominated by aspen canopy cover, litter decomposition initially occurs at greater rates than in stands dominated by conifer cover (Maclean and Wein 1978; Prescott et al. 2000). Decomposition in forests is driven by litterfall, and rapid decomposition underneath aspen has been attributed to litter quality (Bartos and DeByle 1981; Legare et al. 2005; Stump and Binkley 1993). All litter has a pool of labile compounds that decompose rapidly, an intermediate pool representing cellulose, and a recalcitrant pool representing lignin (Adair et al. 2008). Aspen litter contains more labile forms of organic matter resulting in rapid decomposition and nutrient mineralization compared to conifer litter, which includes more woody material and a smaller pool of labile compounds (Taylor and Parkinson 1988). Due to the large proportion of fine litter inputs and rapid decomposition, aspen stands support a thin O horizon (3–4 cm) relative to conifer stands, consisting of accumulated highly decomposed plant materials (Jones and DeByle 1985). The initial quality of litterfall influences the composition of the microbial communities that become established in the litter, so that aspen and conifer stands support different microbial communities (Giardina et al. 2001).

Much of what is known about quaking aspen in the western USA comes from the Rocky Mountain region, where subalpine stands believed to date to the end of the last glacial period occupy thousands of hectares. However, in California, aspen is at the edge of its range and stands are small and isolated. Aspen stands occupy a small proportion (~1 %) of forests in the Sierra Nevada and Southern Cascades (Jones et al. 2005; Shepperd et al. 2006). In this region, many stands date to only 300 years of age due to recent volcanic activity. Stands occupy sites such as meadow edges, rock outcrops, riparian areas, and wetlands, and many stands are composed of one cohort that is periodically renewed, often interspersed with a few large conifers (Potter 1998; Shepperd et al. 2006).

Concern and debate about aspen succession to conifer in the Rockies has existed for many years (Kashian et al. 2007; Kay 1997). Aspen are clonal, relying on vegetative sprouting from the root system to maintain clones over the periods between successful seeding events. Stands initiate sprouts most successfully after a major disturbance such as fire, and occupy disturbed sites first through rapid sprout growth (Romme et al. 1997). In the Rockies, it has been shown that aspen persist over long time scales when the fire interval is short enough to regenerate aspen before it succeeds to conifer (Kashian et al. 2007). This growth strategy is not always successful though, due to the intolerance of aspen to shade and crowding. One mechanism for competition occurs when conifer seedlings establish first, under lower understory light conditions than aspen can tolerate. When disturbance does create light conditions favorable for aspen growth, conifers already occupy the site, leading to eventual conifer succession (Pierce and Taylor 2010).

While succession to conifer is a natural process, recent trends are influenced by human-mediated changes to fire intervals. Since fire suppression policy began in California in the early 1900s, shifts in forest structure towards increased densities of shade-tolerant conifer species have been documented (Beaty and Taylor 2001; Taylor 2000). It has been proposed that this shift is occurring throughout the entire range of mixed conifer forest, and the trend is consistent with forest structure trends in other western regions (Allen et al. 2002; Minnich et al. 1995). Browsing pressure is another risk factor because it suppresses aspen sprout recruitment (Jones et al. 2009; Kay and Bartos 2000). The ages of current aspen cohorts in California correspond with the end of intensive sheep grazing and the beginning of fire suppression management early in the twentieth century, underscoring the influence of management policies on aspen (Potter 1998).

Many stands in California are in a deteriorated condition defined by few mature stems and little or no regeneration (Jones et al. 2005). Root carbohydrate stores may be depleted from multiple years of browsing pressure on sprouts (Bartos 2000). Managers are concerned that when fire causes mortality in mature stems in deteriorating stands of aspen, successful sprouting may not occur if root carbohydrate stores are too depleted. These concerns are supported by findings that when fire does occur, stands with lower prefire aspen densities in the overstory produce fewer postfire sprouts (Smith et al. 2011). But although aspen risk factors are present, few studies have examined aspen stand successional trends in California (Di Orio et al. 2005).

This study follows recent work to quantify biodiversity differences between intact aspen and conifer stands (Kuhn et al. 2011). When aspen stand condition deteriorates, we expect that the key ecosystem services and functions that we expect of aspen also deteriorate. In this study, we focus on a suite of metrics to quantify both aspen stand and understory condition. Stand-scale indicator variables used previously to describe forest condition include tree diameter and age class distributions, native and exotic species richness and abundance, stand growth, and foliar and soil nutrients (Noss 1999; Rutters et al. 1992). We have adapted the indicator variable approach to quantify status and trend in aspen stand condition; but in this case, we are not using it for either rapid assessment or long term monitoring.

