

# Aspen (*Populus tremuloides*) stands and their contribution to plant diversity in a semiarid coniferous landscape

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**Abstract** We conducted a field study to determine the relative contributions of aspen (*Populus tremuloides*), meadow, and conifer communities to local and landscape-level plant species diversity in the Sierra Nevada and southern Cascade Range, northeastern California, USA. We surveyed plant assemblages at 30 sites that included adjacent aspen, conifer, and meadow communities across a 10,000-km<sup>2</sup> region. We statistically investigated patterns in local and landscape-scale plant diversity within and among the three vegetation types. Summing across sites, aspen stands supported more plant species overall and more unique plant species than

either meadow or conifer communities. Local richness and diversity did not differ between aspen and meadow plots; conifer forest plots were significantly lower in both measures. Heterogeneity in species composition was higher for aspen forest than for meadows or conifer forest, both within sites and between sites. Plant communities in aspen stands shared less than 25% of their species with adjacent vegetation in conifer and meadow plots. Within aspen forest, we found a negative relationship between total canopy cover and plant diversity. Our results strongly support the idea that plant communities of aspen stands are compositionally distinct from adjacent meadows and conifer forest, and that aspen forests are a major contributor to plant species diversity in the study region. Current patterns of aspen stand succession to conifer forest on many sites in the semiarid western US are likely to reduce local and landscape-level plant species diversity, and may also have negative effects on other ecosystem functions and services provided by aspen forest.

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## Introduction

Quaking aspen (*Populus tremuloides*) has been identified as a keystone species on many western North

American landscapes (Kay 1997; Stohlgren et al. 1997b; Bartos and Campbell 1998; Knight 2001). Kay (1997) speculated that aspen stands support the second highest level of biodiversity of any western US vegetation type, after riparian plant communities. Mitton and Grant (1996) similarly suggested that in the semiarid western US, aspen habitats were second only in habitat importance to riparian zones. Research from the Intermountain West indicates that aspen stands contribute a variety of ecosystem functions and services, including augmented water yields and soil moisture (Mueggler 1985; Bartos and Campbell 1998; LaMalfa and Ryel 2008) and enhanced diversity of vascular plants (Chong et al. 2000; Stohlgren et al. 1997a, 1999), avifauna (Johns 1993; Griffis-Kyle and Beier 2003; Richardson and Heath 2004), mammals (DeByle 1985), and macroinvertebrates (Jones et al. 1985). Aspen are also widely valued for their esthetic appeal, and for their ability to act as “natural firebreaks” because of their typically high water content (Fechner and Barrows 1976; Kilpatrick et al. 2003).

Many studies report declining aspen extent and health in the western US (Bartos and Campbell 1998; Shepperd et al. 2006). Bartos (2001) estimated aspen extent before Euro-American settlement was 49–95% greater than current extent in seven intermountain states. Di Orio et al. (2004) estimated more than 28% loss of aspen acreage since 1946 in the Warner Mountains in northeastern California. Potter (1998) reported the majority of aspen stands he studied in the Sierra Nevada were heavily encroached by conifer and Jones et al. (2005) found that nearly 80% of aspen stands still extant on the eastern half of the Lassen National Forest in California were at risk of being lost from the landscape because of lack of successful regeneration. At the same time, studies report aspen persistence on many western landscapes (Zier and Baker 2006; Binkley 2008; Sankey 2008). Recent findings indicate drivers of aspen decline or persistence are spatially and temporally heterogeneous across the West (Rogers et al. 2010). Incidents of aspen decline have been attributed in part to reduction in fire frequency and introduction of livestock grazing during the past 150 years, which have the synergistic effect of suppressing aspen sucker recruitment and facilitating successional conversion of shade-intolerant aspen to more shade-tolerant conifer species (Bartos 2001; Kilpatrick and Abendroth 2001; Shirley and Erickson 2001; Jones et al. 2010).

In the last 10 years, aspen conservation and restoration have become a priority for public land management agencies in California (Jones et al. 2005; Shepperd et al. 2006). A common argument for aspen restoration is to conserve unique plant species and assemblages associated with aspen stands and to maintain landscape-level plant diversity (e.g., Potter 1998, 2005). Studies have found that maintaining species diversity at local and landscape scales may result in augmented ecosystem resilience (Tilman and Downing 1994), reliability (Naeem and Li 1997), productivity (Naeem et al. 1996), nutrient retention (Ewel et al. 1991), and resistance to invasive plant species (Symstad 2000). Rare species associated with aspen communities may play critical, but as yet unappreciated, ecological roles (Falk et al. 2006). Loss of keystone species, like aspen, may also lead to threshold ecosystem changes (Power et al. 1996).