We measured current conifer cover in 29 aspen stands, and assessed current ecological condition with ten metrics representing aspen recruitment, understory plant diversity and richness, litter quality, and decomposition. We examined aerial photography for the stands to determine whether aspen succession to conifer had occurred in the past half century. We then evaluated associations between (1) the ten metrics and current conifer cover and (2) the ten metrics and the amount of conifer cover change over the past half century. We hypothesized that as conifer succession proceeds, the metrics representing the ecological values of aspen stands decline.

Materials and methods

Study area

Lassen Volcanic National Park (Lassen NP) is 42,900 ha in area and located in the transition zone between the northern Sierra Nevada and southern Cascade mountain ranges. Elevation ranges from 1,620 to 3,190 m on Lassen Peak, the southernmost volcano of the Cascade Range. The area experiences a Mediterranean-type climate; summers are dry with occasional thunderstorm events; winters are cold and wet with deep snowpack formation. Annual precipitation is spatially variable, with mean annual precipitation ranging from over 200 cm at the higher elevations of the southwest to less than 100 cm in the northeast, mostly occurring as snow (Davey et al. 2007). The dominant forest types within the elevation range containing aspen (1,620–1960 m) are typified by yellow pine (*Pinus ponderosa* and *Pinus jeffreyi*), lodgepole pine (*Pinus contorta*), and white fir (*Abies concolor*) at lower elevations, and red fir (*Abies magnifica*) at higher elevations. The three major sites of aspen occurrence within Lassen NP are characterized by different geologic disturbance histories that include the 1915 eruption of Lassen Peak, a cinder cone eruption in the mid 1700 s, and the last period of glacial retreat (Conlin 2010).

A stratified random approach was used to enroll 29 aspen stands in this observational survey. Aspen stand selection was stratified first by the three major sites of aspen occurrence, to account for differences in geologic disturbance history, and then by conifer cover class at the time of the study (<20, 20–40, 40–60, >60 % conifer cover) nested within site, so that the sample represented geologic disturbance and current conifer cover gradients at Lassen NP.

Field data collection

Field data collection occurred July to September during 2007 and 2008. All field data collection was based upon a modified Whittaker plot sampling design (Keeley et al. 2003). Plots were multi-scale, with a single main plot (300–1,000 m^2) comprising three to ten adjacent 100 m^2 plots. Each 100-m^2 plot included five 1-m^2 subplots within which understory percent cover by species and litter was measured. Species richness was recorded for each 100-m^2 plot using a standardized search effort (equal time). The range in the size of the main plot area was due to existing variability in aspen stand size. The smallest stands were only 300 m^2 in area, while the largest were much larger than the full 1,000-m^2 plot size. This multi-scale plot design allowed measurement of the species cover estimates required to calculate diversity, while ensuring the inclusion of locally rare species (Barnett and Stohlgren 2003). It also provided the flexibility in main plot size necessary to sample stands smaller than the standard 1,000-m^2 Whittaker main plot. We placed as many 100-m^2 plots as possible within each stand, up to a maximum number of ten plots (1,000 m^2). Many stands were small enough that the majority of the stand was included within the main plot.

For each stand, we recorded elevation, spatial (GPS) coordinates, slope, and aspect. Forest strata were delineated by stand in terms of canopy, intermediate, and understory, and the height of one representative tree from each stratum was measured. For each tree in the 100-m^2 plots, we recorded strata, diameter at breast height, and species. At the center of each 100-m^2 plot we measured percent overstory cover with a spherical densiometer and measured solar availability with a solar pathfinder. Deer browse on aspen sprouts was recorded as a categorical variable (neither/browsed/hedged) (Keigley and Frasina 1998). “Browsed” was defined as browse damage to current year growth, and “hedged” was defined as evidence of browsing on three or more shoots of current and previous year growth.

We measured ten stand condition metrics: aspen sprouting and aspen establishment; understory species richness and diversity; O horizon depth; total, fine, and woody litter C:N; the ratio of the masses of woody to fine litter; and litter decomposition (Table 1). Sprouting is defined as sprout density (aspen stems less than 1.4 m tall), and the basal area of aspen in the intermediate stratum was considered to be evidence of establishment. Aspen sprouting and aspen establishment, understory species richness and diversity, and O horizon depth were measured in all 29 stands. Due to laboratory resource constraints, litter quality (total, fine, and woody litter C:N; the ratio of the masses of woody to fine litter; and litter decomposition) was determined for samples from only 12 of the 29 stands. To ensure the subsample was representative of the full sample of 29 stands, we selected the 12 stands from the same stratified gradient of conifer classes (<20, 20–40, 40–60, >60 % conifer cover) as the full sample, so that stands representing high, medium, and low levels of conifer encroachment were included in the subsample.