It is widely thought that aspen stands support high numbers of unique plant species and communities, and aspen restoration projects are occurring throughout northern California with the enhancement of plant diversity as a primary goal. Interestingly, there is actually no published information that explicitly supports the presumption that aspen stands sustain unique plant species or communities in California (Barbour and Minnich 2000), or that California aspen communities disproportionately contribute to local or landscape-scale plant species diversity, although studies show such patterns in the Rocky Mountains (e.g., Stohlgren et al. 1997a). Potter (1998, 2005) noted that aspen stands were among the most species-rich plant communities in the (southern and central) Sierra Nevada, but he did not analyze compositional relationships between aspen and other vegetation types. Furthermore, our literature review found no studies that quantitatively described understory plant composition, richness, or diversity associated with aspen stands in northern California. Potter (1998, 2005) provided information from the southern Sierra Nevada, but his community types are distinct from the lower elevation, mostly east slope communities that characterize the northern part of the range.

We designed an observational field study to investigate the contribution of aspen to plant diversity in conifer-dominated mountain landscapes in the northern Sierra Nevada and southern Cascade Range, California, USA. We conducted a cross-sectional survey to assess the extent to which aspen stands

support unique plant assemblages and contribute to local and landscape-level plant diversity. We assessed and contrasted plant species metrics among adjacent aspen, meadow, and conifer plant communities at 30 study sites across northeastern California. Based on results from the Rocky Mountains (e.g., Stohlgren et al. 1997a, 1999; Shepperd et al. 2001) and qualitative evidence from elsewhere in California (e.g., Potter 1998, 2005), we hypothesized that aspen stands support higher plant species richness and diversity than either meadow or conifer communities, and that aspen also supports unique plant species and species assemblages not found in meadow or conifer communities. We also examined associations between aspen community species richness and diversity and local environmental conditions.

## Methods

### Study area

Our study area encompassed roughly 10,000 km<sup>2</sup> of northeastern California, centered on the eastern slope of the Sierra Nevada and southern Cascade mountain ranges. From north to south, 30 study sites were located from Eagle Lake (north of Susanville, CA) in the southern Cascade Range, to Carson Pass in the central Sierra Nevada, a linear distance of approximately 240 km (Fig. 1). Table 1 summarizes environmental conditions across the study sites. The study area is mountainous and characterized by a Mediterranean climate with a marked Great Basin influence (i.e., drier, with cold winters and some summer thundershowers). Being east of the Pacific Crest, the area experiences a strong rain-shadow effect. Summers are dry and warm with occasional thundershowers, whereas winters are cold and wet. The majority of precipitation falls from October to March as snow. Lower- and upper-montane zones (1,200–2,500-m elevation) are typified by coniferous forest on upland slopes dominated by Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), red fir (*A. magnifica*), and lodgepole pine (*P. contorta*), interspersed with comparatively small patches of Great Basin sagebrush (*Artemisia* spp.) scrub, and meadow communities in glacial and alluvial valleys. Aspen is a minor hardwood component of montane ecosystems in the study region, with spatially disjunct stands occurring in favorable sites, usually near a surface or ground

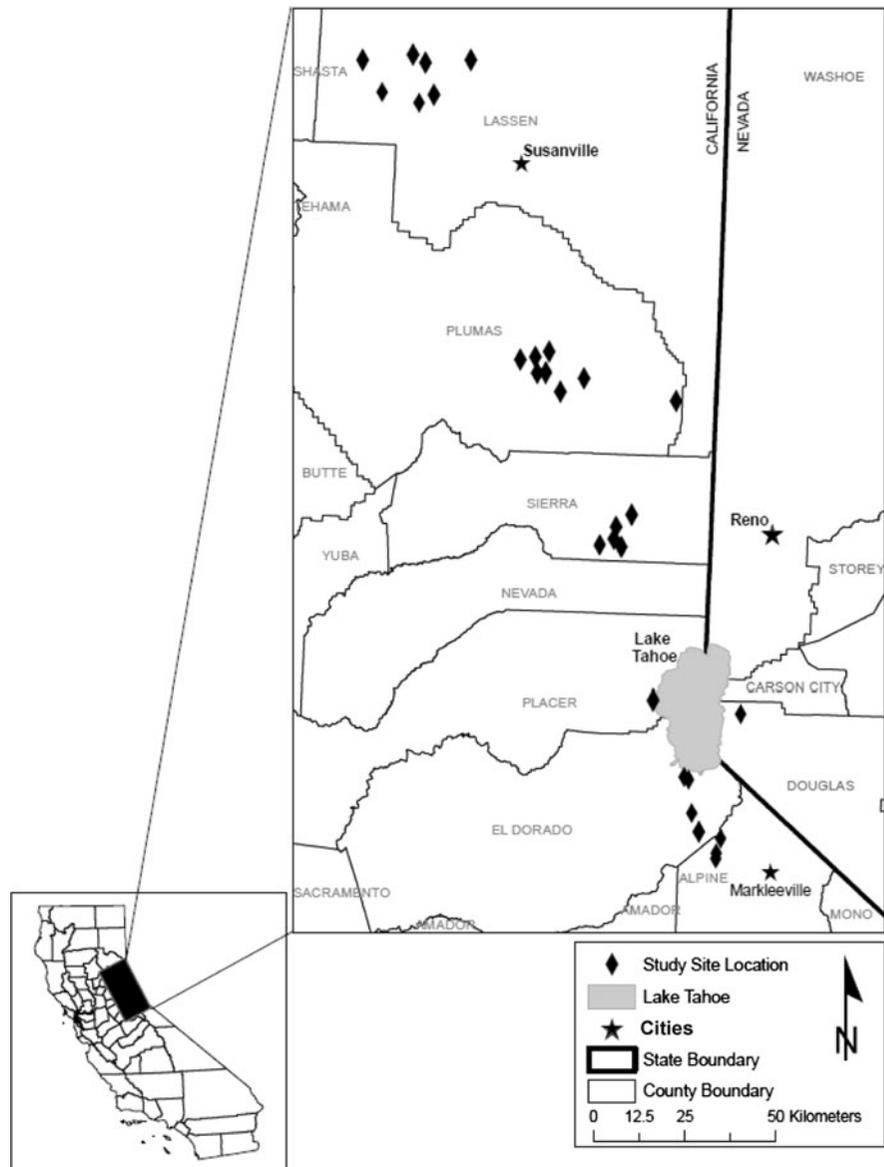
water source. Aspen stands in the study region average less than one hectare in size and constitute <2% of overall forest cover (unpublished survey data, Lassen and Plumas National Forests, 2000–2006). All study sites were found on land administered by the United States Forest Service (USFS).