Litter quality analysis

We composited three samples per 100-m^2 plot, and sorted woody litter, defined as twigs and bark greater than 1-mm diameter, from fine litter, to distinguish between relatively labile and recalcitrant organic matter pools. Samples were dried to a constant mass, and total mass of each fraction was determined. Percentage organic material and mineral soil was determined by loss on ignition for a 2-g subsample (Nelson and Sommers 1996). The ratio of the mass of woody to fine fractions was expressed as grams woody per cubic centimeter/grams fine per cubic centimeter. We analyzed a separate 3-g subsample of fine and woody litter fractions for mass of C and N by a combustion method (AOAC 1997).

The degree of litter decomposition was determined through extraction of hemic and fulvic compounds with a pyrophosphate color method (Soil Survey Staff 1999). This method provides an initial comparison of the degree of decomposition between samples; here, it was utilized to gauge whether differences in decomposition could be distinguished at the temporal and spatial scales of this study. We treated a subsample of 2.5-g fine litter

Table 1 Descriptive statistics for stand conditions observed for 29 stands surveyed on Lassen Volcanic National Park, CA

	Metric	Units	Mean	SE	Range
Plant (*n*=29)	Conifer cover	% cover	50	4	2–77
	Aspen cover	% cover	24	3	4–71
	Sprouting	Sprouts/100 m^2	52	8	3–127
	Establishment	m^2/ha	5.8	1.9	0.0–35.8
	Shannon Index		1.95	0.10	0.69–2.74
	Herbaceous species richness	number of species	31	2	11–54
	O horizon depth	cm	5	0.3	1–8
Litter (*n*=12)	Litter C:N	g C/g N	30.8	1.1	26.0–36.4
	Fine C:N	g C/g N	27.3	1.0	23.3–35.3
	Woody C:N	g C/g N	50.8	2.4	40.1–70.2
	Woody:fine mass	g woody cm^{-3}/ g fine cm^{-3}	0.26	0.03	0.11–0.50
	Decomposition	Munsell value	5.2	0.1	4.6–5.6

Litter quality indicators were measured for a subsample of 12 stands with a solution of 4 mL H_20 and 1 g sodium pyrophosphate decahydrate ($Na_4P_2O_7 \cdot 10\ H_20$). After 9 h, we extracted the solution and read the degree of darkness as "value" from the Munsell color notation with a colorimeter. The 1–10 scale represents dark (lower numbers representing more decomposed plant material) to light (higher numbers representing less decomposed plant material).

Photo interpretation

Aerial photo interpretation was conducted to calculate the direction and rate of cover change in aspen stands. Black and white panchromatic images (nominal scale 1:20,000), dated 1952 and 1954, were interpreted for all stands. The photos were rectified in ERDAS IMAGINE software, version 9.3.2. Recent aspen stand status was represented by grayscale Digital Orthophoto Quadrangle imagery from panchromatic black and white film, dated August and September 1998 (nominal scale 1:12,000).

We estimated historical and current percent aspen and conifer cover with Digital Mylar Cover Interpreter for ArcGIS version 9.x (Clark et al. 2004). We read aspen and conifer cover as ocular estimates from a circular buffer (diameter 28 m) around the field-collected GPS point from the center of the full Whittaker plot. The analysis was conducted at the scale of the full plot, rather than the 100-m^2 scale used for field measurements, due to detectability limits. The classification system had an interval width of 10 percentage points per class, and the class midpoint was recorded for each data point. To improve accuracy, we read additive estimates of percent conifer, aspen, and open cover for a total of 100 % cover in each plot. Stands were read in a randomized order, and identifying information was blocked out to ensure independence of cover estimates. Photointerpretation validation was conducted by regressing 1998 aspen and conifer cover values against the field-collected densiometer percent cover values for a sample of 12 sites.

Data analysis

We calculated species richness and the Shannon-Wiener index of diversity with PC-ORD4 (McCune and Mefford 1999) for each 100-m^2 subplot. Associations between current percent conifer cover and the stand condition metrics were evaluated for the 100-m^2 plots using linear mixed effects regression (Table 1) (Insightful Corporation 2001). The models were analyzed with current percent conifer cover as the predictor, stand as a random (group) effect, and the stand condition metric as the response variable. The inclusion of stand as a random effect accounted for variable Whittaker plot size. Assumptions of normality and homogeneity of variance were confirmed by evaluation of standard residual plots. Data were transformed if necessary. A p value of 0.05 ($p \leq 0.05$) was considered significant, and p values of 0.1 ($p \leq 0.1$) were noted to indicate possible trend.