### Site selection and study design

Our study was a cross-sectional survey of 30 randomly selected study sites. Each study site included an adjacent aspen stand, meadow, and upland conifer forest. Study site distribution was stratified to reflect the range of environmental conditions typical of the eastside Sierra Nevada and southern Cascade landscape. From north to south, sites were distributed across eastern portions of the Lassen ( $n = 6$ ), Plumas ( $n = 9$ ), and Tahoe ( $n = 5$ ) National Forests, the Lake Tahoe Basin Management Unit ( $n = 7$ ), and the western portion of the Humboldt-Toiyabe National Forest ( $n = 3$ ). Study sites were randomly selected from the pool of known aspen stands occurring on each USFS management unit that met the following criteria: the aspen stand (1) was bordered by a meadow and conifer uplands; (2) had an overall average of  $\leq 25\%$  conifer overstory and  $\geq 25\%$  aspen overstory (by ocular estimate); (3) had been undisturbed by wildfire events or timber harvest activities in the previous 25 years; and (4) had  $< 5\%$  annual aspen browse by livestock or wild ungulates (as determined by USFS aspen stand surveys). Aspen stands chosen in the field for sampling averaged 65.7% ( $\pm 27.6$  SD) overstory cover (median = 69%); aspen cover averaged 55.2% ( $\pm 25$  SD), and conifer cover averaged 8.1% ( $\pm 13.8$  SD).

Plant species data were collected at seven sites between May and September 2005, to determine minimal sampling areas for our study. At these sites, within each aspen and conifer forest stand, we established one 1,000-m<sup>2</sup> modified-Whittaker macroplot (Keeley et al. 1995), with ten 100-m<sup>2</sup> subplots nested in a 2 × 5 design and two 1-m<sup>2</sup> quadrats nested within each 100-m<sup>2</sup> subplot (for 20 total 1-m<sup>2</sup> quadrats per macroplot). At each meadow site, we established either 200- or 300-m<sup>2</sup> modified-Whittaker macroplots, which consisted of either two or three linearly adjacent 100-m<sup>2</sup> subplots and nested 1-m<sup>2</sup> quadrats as above. These plot sizes (1,000 m<sup>2</sup> for forest vegetation, 200–300 m<sup>2</sup> for herbaceous vegetation) are typical

**Fig. 1** Map of 30 study sites sampled in this study. Sites were distributed from Eagle Lake (north of Susanville) in the southern Cascade Range south to Carson Pass in the central Sierra Nevada. Each site contained an aspen stand fringed by a meadow and adjoined by conifer-dominated uplands. Susanville (in the north) is at  $40^{\circ} 24.91$  N,  $120^{\circ} 39.04$  W and Markleeville (in the south) is at  $38^{\circ} 41.72$  N,  $119^{\circ} 46.87$  W



sizes for vegetation sampling in forest and meadow habitats (Brohman and Bryant 2004). To determine a standard area to sample for comparisons between the three vegetation types, we used the nested sampling design to construct species accumulation curves for each of the seven study sites. Based on these curves, we settled on  $200 \text{ m}^2$  as a reasonable balance between sampling effort and species sampled.

Subsequently, we established one  $200\text{-m}^2$  modified-Whittaker macroplot in each plant community (aspen stand, conifer forest, and meadow) at each of the 30 study sites. We used methods for plot

orientation similar to those of Keeley and Fotheringham (2005). All plots were located in relatively homogeneous stands of vegetation, with the long-axis perpendicular to the evident moisture gradient. Plots within a study site were separated by less than 300 m linear distance.

#### Species data and environmental variables

We used a standard plant species data collection protocol (Keeley et al. 1995) at each study site. Plant species and environmental data were collected at the

**Table 1** Descriptive statistics for environmental variables observed across the 30 study sites

Metric	Minimum	Mean	Median	Maximum
Elevation (m)	1,614	1,897	1,825	2,443
Slope (%)	0	8	7	28
Mean annual ppt (mm)	420	890	870	1,800
Aspen stand area (ha)	0.3	0.9	0.7	4.4
Aspen stand–aspen cover (%)	21	62	63	98
Aspen stand–conifer cover (%)	0	9	0	50
Aspen stand–total cover (%)	26	77	72	100
Conifer stand–total cover (%)	10	59	60	100

Site distribution was designed to represent the range of environmental conditions typical of eastside Sierra Nevada and southern Cascade landscapes

30 study sites between May and September of 2005 and 2006. All plants were identified to species, subspecies, or variety following Hickman (1993). Species richness and dissimilarity (1-Jaccard Index of Similarity; McCune and Grace 2002) were determined by species occurrence in each 200-m<sup>2</sup> plot. Relative abundances for calculation of species diversity (Shannon–Wiener Index), species evenness (Pielou 1969), and species dominance (Simpson's Index) were determined from the mean cover of species occurring in the 1-m<sup>2</sup> quadrats nested within the 200-m<sup>2</sup> macroplot.

Environmental conditions were quantified for each plot at each study site. Aspect was a categorical variable based on compass azimuth, with four categories (north = 315°–44°, east = 45°–134°, south = 135°–224°, and west = 225°–314°). Slope (%) was measured using a clinometer. Total overstory canopy closure (%), canopy closure by aspen (%), and canopy closure by conifer (%) were visually estimated for each aspen and conifer plot. Geographic position for each 200-m<sup>2</sup> plot was recorded with a global positioning system. Positions were then geo-referenced with ArcMap GIS software (ESRI 2005) and projected onto various base map layers. Values for mean annual precipitation were determined for each study site by projecting site positions onto 800-m Grid Prism precipitation data layers (Gibson 2006). Stand size for each aspen stand at each study site was determined by delineating polygons around areas of contiguous overstory aspen canopies after overlaying geo-referenced plot positions onto digital color aerial imagery (California Spatial Information Library System [CaSil] 2006).

### Data analysis

Numbers and identities of unique plant species were determined through assessment of unweighted species presence lists for each community type. We followed procedures described in McCune and Grace (2002) using PC-Ord version 5 software (McCune and Mefford 2005) to calculate species richness, diversity, evenness, dominance, turnover, and similarity for each modified-Whittaker macroplot ( $n = 90$ , 30 per plant community type). We used analysis of covariance and post hoc pairwise Tukey–Kramer HSD mean separation to test for differences in species richness, diversity, evenness, dominance, and turnover among the three community types (JMP version 5.1). Study site identity was used as a grouping variable to account for spatial correlation among the three modified-Whittaker plots located at the same study site (Sall et al. 2005). Assumptions of linearity, normality, and homogeneity of variance were confirmed by evaluation of standard residual plots.

We calculated species dissimilarity measures (1-Jaccard similarity) among all pairwise groups of meadow plots, aspen plots, and conifer plots. We took the mean and standard deviation of the dissimilarity measures for each vegetation type and compared them using ANOVA.

We used simple linear regression to examine correlations between environmental conditions at aspen communities and plant species richness and diversity within aspen communities. We first evaluated colinearity among the variables describing environmental conditions at each aspen stand shown

in Table 1, as well as aspect. Elevation, aspen stand area, and mean annual precipitation were strongly positively correlated (Pearson's  $r_1 > 0.5$ ), possibly because of the fundamental role that elevation plays in determining annual precipitation and growing conditions in the Sierra Nevada and Cascade region. We excluded stand area and mean annual precipitation from the analysis, but included elevation that reflected these conditions as well as others (e.g., growing season duration). Species richness and diversity were regressed by elevation, total canopy cover, slope, and aspect. Assumptions of linearity, normality, and homogeneity of variance were confirmed by evaluation of standard residual plots.

## Results

### Plant species differences among aspen, meadow, and conifer communities

Across all 90 modified-Whittaker macroplots and plant communities, we recorded a total of 444 plant species. We found 316 species in aspen stands, 257 in meadows, and 206 in conifer stands (Table 2). Table 2 also displays the functional types (lifeforms) of species observed within each plant community. The overall species list was strongly skewed toward

perennial plants—73% (323) were perennial and 27% (121) annual or biennial—and included 9 trees, 31 shrubs (and subshrubs), 265 forbs, 100 graminoids, and 6 vines. Across all three plant communities, graminoids (22.5%) and forbs (59.7%) were substantially more abundant than other growth habits.

We found 63, 61, and 55 unique plant species in aspen, meadow, and conifer communities, respectively. Unique plant species identified in the aspen community are listed in Table 3 along with relative frequency of occurrence (or constancy), plant class/growth habit, lifespan, and nativity status in California for each species. Table 4 reports the functional type spectra for unique species observed within each community. The distribution of growth habits for the unique species observed in each community type was also dominated by graminoids and forbs.