To examine change in conifer and aspen cover, we calculated the difference in 1998 and 1952 percent cover values for all stands (Fig. 1). Because it appeared that two distinct dynamics were occurring, we assigned stands to two levels of a categorical variable, stand dynamic: "persistent aspen" and "increasing conifer" for subsequent analyses. The persistent aspen stands were defined as those with conifer cover change less than or equal to 10 %, and the conifer-encroached stands as those with conifer cover change greater than 10 %. Using this categorical variable, generalized least squares regression models were developed for each of the ten metrics of current ecological condition using a backwards stepwise approach, at the scale of the full Whittaker plot. The full variable set included stand dynamic, conifer cover 1952, conifer cover 1998, aspen cover 1952, aspen cover 1998, total cover 1998, and conifer change 1952–1998. Model selection was evaluated with Akaike's information criterion (Burnham and Anderson 2002). Plot size was evaluated as a covariable. The smallest p value for plot size was for fine C:N ($p = 0.22$), and therefore plot size was eliminated from the model. Data were transformed if necessary. Variance functions were employed in cases where heteroscadiscity was indicated by residual plots (Pinheiro and Bates 2000).

Results

Associations between current percent conifer cover and stand condition metrics

Herbaceous species richness, the Shannon-Wiener index of diversity, and O horizon depth were associated with current percent conifer cover ($p < 0.1$) (Table 2).

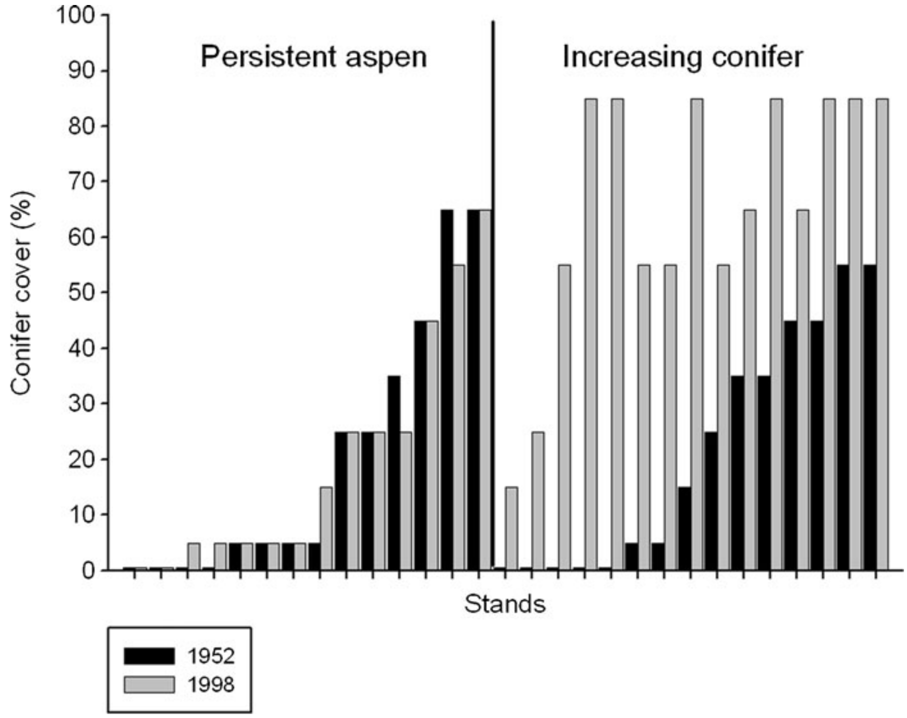

Fig. 1 Trends in conifer cover 1952–1998 by stand from photo interpretation. The persistent aspen category is defined as conifer cover change less than or equal to 10 % and increasing conifer is defined as conifer cover change greater than 10 %

For each 10 % increase in percent conifer cover, species richness decreased by one species, the Shannon index decreased by 0.01, and O horizon depth increased by 0.4 cm. Significant *p* values were

Table 2 Results for linear mixed effects regression analysis with stand condition indicator as the dependent variable, percent conifer cover as the independent variable, and stand as a random effect

	Metric	Units	Percent conifer cover coefficient	*p* value[a]
Plant (*n*=219)	Sprouting[b]	Sprouts/100 m^2	−0.03	<0.01*
	Establishment[c]	m^2/ha	−0.001	0.46
	Shannon Index		−0.01	<0.01*
	Herbaceous species richness	number of species	−0.09	<0.01*
	O horizon depth	cm	0.04	<0.01*
Litter (*n*=89)	Litter C:N	g C/g N	−0.003	0.92
	Fine C:N[d]	g C/g N	0.001	0.17
	Woody C:N[e]	g C/g N	0.0001	0.95
	Woody:fine mass	g woody cm^{-3}/ g fine cm^{-3}	0.0003	0.93
	Decomposition	Munsell value	−0.004	0.10**

All plant variables were measured in 29 stands surveyed on Lassen Volcanic National Park, CA. Litter variables were measured for a subsample of 12 stands. Transformed coefficients are reported

*p=0.01; **p=0.1 (Significant results at each *p* value)

[a] *P* value associated with each variable

[b] Sprouting was square root-transformed

[c] Establishment was square root-transformed

[d] Fine C:N was natural log-transformed

[e] Woody C:N was natural log-transformed

also found for aspen sprouting and decomposition, but small coefficients indicate that the trend was minor. The percentage of sprouts showing evidence of herbivory (browsing and hedging) ranged from 45 to 100 % for all stands.

Trends in conifer cover within aspen stands

While total cover increased in all stands over time as canopies filled in, we observed two distinct dynamics based on photointerpretation. Conifer encroachment occurred in 15 of the 29 aspen stands over the 50-year period (Fig. 1). In stands with conifer encroachment, conifer cover increased by an average of 1 % a year, while percent aspen cover declined by 0.3 % a year. By 1998, the mean value of percent conifer cover was 46 % higher in encroached stands than in persistent aspen stands (Table 3). Mean percent aspen cover was 29 % lower in encroached stands than in persistent aspen stands. Within persistent aspen stands, aspen canopy cover was 50 %, relative to a mean conifer canopy cover of 20 % (Table 3). In persistent stands, mean aspen sprouting was higher by three sprouts/100 m^2, establishment by 3.7 m^2/ha, species richness by 6 species, and the Shannon index by 0.3 units (Table 4). The C:N of the woody fraction and the mass of the woody to fine fractions were lower, and fine litter C:N and O horizon depth were apparently lower. In the validation of the photo interpretation, percent cover estimates regressed on field densiometer cover values were significant for both aspen and conifer cover (aspen: $p<0.001$, $R^2=0.69$, conifer: $p<0.001$, $R^2=0.73$).

Table 3 Comparison of conifer, aspen, and open cover values from photo interpretation at the two defined levels of stand dynamic (persistent aspen and increasing conifer)

	Stand dynamic	
	Persistent aspen[a]	Increasing conifer[b]
Number of stands	14	15
Sample %	48	52
Mean cover values (%)		
Conifer 1952	20 (6)	22 (6)
Conifer 1998	20 (6)	66 (6)
Conifer Δ/year	0 (0.03)	0.96 (0.1)
Aspen 1952	38 (11)	35 (9)
Aspen 1998	50 (10)	21 (7)
Aspen Δ/year	0.28 (0.14)	−0.32 (0.13)
Total cover 1952	62 (9)	61 (8)
Total cover 1998	80 (7)	92 (3)
Total cover Δ/year	0.39 (0.15)	0.69 (0.16)

[a] Persistent aspen is defined as conifer cover change less than or equal to 10 % and increasing conifer is defined as conifer cover change greater than 10 %.

[b] Mean (standard error)

Correlations between temporal trends in conifer cover and stand condition metrics

In multiple regression modeling, the significant interactions of stand dynamic by 1998 percent total cover indicated that stand dynamic influenced the relationship of stand condition metrics to percent total cover (Table 5). Stand dynamic by percent total cover interactions were found for species richness ($p=0.07$), the Shannon-Wiener index of diversity ($p=0.08$), and sprouting ($p=0.03$). For example, for every 10 % increase in percent total cover, the number of aspen sprouts increased by 16 sprouts/100 m^2 in encroached stands, but decreased by three sprouts/100 m^2 in stands with persistent aspen (Fig. 2a and b). For every 10 % increase in percent total cover, species richness decreased by less than one species in stands with persistent aspen, but decreased by five species in encroached stands (Fig. 2c and d). Establishment was associated with stand dynamic ($p=0.09$). In stands with conifer encroachment, the basal area of aspen in understory cohorts was less than in persistent stands.

O horizon depth was not significantly associated with either stand dynamic or percent total cover, although a positive regression coefficient indicated a trend of increasing O horizon depth in stands with conifer encroachment (Table 5). A significant relationship was not detected in the C:N ratio of the litter as a whole; however, a significant positive relationship between C:N of the woody fraction and percent total cover was observed ($p=0.02$), as well as a significant stand dynamic by percent total cover interaction for the ratio of woody to fine mass ($p<0.01$). For decomposition, the measured range of Munsell values was narrow (4.6–5.6) (Table 1), and was not significantly associated with stand dynamic or percent total cover.