Descriptive statistics for mean species richness, diversity, evenness, and dominance by plant community are displayed in Fig. 2. Aspen and meadow communities did not significantly differ for any of these metrics ( $P > 0.05$ ). Aspen and meadows were significantly higher in local species richness, diversity, and evenness than conifer stands while dominance was significantly greater in conifer stands than either aspen or meadows ( $P < 0.05$ ).

Mean species turnover (beta diversity) among study sites, as measured by Jaccard dissimilarity, was

**Table 2** Summary of functional types for plant species observed within aspen, meadow, and conifer community types and across all community types (overall)

	Number of species				Percent of total species			
	Overall	Aspen	Meadow	Conifer	Overall	Aspen	Meadow	Conifer
Total species	444	316	257	206	–	–	–	–
Graminoid	100	71	70	31	22.5	22.5	27.2	15.0
Forb	265	191	161	112	59.7	60.4	62.6	54.4
Tree or shrub	8	6	1	7	1.8	1.9	0.4	3.4
Vine or forb	6	6	5	2	1.4	1.9	1.9	1.0
Subshrub or forb	24	16	10	17	5.4	5.1	3.9	8.3
Shrub	23	14	2	21	5.2	4.4	0.8	10.2
Subshrub	5	4	1	4	1.1	1.3	0.4	1.9
Tree	9	6	1	8	2.0	1.9	0.4	3.9
Subshrub or shrub	3	1	1	3	0.7	0.3	0.4	1.5
Subshrub, shrub, or forb	1	1	1	1	0.2	0.3	0.4	0.5

The majority of plant species observed in all three communities were graminoids or forbs. About 10% of the species sampled can take more than one lifeform

**Table 3** Plant species (63) observed only in aspen plant communities

Species scientific name	Frequency	Growth habit/class	Lifespan
<i>Acnatherum lemmonii</i>	3.3	G/M	P
<i>Aconitum columbianum</i>	3.3	F/D	P
<i>Actaea rubra</i>	3.3	F/D	P
<i>Allophylum gilioides</i>	3.3	F/D	A
<i>Alnus incana</i>	3.3	T, S/D	P
<i>Arnica mollis</i>	3.3	F/D	P
<i>Artemisia douglasiana</i>	16.7	F/D	P
<i>Aster foliaceus</i>	3.3	F/D	P
<i>Berula erecta</i>	3.3	F/D	P
<i>Bromus suksdorfii</i>	3.3	G/M	P
<i>Calamagrostis canadensis</i>	3.3	G/M	P
<i>Camissonia subacaulis</i>	3.3	F/D	P
<i>Carex canescens</i>	3.3	G/M	P
<i>Carex feta</i>	3.3	G/M	P
<i>Carex fracta</i>	3.3	G/M	P
<i>Carex heteroneura</i>	3.3	G/M	P
<i>Carex specifica</i>	3.3	G/M	P
<i>Castilleja lacera</i>	10.0	F/D	A
<i>Cerastium fontanum</i> ssp. <i>vulgare</i> *	3.3	F/D	B, P
<i>Cirsium douglasii</i> var. <i>breweri</i>	6.7	F/D	B, P
<i>Clarkia rhomboidea</i>	3.3	F/D	A
<i>Claytonia exigua</i>	3.3	F/D	A
<i>Claytonia perfoliata</i>	3.3	F/D	A, P
<i>Crepis pleurocarpa</i>	3.3	F/D	P
<i>Dactylis glomerata</i> *	6.7	G/M	P
<i>Delphinium polycladon</i>	3.3	F/D	P
<i>Descurainia incana</i>	3.3	F/D	A, B, P
<i>Descurainia incisa</i> ssp. <i>incisa</i>	3.3	F/D	B
<i>Elymus glaucus</i> ssp. <i>glaucus</i>	3.3	G/M	P
<i>Epilobium angustifolium</i> ssp. <i>angustifolium</i>	13.3	F/D	P
<i>Epilobium minutum</i>	3.3	F/D	A
<i>Eryngium pinnatisectum</i>	3.3	F/D	P
<i>Fragaria vesca</i>	3.3	F/D	P
<i>Galium bifolium</i>	20.0	F/D	A
<i>Galium triflorum</i>	6.7	V, F/D	P
<i>Geranium californicum</i>	3.3	F/D	P
<i>Geum triflorum</i>	3.3	F/D	P
<i>Glyceria elata</i>	6.7	G/M	P
<i>Helenium bigelovii</i>	3.3	F/D	P