Table 4 Descriptive statistics for stand condition indicators by stand dynamic (persistent aspen/increasing conifer)

	Metric	Units	Stand dynamic	
			Persistent aspen[a]	Increasing conifer[b]
Plant (n=29)	Aspen cover	% cover	28 (5)	20 (3)
	Sprouting	Sprouts/100 m^2	54 (11)	51 (10)*
	Establishment	m^2/ha	7.7 (3.0)	4.0 (2.4)**
	Shannon Index		2.1 (0.1)	1.8 (0.1)**
	Species richness	Number of species	34 (2)	28 (3)**
	O horizon depth	cm	4.5 (0.5)	5.2 (0.4)
Litter (n=12)	Litter C:N	g C/g N	30.1 (1.7)	31.3 (1.4)
	Fine C:N	g C/g N	25.6 (1.4)	28.5 (1.4)
	Woody C:N	g C/g N	49.0 (2.8)	52.0 (3.7)*
	Woody:fine mass	g woody cm^{-3}/ g fine cm^{-3}	0.24 (0.02)	0.28 (0.06)***
	Decomposition	Munsell value	5.3 (0.2)	5.2 (0.1)

Plant variables were measured in the field during summers of 2007 and 2008, from 29 stands in Lassen Volcanic National Park, CA. Litter variables were measured for a subsample of 12 stands

*p=0.05; **p=0.1; ***p=0.01

[a]Mean (standard error)

[b]Results that are significantly different between stand dynamics (from models in Table 5)

Discussion

Declines in stand condition with increasing conifer cover

Along the sampled gradient of current percent conifer cover (2–77 %), increasing conifer cover was associated with declines in aspen stand condition, as evidenced by decreased herbaceous species diversity and richness and increased O horizon depth (Table 2). Analyses based on recent field observations are limited to providing a snapshot of current conditions, without taking into account local stand history. Interpretation of aerial photos allowed us to conclude that percent conifer cover has increased in some aspen stands over the past 50 years; however, it is clear that variability is present in aspen dynamics within Lassen NP. Determination of the factors behind aspen persistence or conifer encroachment at each stand was outside the scope of this study; however, the observed variability in stand dynamics is similar to the Kashian et al. (2007) findings of localized areas of aspen persistence or increasing conifer, and supports the conclusion that the drivers of aspen dynamics are spatially and temporally heterogeneous across the landscape. Strand et al. (2009) provides an extended discussion of factors driving succession in aspen. Many aspen stands at Lassen co-occur with springs, frequently flooded streams, and wet meadows. Slower rates of conifer encroachment have been measured in these types of wet microsites (Strand et al. 2009).

Aspen and conifer dynamics

The interaction of stand dynamic and total cover on sprouting and establishment provides evidence of aspen deterioration with conifer encroachment. Aspen sprouting increased sharply in encroached stands (Fig. 2b), indicating that deterioration of mature aspen stems may be disrupting the hormonal inhibition of sprouting. In persistent aspen stands, where sprouting decreased with increased total cover, aspen may be directing energy into growth of existing stems rather than releasing sprouts. Only four of the 29 stands showed more than minimal establishment of aspen basal area in intermediate strata (three of the four were persistent stands), and the rest appeared to have a single age class structure. The low level of successful establishment, even though some stands are releasing large numbers of sprouts in an attempt to regenerate, may be due to herbivory impacts. The percentage of sprouts showing evidence of herbivory was very high, even for the four stands with higher establishment (81–96 % sprouts browsed). Stands with a single age class are not necessarily in poor condition, but the apparent impacts of herbivory decrease the probability of successful replacement of stems as stands age and decline.

Table 5 Regression models for each stand condition indicator, with stand dynamic and total conifer and aspen cover in 1998 as independent variables

	Metric	Units		Coefficient[a]	*p* value[b]
Plant *n*=29	Sprouting[c]	Sprouts/100 m^2	Intercept	1.79	<0.01
			Stand dynamic[d]:		
			Pers. aspen	0	
			Incr. conifer	−2.63	0.02*
			Total cover [e]	−0.003	0.55
			Stand dynamic x total cover	0.03	0.03*
	Establishment[f]	m^2/ha	Intercept	0.29	0.82
			Stand dynamic:		
			Pers. aspen	0	
			Incr. conifer	−1.26	0.09**
			Total cover	0.02	0.18
	Shannon Index		Intercept	1.86	<0.01
			Stand dynamic:		
			Pers. aspen	0	
			Incr. conifer	2.10	0.12
			Total cover	0.003	0.57
			Stand dynamic x total cover	−0.03	0.08**
	Herbaceous species richness	species	Intercept	40.06	<0.01
			Stand dynamic:		
			Pers. aspen	0	
			Incr. conifer	37.43	0.10**
			Total cover	−0.07	0.44
			Stand dynamic x total cover	−0.47	0.07**
	O horizon depth	cm	Intercept	5.06	<0.01
			Stand dynamic:		
			Pers. aspen	0	
			Incr. conifer	0.83	0.20
			Total cover	−0.01	0.65
Litter *n*=12	Litter C:N	g C/g N	Intercept	26.96	<0.01
			Stand dynamic:		
			Pers. aspen	0	
			Incr. conifer	0.87	0.72
			Total cover	0.04	0.54
	Fine C:N[g]	g C/g N	Intercept	3.1	<0.01
			Stand dynamic:		
			Pers. aspen	0	
			Incr. conifer	0.09	0.25
			Total cover	0.002	0.42
	Woody C:N[h]	g C/g N	Intercept	3.43	<0.01
			Stand dynamic:		
			Pers. aspen	0	
			Incr. conifer	0.01	0.88
			Total cover	0.01	0.02*