**Table 3** continued

Species scientific name	Frequency	Growth habit/class	Lifespan
<i>Helianthella californica</i> var. <i>nevadensis</i>	3.3	F/D	P
<i>Heterotheca villosa</i> var. <i>hispida</i>	3.3	SS, F/D	P
<i>Hieracium horridum</i>	3.3	F/D	P
<i>Juncus cyperoides</i>	3.3	G/M	P
<i>Lilium pardalinum</i> ssp. <i>shastense</i>	6.7	F/M	P
<i>Luzula comosa</i> var. <i>congesta</i>	3.3	G/M	P
<i>Luzula subcongesta</i>	3.3	G/M	P
<i>Nemophila parviflora</i> var. <i>austinae</i>	6.7	F/D	A
<i>Penstemon rydbergii</i> var. <i>oreocharis</i>	3.3	SS, F/D	P
<i>Phlox diffusa</i>	3.3	SS, F/D	P
<i>Polemonium californicum</i>	6.7	F/D	P
<i>Polygonum phytolaccifolium</i>	3.3	F/D	P
<i>Prunella vulgaris</i> var. <i>lanceolata</i>	6.7	F/D	P
<i>Ribes nevadense</i>	6.7	S/D	P
<i>Scutellaria antirrhinoides</i>	3.3	F/D	P
<i>Senecio streptanthifolius</i>	10.0	F/D	P
<i>Smilacina stellata</i>	26.7	SS/D	P
<i>Solidago canadensis</i> ssp. <i>elongata</i>	3.3	F/D	P
<i>Spiraea densiflora</i>	3.3	S/D	P
<i>Stachys ajugoides</i> var. <i>ajugoides</i>	26.7	F/D	P
<i>Stellaria media</i> *	6.7	F/D	A, P
<i>Stellaria obtuse</i>	3.3	F/D	P
<i>Thelypodium crispum</i>	3.3	F/D	A, B, P
<i>Viola macloskeyi</i>	6.7	F/D	P

Asterisk (\*) denotes introduced species. Only seven species had sufficient relative frequency of occurrence (>10.0) to serve as useful indicators of aspen plant assemblages

Growth habit: *F* forb/herb, *G* graminoid, *V* vine, *SS* subshrub, *S* shrub, *T* tree; Class: *D* dicot, *M* monocot; Lifespan: *A* annual, *B* biennial, *P* perennial

highest for the aspen community (1-J = 0.166, SD = 0.068), intermediate in the meadow community (1-J = 0.155, SD = 0.081), and lowest in the conifer community (1-J = 0.140, SD = 0.067). All pairwise comparisons were significantly different at  $P < 0.05$ . The species accumulation curves derived

**Table 4** Summary of functional types for unique plant species observed within aspen, meadow, and conifer plant communities

Functional types	Aspen	Conifer	Meadow
Total number of unique species	63	55	61
Graminoid	13	5	20
Forb	42	27	39
Tree or shrub	1	2	0
Vine or forb	1	0	0
Subshrub or forb	3	7	1
Shrub	2	9	0
Subshrub	1	1	0
Tree	0	2	1
Subshrub or shrub	0	2	0
Subshrub, shrub, or forb	0	0	0

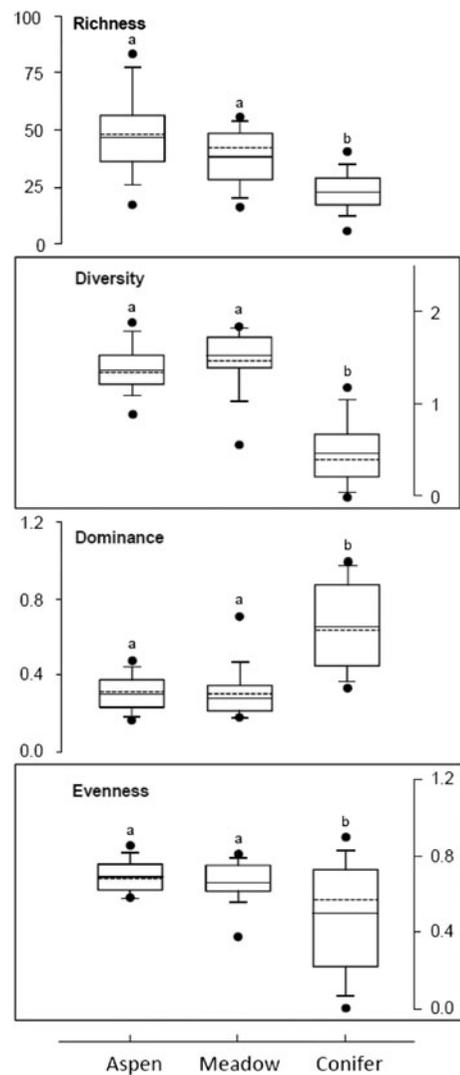
Values are number of species within each functional type. Five of the 63 species can occur as multiple lifeforms

from the first seven pilot sites indicated that the aspen sites also supported higher heterogeneity in species composition at the within-plot scale. From 1 to 200 m<sup>2</sup>, the rate of species accumulation per square meter was 0.08 in meadow sites, 0.11 in conifer sites, and 0.20 in aspen sites.

Figure 3 illustrates the number of species shared between aspen, meadow, and conifer plant communities. Community dissimilarity (calculated as 1-Jaccard) between aspen, conifer, and meadow plant communities was high. On a site-by-site basis, the species list for aspen communities differed by an average of 86% from conifer and 75% from meadow; mean species dissimilarity between conifer and meadow was 95%. Aspen communities represent highly distinct plant assemblages and exhibit little species redundancy with adjacent meadow or conifer communities.