Table 5 (continued)

Metric	Units		Coefficient[a]	*p* value[b]
Woody:fine mass	g woody cm^{-3}/ g fine cm^{-3}	Intercept	0.33	0.01
		Stand dynamic:		
		Pers. aspen	0	
		Incr. conifer	−1.05	<0.01***
		Total cover	−0.001	0.29
		Stand dynamic x total cover	0.01	<0.01***
Decomposition[i]	Munsell value	Intercept	1.72	<0.01
		Stand dynamic:		
		Pers. aspen	0	
		Incr. conifer	−0.01	0.83
		Total cover	−0.001	0.54

Stand dynamic and total cover are from aerial photo interpretation and plant variables were measured in the field during summers of 2007 and 2008, from 29 stands in Lassen Volcanic National Park, CA. Litter variables were measured for a subsample of 12 stands

*p=0.05; **p=0.1; ***p=0.01 (significantly different results at each indicated p value)

[a] Coefficient for each variable in the linear model. The value of the coefficient indicates the direction (+ or −) and magnitude of the relationship between each predictor variable to the response variable. For continuous predictor variables, the coefficient indicates the change in the response variable associated with each incremental change in the predictor variable

[b] *P* value associated with each variable

[c] Sprouting was log-transformed

[d] Stand dynamic is a categorical variable with two levels, persistent aspen and increasing conifer cover. The coefficient for the referent condition (persistent aspen) is set to 0.0; the coefficient for increasing conifer represents the estimated difference of the response variable (e.g., stands with increasing conifer dynamic have 10 % less aspen cover than stands with a persistent aspen dynamic given that all other variables are held constant)

[e] Total cover is the sum of aspen and conifer cover in 1998, from photo interpretation

[f] Establishment was square root-transformed

[g] Fine C:N was ln-transformed

[h] Woody C:N was ln-transformed

[i] Decomposition was ln-transformed

Forest floor processes also undergo transition as conifer cover increases. Under persistent aspen canopies, the ratio of woody to fine litter is influenced by the large mass of fine leaf litter produced annually. In stands with conifer encroachment, the ratio of woody to fine litter increases as conifers shed woody litter. Woody litter C:N increases as recalcitrant materials build up on the forest floor. The absence of significant results for decomposition is probably due to the mixed conifer and aspen canopies present in all sampled stands. While significant differences in forest floor factors are found between stands with unmixed canopies of either aspen or conifer, Prescott et al. (2000) found that decomposition rates for mixed deciduous and conifer litter were the same as pure conifer litter. Differences along the gradient of conifer cover may be masked by the persistence and buildup of conifer needles.

The finding of rapid species loss in stands with increasing conifer cover emphasizes the loss of understory diversity as aspen stands succeed to conifer. Significant decreases in diversity have been correlated with increasing canopy cover and litter depth in Sierran mixed conifer communities (Wayman and North 2007). The canopy influences the quantity and quality of light that reaches the forest floor, soil surface temperatures, and the quantity and quality of litter inputs. Litter directly affects understory plant communities by insulating soil from temperature fluctuations, altering moisture retention, and by acting as a physical barrier (Facelli and Pickett 1991). Litter quality and type impacts seedling germination and establishment (Xiong and Nilsson 1999). Experimental work