Correlation of environmental conditions with aspen species richness and diversity

As total canopy cover increased, there was a significant decrease in aspen stand plant species diversity (Fig. 4). There were no other significant relationships between diversity or richness and any of the environmental variables examined ( $P \geq 0.30$  in all cases).

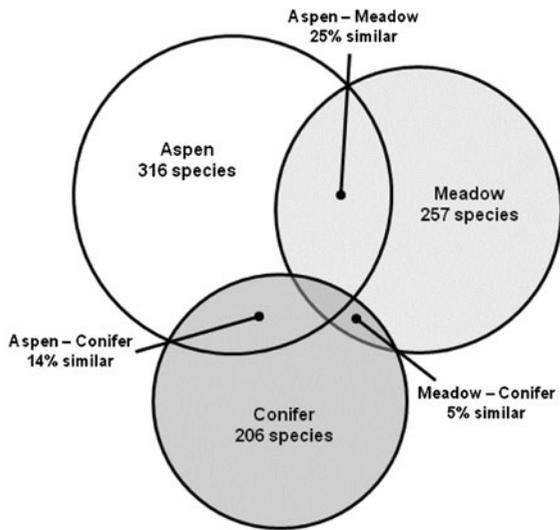


**Fig. 2** Plant species metrics observed for aspen, meadow, and conifer plant communities across the 30 study sites. “Diversity” is the Shannon–Wiener species diversity index and “dominance” is the Simpson’s index of dominance. For each metric, the *box* represents the 25th and 50th percentiles; within the *box*, the *dotted line* is the median, the *solid line* is the mean; the *dots* are the fifth and 95th percentiles. Boxes with different letters in each metric panel are significantly different ( $P < 0.05$ ; Tukey–Kramer HSD)

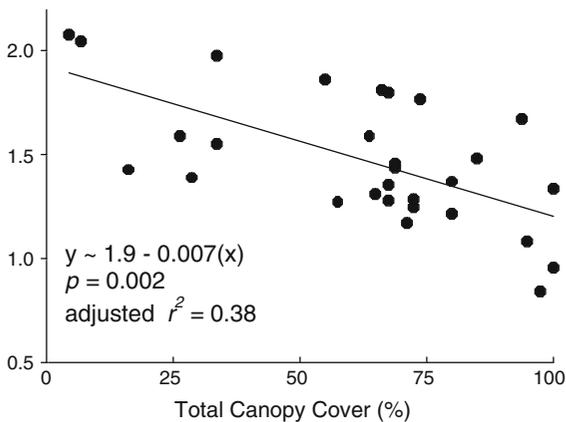
## Discussion

Aspen contributions to diversity

Our results demonstrate that aspen communities in northeastern California are not simple amalgamations



**Fig. 3** Venn diagram illustrating proportional number of plant species found and similarity in species found between aspen, meadow, and conifer plant communities. *Overlap* indicates species redundancy between and among community types



**Fig. 4** For aspen sites, the relationship between total overstory tree canopy cover (aspen and conifer combined) and the Shannon–Wiener species diversity index. Diversity declined significantly as total overstory tree canopy cover increased

of species from adjacent conifer and meadows, but represent unique and highly diverse plant assemblages. Species accumulation curves showed that aspen stands supported higher site-scale heterogeneity in species composition than meadows or conifer forest, and species turnover among different sampling sites in the study region was higher for aspen stands than for the other vegetation types. Aspen stands are thus not only more species diverse at the site scale than conifer forest but also they support higher site-

to-site heterogeneity in species assemblages across the northern California landscape. Given the decline of aspen throughout our region (Di Orio et al. 2004; Jones et al. 2005; Shepperd et al. 2006), our findings support aspen conservation and restoration as a means to reduce loss of local and landscape plant species diversity. Our data, which assessed the extremes of a successional continuum from pure aspen stand to pure conifer forest stand on similar neighboring sites, suggest that succession of aspen to conifer communities might reduce landscape and local plant diversity in the northern Sierra Nevada landscape by precipitating a decrease in the abundance of plant species that are either restricted to or predominantly found in aspen stands.

We found 63 unique understory plant species occurring within aspen stands that were not observed in adjacent conifer or meadow vegetation types (although most of these species are found outside of aspen stands in some part of their range). Seven of these species (*Artemisia douglasiana*, *Castilleja lacera*, *Epilobium angustifolium* ssp. *angustifolium*, *Galium bifolium*, *Senecio streptanthifolius*, *Smilacina stellata*, and *Stachys ajugoides* v. *ajugoides*) were observed in sufficient relative frequency (in greater than 10% of plots) to be considered “indicator species” of aspen (and perhaps other montane hardwood) habitats in our study region. We found that conifer and meadow types supported a similar number of unique species, 55 and 61, respectively, and dissimilarity in plant community composition between the three vegetation types was high. Our data substantiate the idea that aspen, meadow, and conifer stands support largely distinct floras, each contributing importantly to landscape plant diversity in the study region.

Declines in abundances of species restricted to or found primarily in aspen stands might cause loss of ecological function and ecosystem services. Aspen itself is an important browse species for ungulates, and is a major focus of feeding by deer, elk, and cattle in the late summer and fall (Jones et al. 2010). Aspen understory species are also an important source of food for many vertebrates, and provide equal if not higher payoff than meadow vegetation in fiber, crude protein, phosphorus, and calcium (Jones et al. 2010). Of the 63 species we found only in aspen stands, more than 20% of the genera represented have documented use as foodstuffs by indigenous North

Americans (Weeden 1996). In addition, many species present in other vegetation types but more abundant in aspen stands are important wildlife and livestock food sources, including species of the genera *Symphoricarpos*, *Lupinus*, *Poa*, and *Carex* (Potter 1998, 2005). Further loss of aspen habitat and associated species in the study region would also negatively affect wildlife habitat and compromise an important esthetic component of the regional landscape.

Plant species richness, diversity, and evenness were significantly higher for aspen stands and meadows than for conifer. This was because of higher overall species numbers per plot in the aspen and meadow sites, and the strong dominance of most conifer sites by one or two tree species and a few understory species. When added across sites, we found that the aspen habitat was more species rich at the landscape scale than either meadows or conifer forest. This was because of high local diversity, but also to high-beta diversity (species turnover) among sites. These results corroborate studies carried out in the Colorado Rockies (Stohlgren et al. 1997a, 1999). The Colorado studies also found that plant species richness per unit area in aspen habitats was much higher than in any other montane vegetation type. We did not incorporate area into our analysis, but we would doubtless find the same pattern in our study region, because aspen comprises such a small part of the landscape. In summary, aspen habitats are important islands of diversity in the northern Sierra Nevada and southern Cascades, and their significance is highly and positively disproportionate to their meager representation on the contemporary landscape.

Our research focused on relatively pure aspen stands. From these 30 stands, we observed that increasing total canopy cover was negatively correlated with understory plant diversity. This pattern corroborates the results of other studies that included aspen habitats, where a variety of understory characteristics have been shown to strongly correlate with canopy-light transmission (e.g., Messier et al. 1998; Lieffers et al. 1999; Hart and Chen 2006). The effect of reduced plant species diversity as aspen overstory canopy increases could be attributed to canopy interception of available resources (Anderson et al. 1969; Ricklefs 1977; Lavers and Field 2006), competition from tree roots under canopies (Ellison and Houston 1958; Callaway and Walker 1997), and compositional shifts from mixed forbs and grasses

under partial canopies to increased dominance by forbs under increasingly closed overstory canopies (Powell and Bork 2006). Aspen forests are successional to conifer forests in many environments in our study region (Potter 1998; Shepperd et al. 2006). Conifer species cast much deeper shade than aspen, and the results of our study point to the pattern of plant community impoverishment that can occur when conifers overtop and replace aspen stands in these successional sites.

Total canopy cover accounted for only a minor portion of the variation within the data set, and significant correlations among a suite of other measured environmental variables with either aspen richness or diversity were not observed (note that there are numerous variables that we did not measure). Although the correlation of total canopy cover with species diversity was statistically significant, the slight negative slope indicates only minor ecological effects. Plant assemblages are ultimately a result of complex interactions among local characteristics, regional processes, phylogenesis, and disturbance regimes (Ricklefs and Schluter 1993; Rosenzweig 1995). It is likely that environmental processes operating at broader spatial or temporal scales are important drivers of much of the variation in aspen plant assemblages in our study.

## Conclusions

In our study region in northeastern California, aspen stands are very distinct vegetation types, and they support extremely high-local and landscape plant species diversity. Current trends in aspen populations in northern California are negative, and land management agencies are developing and implementing aspen-focused restoration activities (Jones et al. 2005, 2010; Shepperd et al. 2006). We encourage land management approaches that reintegrate natural disturbance regimes or more directly seek to preserve or restore distinct aspen plant communities in our study region. Aspen stands are dependent on ecological disturbances, such as fire to remain competitive with shade-tolerant conifer species, such as *Abies concolor* and *Pinus contorta*, and anthropogenic changes to natural disturbance regimes may be at the root of regional trends of aspen habitat loss to forest successional processes (Shepperd et al. 2006).

Wholesale reversion to pre-Euro-American settlement disturbance regimes may be impractical or impossible in many parts of northern California and other parts of the western US. In its place, research shows that more localized restoration approaches, such as mechanical thinning of encroaching conifer, prescribed fire, and reduced livestock browse pressure, can stimulate aspen recruitment and ensure stand persistence or expansion (Shepperd 2001; Jones et al. 2005, 2010; Shepperd et al. 2006). Current national priorities of federal land management agencies are centered on ecological restoration and enhancement of ecological resilience to climate change (e.g., US Department of Agriculture 2010). Policies and practices that preserve or restore aspen habitat and effectively maintain habitat heterogeneity and landscape diversity fit well within these objectives and should continue to be encouraged as a land management priority throughout the semiarid West.

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