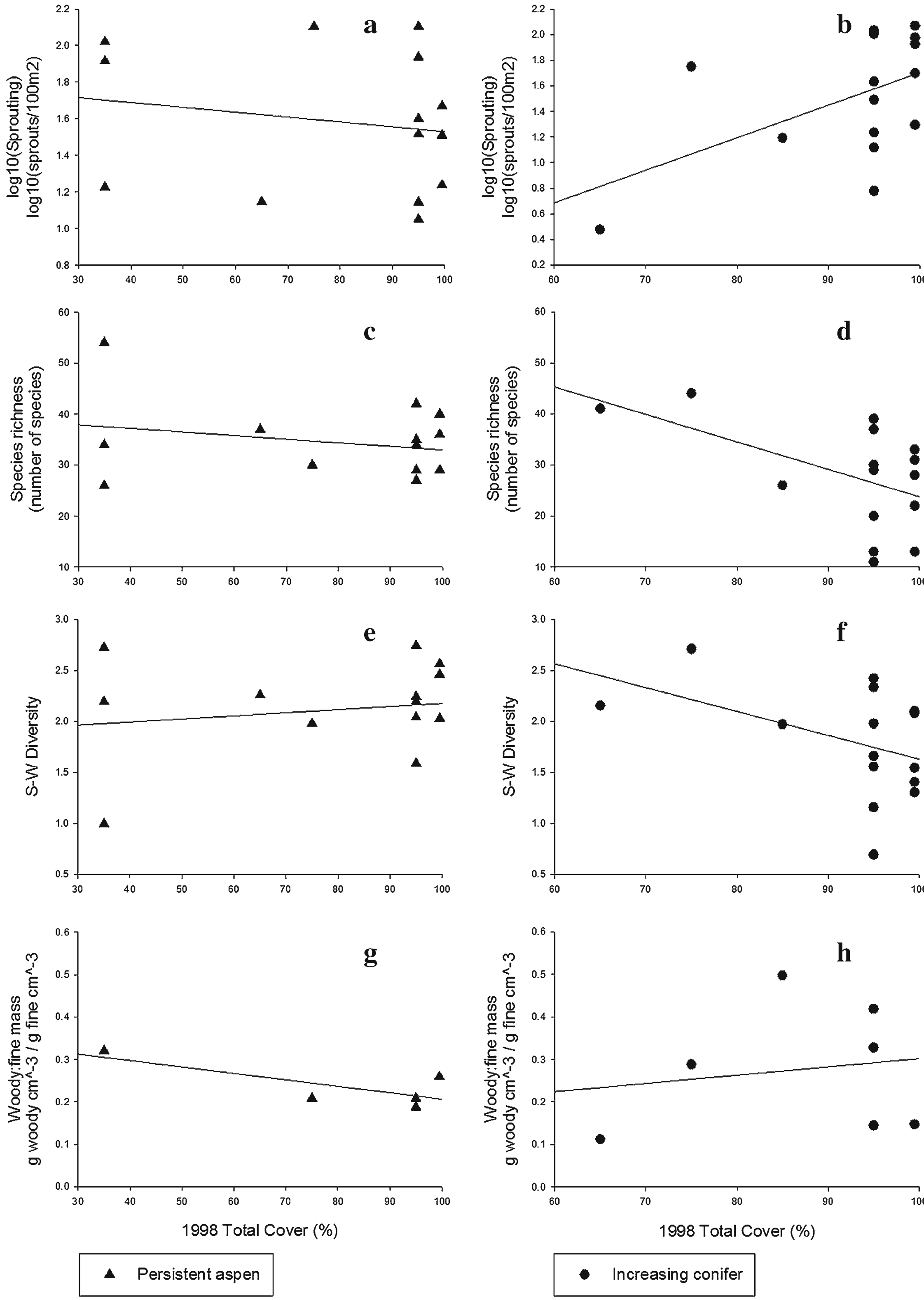

Fig. 2 **a**–**h** Regression of stand condition metrics for which the interaction of percent total cover and stand dynamic were significant

conducted with coniferous litter found germination decreased for all tested herbaceous species as litter depth increased (Horman and Anderson 2003). Seeds fail to come into contact with mineral soil, or fail to establish after germination. Reductions in conifer cover and litter depth have the opposite effect. Species richness and cover increased in response to a combination of burning (reducing litter and woody debris) and thinning treatments (increasing light and soil moisture) (Wayman and North 2007).

Management of aspen stands in national parks

Maintenance of biological diversity is a primary goal of national parks and wilderness (Cole et al. 2008), and a better understanding of the ecosystems and processes supporting diversity is essential to preserve biodiversity in the current context of rapid environmental change (Millar 2009). Aspen contribute to landscape-level diversity in coniferous landscapes such as those found across western North America. Anthropogenic impacts to fire regimes have promoted widespread shifts in forest structure, and further impacts due to climate are expected. In California, current predictions include greater fire frequency in forested areas through effects of higher temperature and drought on fuel flammability (Westerling and Bryant 2008). The national park setting of this study highlights the tension between two stand-scale management options: managing for values provided by the presence of aspen, such as higher understory diversity, or allowing conifer succession to proceed as an ecological process. The management policy of the U.S. National Park Service calls for limited intervention but acknowledges the need for active management of impacts that diminish the integrity of protected systems. The policy cites anthropogenic successional trends and loss of habitat for fire-adapted plant and animal species as appropriate justifications for active management (NPS 2006). The small size and limited extent of aspen stands in the Southern Cascades and northern Sierra Nevada underscore the need for management decisions before further deterioration occurs.

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